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# Information socialement acquise chez le lézard vivipare *Lacerta vivipara*

**Thèse dirigée par :**

Jean CLOBERT et Patrick FITZE

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**Jury :**

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**PhD**

Ecology

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# Socially acquired information in the common lizard *Lacerta vivipara*

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19/12/2006

**Jury:**

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*"Tout dans la vie est affaire de choix, ça commence par la tétine ou le téton,*
*ça se termine par le chêne ou le sapin, et puis d'ici à là,*
*de sa naissance à sa mort, l'homme est en permanence confronté à des choix*"
Pierre Desproges, La Scène

*Je remercie Jean et Patrick pour m'avoir appris à développer des idées, à construire des expériences, et à diffuser mon savoir aux autres. Pour faire un parallèle avec mon sujet de thèse, ils m'ont permis d'accéder à leurs informations personnelles et d'être à mon tour une source d'informations scientifiques. Merci à Jean pour m'avoir soutenu et pour avoir été présent sur le terrain durant ce 'fameux' été 2005.*

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Cette thèse est composée de huit manuscrits rédigés en anglais, qui sont le corps de mon travail. Trois de ces articles sont publiés tandis que les autres sont en cours de soumission.

Une introduction générale resitue ma thématique dans un contexte scientifique général et amène les manuscrits en les regroupant dans une problématique commune. Je discute, ensuite, des implications de ce travail et des perspectives utiles au développement de ces idées.

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# INTRODUCTION

## I. L'INFORMATION : DE LA PHYSIQUE A LA BIOLOGIE

Dans un environnement inconstant et incertain, prendre une décision adéquate est difficile mais néanmoins crucial. Décider de quitter son lieu de vie, de s'installer dans un nouvel habitat, de se reproduire et d'interagir avec d'autres individus, sont autant de décisions inévitables. Pour réduire cette incertitude, et donc prendre la meilleure décision, les individus ont accès à une multitude d'indices sur le monde environnant. Les signaux et les indices émis par les éléments biotiques et abiotiques de l'environnement servent, ainsi, de sources d'informations sur la qualité et les particularités de l'habitat et de ses résidents. Dans cette perspective, les théories du signalement, de la communication, et plus généralement de l'information, sont devenus des axes majeurs de recherche en écologie évolutive. Les fondements de ces théories sont pourtant ancrés dans une discipline très éloignée de la biologie : la physique.

### L'information : Une vision commune pour des disciplines éloignées ?

*"Information is a very elastic term"*
Ralph V.L. Hartley

#### *Tout est physique…*

Avec sa théorie mathématique de la communication (1948), Claude Shannon a fourni le document fondateur de la majorité des études futures sur la théorie de l'information. Bien que l'intégration de la notion d'information de Shannon (1948) au sein des systèmes de communication ait abouti à des applications diverses, les études de Nyquist (1924) et d'Hartley (1928)sont à l'origine du concept de l'information. Aucun ne fournit de définition exacte de l'information mais Shannon décrit le modèle général du transfert d'information en ces termes : 'The fundamental problem of communication is that of reproducing at one point either exactly or approximately a message selected at another point.' Ce problème fondamental de la communication trouve sa résolution à travers cinq étapes distinctes (Fig. 1). A l'origine de la communication, une source d'information produit le message, ou la séquence

de messages, destiné à être communiqué au récepteur. Ce message est ensuite codé en un signal 'transférable'. Le signal ainsi produit est transmis de l'émetteur au récepteur, à travers un média ou canal de transmission. Au cours de cette transmission, diverses sources de bruit peuvent modifier le signal. Finalement, le récepteur effectue l'opération inverse de celle réalisée par l'émetteur, pour pouvoir reconstruire le message à partir du signal et le transférer à la destination.

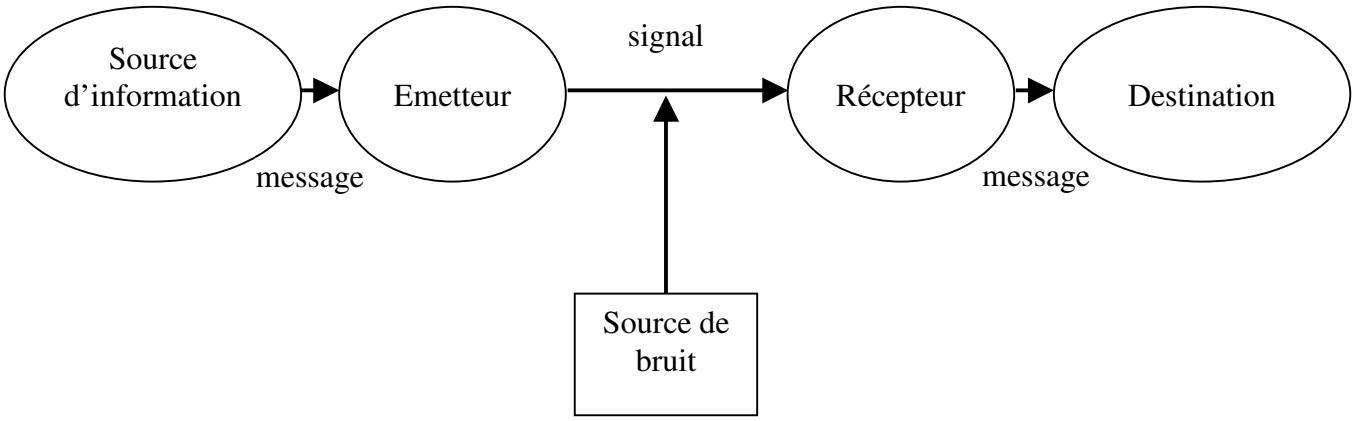


**Figure 1 :** Schéma général d'un système de communication (d'après Shannon (1948))

La théorie de l'information a servi de support à la compréhension de toutes les formes de communication, des réseaux informatiques et téléphoniques aux relations humaines. Parallèlement, les scientifiques de nombreuses disciplines ont vu dans la théorie de l'information une base de recherche pour des questions variées. Ainsi, les psychologues, les comportementalistes, les philosophes et les biologistes ont employé des termes tels que le code, la traduction, le transfert d'information, le signal pour illustrer et expliquer leurs systèmes. L'information est évoquée en biologie dans de nombreux contextes (Maynard-Smith 1999, Downes 2006). Les domaines majeurs d'application biologique, la neurobiologie (Borst et Theunissen 1999), la génétique (Maynard-Smith 1999) et l'éthologie au sens large (Johnstone 1997, Giraldeau 1997, Dall *et col.* 2005), ont développé des approches différentes à partir d'une même base théorique.

## *Différentes approches pour des questions communes*

La façon d'appréhender les questions techniques et implications liés à la théorie de l'information diffèrent entre disciplines. Cependant, les principes soulignés par ces questions sont fortement similaires. John Maynard-Smith donne sûrement la meilleure métaphore en illustrant le passage du génotype en un phénotype : « The genotype is not a description of the adult organism, but a recipe for making one, given an environment, initial conditions, and the laws of physics. ». Cette métaphore souligne les 'problèmes' importants de la théorie de l'information en biologie. Pour faire une copie exacte d'un organisme, ou plus généralement d'une information, les conditions environnementales doivent être les mêmes. Mais il faut également que la recette soit complète (*i.e.* fiabilité et honnêteté du signal), qu'elle ne soit pas détériorée lors de la transmission (*i.e.* conditions environnementales lors du transfert de l'information), et finalement qu'elle soit correctement lue par le récepteur (*i.e.* capacité individuelle de décodage du signal). Les études se sont, ainsi, axées autour de trois étapes de la théorie de l'information : l'encodage de l'information, le bruit modifiant le signal dans le canal de transmission, et l'utilisation du signal par le récepteur.

### *Comment encoder un message ?*

Encoder un message revient à traduire ce message en un signal transférable dans le canal de transmission. Cette traduction du message en signal, effectué par l'émetteur, fait intervenir la théorie du codage, ainsi que les notions de coût et de fiabilité de l'encodage. En biologie, l'encodage prend plusieurs formes, et conduit à différents signaux selon le type d'information, d'émetteur et de récepteur. Nous pouvons ainsi distinguer trois visions, correspondant à trois disciplines de la biologie, plus ou moins distantes de la théorie 'physique' de l'information : la neurobiologie, la génétique et l'étude du comportement. Les neurobiologistes font référence à l'information le long des neurones et à travers les synapses dans le système nerveux. Ce transfert d'information neuronale a un fonctionnement très similaire au transfert de l'information dans la théorie de la communication (Borst et Theunissen 1999). Le système neuronal traduit le message à transférer en potentiels d'action modulés par leur nombre et leur espacement temporel (*i.e.* trains de potentiels d'action). Cet encodage est simple et facilement traduisible en bits. Cela a permis une utilisation considérable des modèles de Shannon, et plus généralement des modèles 'physiques' de l'information (Borst et Theunissen 1999). L'information génétique a soulevé des conflits conceptuels plus importants de la part des philosophes de la science (Maynard-Smith 1999,

Downes 2006). La notion d'information génétique, évoquée pour expliquer l'hérédité et le développement, est basée sur une idée simple. Les gènes seraient porteurs d'une information, au travers du code génétique, fournissant les instructions (*i.e.* recette) pour la construction d'un phénotype. A partir de cette idée, les biologistes moléculaires ont introduit une terminologie consistante avec cette vision : l'information, codée en ADN à partir des bases d'acides aminés, est répliquée, transcrite de l'ADN en ARN, et traduite de l'ARN en protéines. L'information génétique est, donc, construite sur deux niveaux. Premièrement, les gènes contiennent une information transmise d'une génération à une autre, et qui correspond à une protéine ou un polypeptide donné. L'émetteur et le récepteur sont donc deux générations, le message est la protéine, et le signal est une séquence nucléotidique. La seconde vision informationnelle correspond au développement. Le développement est ainsi vu comme la transmission de l'information de l'ADN en ARN, via un codage en bases complémentaires, et cette information est traduite en une protéine donnée, via un codage reliant les triplets de bases aux acides aminés (Downes 2006). L'information génétique semble bien intégrée dans la vision générale. Cependant, elle a conduit à de nombreux débats, tels que la vision réductionniste d'une information portée uniquement par les gènes, et ne laissant pas de place à la modulation développementale de cette information, et donc à la plasticité phénotypique.
Dans la communication animale, le transfert d'information fait intervenir des signaux plus complexes, plus diversifiés, souvent multiples pour une information, et il est donc moins facilement modélisable. Nous le développerons plus en détail dans le chapitre suivant.

*Comment le signal est-il bruité ?*

Les seconds modèles de Shannon introduisent une notion essentielle à la théorie de l'information. Le signal reçu n'est pas nécessairement le même que le signal émis à sa source. Durant sa transmission (*i.e.* dans le canal de transmission), le signal peut être perturbé par différents bruits modifiant ce signal, et donc l'information transmise. Cette notion a évidemment des répercussions énormes sur l'efficience de la communication, et a donc conduit les chercheurs à s'y intéresser. Le protocole d'étude du bruitage du signal est simple et commun à toutes les disciplines : mesurer la précision du transfert d'information en comparant les caractéristiques du signal reçu (*i.e.* output) pour un signal donné (*i.e.* input). Dans le codage neuronal, la théorie de l'information peut être appliquée précisément pour quantifier la fiabilité d'un système input-ouput. La transmission d'information neuronale est bruitée car les potentiels d'actions produits par le neurone possèdent une forte entropie (Borst

et Theunissen 1999, Chacron *et col.* 2004). Cependant, les mesures de transfert d'information révèlent que chaque potentiel d'action possède une quantité importante d'information et que le bruit neuronal est relativement faible (Borst et Theunissen 1999). De plus, certains mécanismes réduisant le bruit ont pu être mis en évidence. Par exemple, les intervalles corrélés entre les potentiels d'action d'un neurone permettent de réduire le bruit, et ainsi d'augmenter le transfert d'information (Chacron *et col.* 2004). En génétique et en comportement animal, le transfert de l'information est soumis à des modifications du signal plus importantes. La notion de canal de transmission en génétique a soulevé plus d'interrogations. Comme l'avait illustré Maynard-Smith (1999), le génotype est une recette pour faire un phénotype particulier dans des conditions initiales et environnementales données. Le développement a, ainsi, été considéré comme le canal de transmission, et les conditions lors du développement comme le bruit modifiant le signal. Il est alors possible d'obtenir des phénotypes différents à partir d'un même signal (*i.e.* gène) par le biais de bruits développementaux. Et c'est à partir de cette conclusion qu'une ambiguïté est née. Si le développement peut affecter l'information reçue, les conditions de développement, en elles-mêmes, peuvent être considérées comme une source d'information dans la production du phénotype. Ainsi, connaître les conditions de développement serait une information importante dans la production du phénotype. Cette double fonction canal-émetteur se retrouve également dans le comportement animal et particulièrement dans la vision écologique de la communication animale. L'information est transférée à travers l'environnement (*i.e.* canal de transmission) qui représente une source de bruit importante. En effet, lors d'une communication entre deux individus, l'émetteur et le récepteur sont souvent distant, en contact occasionnel, et dans un environnement fluctuant. Nous verrons, par la suite, que certains mécanismes de réduction du bruit existent, tels que la redondance du signal, la présence d'émetteurs multiples, ou l'existence d'un signal constant (*e.g.* couleur). La dépendance environnementale du signal peut également être vue comme une source d'information. Une information donnée et son signal n'ont pas la même valeur dans des environnements variés. Par exemple, une couleur de camouflage ne donnera pas la même information au récepteur dans l'environnement où le camouflage est adéquat que dans un environnement totalement différent. Cette dualité entre source de bruit et information en elle-même, rend l'étude des canaux de transmission plus compliquée et donc plus intéressante.

*Comment le récepteur extrait-il l'information du signal ?*

Cette question n'a de réel intérêt que dans un système asymétrique. La théorie de Shannon décrit des systèmes symétriques, dans lesquels le récepteur réalise exactement la traduction signal-message grâce aux mécanismes inverses de ceux utilisés par l'émetteur. De nouveau, le système d'information neuronal possède par sa symétrie un fort point commun avec les modèles de Shannon. L'information génétique ne suit pas un système symétrique. Cependant, dans ces deux systèmes (neuronal et génétique), les récepteurs ne diffèrent pas par leurs capacités à traduire le signal, et une fois le canal de transmission passé, peu de modulation de l'information ne survient. C'est en cela, que cette question a un intérêt modeste pour ces deux systèmes. L'originalité de la communication animale repose sur son niveau d'asymétrie dans le transfert d'information. Le récepteur réalise rarement les mécanismes inverses de ceux utilisés par l'émetteur. Nous pouvons alors voir émerger des problèmes d'utilisation différentielle de l'information par les récepteurs, selon leurs capacités à intégrer et analyser l'information, leurs sensibilités, et les avantages liés à l'utilisation de l'information. De plus, les caractéristiques des individus récepteurs exercent une forte pression de sélection sur les signaux émis. Cela conduit à des signaux dépendants du type de récepteurs, tels que les signaux intra-sexuels versus inter-sexuels, et intra-spécifiques versus inter-spécifiques.

## De l'utilité de la théorie de l'information en écologie évolutive

*« In biology, the notions of meaning and intelligence are replaced by those of function and natural selection »*
John Maynard Smith

Deux visions du transfert d'information sont généralement utilisées. En physique, il est considéré qu'un émetteur émet un signal, et que le récepteur reçoit un signal sans qu'il ne l'ait recherché (Shannon 1948). L'émetteur est au centre du transfert d'information. En communication et psychologie humaines, le récepteur recherche une information et trouve le signal (ou indice) transmis par l'émetteur (Wilson 1999). Ces deux approches se retrouvent en écologie évolutive. Ainsi, l'écologie du signalement axe plus ses recherches sur un individu qui émet 'intentionnellement' un signal informatif sur son état. Même si le récepteur influe sur l'évolution du signal (voir ci-dessous), l'émetteur reste à l'origine du transfert d'information. L'écologie de l'utilisation de l'information considère également un émetteur transférant un 'signal'. Cependant, le 'signal' est parfois émis involontairement (*i.e.* par

inadvertance) et est donc nommé ‘indice’. L’émetteur ne cherchant pas à renseigner, le rôle du récepteur dans le transfert de l’information est mis plus en avant. Le récepteur recherche une information pour réduire son incertitude, et la trouve auprès d’émetteurs. Cette différence de point de vue nous amène à présenter séparément les mécanismes impliqués dans l’émission des signaux de ceux impliqués dans l’émission des autres types d’information.

## *L’écologie du signalement*

Un signal est un trait spécialisé pour la communication (Johnstone 1997). Cela implique qu’il est émis ‘intentionnellement’ par l’animal pour renseigner sur son état (*e.g.* santé, statut de reproduction) et qu’il confère un avantage sélectif. Pour que le rôle du signal dans la communication soit efficace, les pressions de sélection doivent conduire à la sélection de bons émetteurs mais également de bons récepteurs (*i.e.* bonne capacité de lecture du signal). Un animal, émetteur ou récepteur, étant soumis à de nombreuses pressions de sélection, il existe une diversité d’avantages sélectifs des signaux, et plus généralement une diversité des signaux. Ainsi, la couleur, l’agressivité, le chant modulent des interactions intra- et inter-sexuelles, telles que la probabilité de s’accoupler, le choix de partenaire ou la compétition pour l’accouplement. Mais comment ont pu évoluer ces signaux pour permettre une communication efficace ?

L’efficacité d’un signal repose sur deux principes importants. Premièrement, le signal doit être perçu par le récepteur. En d’autres termes, le récepteur doit être capable de lire le signal. Cela implique que 1) l’émetteur produise un signal facilement détectable dans un environnement fortement bruité et instable, et que 2) les capacités d’intégration du signal (*i.e.* traduction) du récepteur soient en adéquation avec le signal émis. Nous avons vu précédemment que le bruit du canal de transmission pouvait conduire à des modifications importantes du signal, voire à l’impossibilité pour le récepteur de lire le signal. Or, la communication animale s’effectue dans un environnement bruité et avec une certaine distance entre l’émetteur et le récepteur. Pour permettre une bonne détectabilité du signal par le récepteur, et ainsi une communication efficace, il existe plusieurs propriétés communes à différents signaux (Johnstone 1997). Parmi celles-ci, la redondance et l’évidence des signaux sont des avantages clairs. Par exemple, les couleurs vives et les émissions sonores des mâles se démarquent facilement des couleurs et des sons des milieux naturels. Les émissions sonores ont également comme avantage d’être détectées à de grandes distances. Les femelles

peuvent, ainsi, détecter facilement les mâles très colorés ou à chants très distincts. L'autre difficulté de la communication est l'irrégularité des interactions. En effet, les individus ne sont pas constamment en interaction avec tous leurs congénères. Par hasard, une femelle peut ne pas recevoir le signal émis par le mâle. Un signal répété, comme le chant, ou un signal constant, comme la couleur, augmente la probabilité de transmission du signal. Cette évidence et cette redondance du signal apportent ainsi un avantage sélectif aux individus. Cependant, ces propriétés des signaux présentent également des coûts. Si les congénères peuvent plus facilement détecter ces signaux, les prédateurs le peuvent également. Il en résulte une balance coûts-bénéfices des signaux que nous développerons par la suite.

Certaines caractéristiques des signaux permettent donc d'être distinguable dans un environnement bruité. Cependant, les environnements, et plus généralement les contextes, dans lesquels sont émis les signaux sont très variables. Un signal donné n'a donc pas la même valeur dans tous les contextes. En conséquence, l'intensité des signaux varie fortement entre les contextes et les environnements. Chez de nombreuses espèces, l'intensité et la variabilité de la couleur diffèrent entre les populations (e.g. Endler 1991, Marchetti 1993, Macedonia *et col.* 2004). Par exemple, Macedonia et col. (2004) montrent que l'intensité de la couleur du lézard à collier (*Crotaphytus collaris*) est différemment exprimée dans trois populations d'Oklahoma. A un niveau plus local, des différences de couleur sont observées selon les substrats de vie chez le lézard à collier. Ces variations locales sont par ailleurs plus importantes chez les mâles de cette espèce. Les auteurs expliquent ces variations dépendantes de la population et du sexe par un niveau de prédation variable dans un contexte de sélection sexuelle pour des mâles colorés. De la même manière, la prédation associée à la sélection sexuelle semble être à l'origine des variabilités locales de la couleur des guppies (Endler 1991).

Le contexte intra-spécifique peut lui aussi affecter l'intensité des signaux. Ainsi, chez les lézards de barrières (*Sceloporus undulatus*), les mâles résidents exhibent une couleur dorsale plus claire en présence de mâles introduits, uniquement lors de la saison de reproduction (Smith et John-Adler 1999). Chez cette espèce, la clarté de la couleur dorsale signale le statut de dominance. Cette couleur a un rôle important dans la compétition intra-sexuelle pour les territoires. Cet éclaircissement du signal coloré aurait ainsi un impact sur la dissuasion des intrus. La présence de congénères modifie donc l'évolution des signaux impliqués dans la communication. Ce rôle de l'audience sur l'émission des signaux illustre

bien l'importance du contexte dans le transfert d'information sur la qualité des individus. Ainsi, chez le poisson combattant, la présence d'une femelle réduit l'agressivité des interactions entre les mâles et intensifie les signaux (Doutrelant *et col.* 2001). Les situations d'interactions obligeraient les mâles à développer des signaux plus honnêtes et donc une information plus juste. Associé à ces mécanismes dépendants du contexte et de l'environnement, un 'bon' transfert de l'information nécessite une bonne exploitation du signal par le récepteur. L'émetteur doit ainsi employer des signaux en adéquation avec les capacités sensorielles et neuronales des récepteurs (e.g. Ryan 1990). Hormis cette adéquation 'mécanique' entre signaux et capacité des récepteurs, l'existence de signaux multiples pourrait permettre au récepteur de mieux estimer l'information émise (Møller et Pomiankowski 1993). En effet, les animaux développent souvent plusieurs signaux évoluant conjointement. Cette diversité des signaux permettrait à la fois l'apport d'informations multiples, mais aussi la détection des signaux dans un contexte où les capacités sensorielles et les sensibilités des récepteurs pour un signal varient (voir partie 'conclusion et perspectives', Møller et Pomiankowski 1993, Johnstone 1997).

La théorie de la communication et de l'évolution du signal implique également un bénéfice pour le récepteur qui exploite l'information. Ce second principe nous amène à considérer l'honnêteté des signaux. Même s'il existe de nombreux exemples de tricherie, l'honnêteté est une nécessité dans l'évolution et le maintien d'un système signal-exploitation du signal. Les progrès en écologie évolutive, et particulièrement l'intégration de disciplines connexes, ont permis de cibler les mécanismes de l'honnêteté. Le principe du handicap de Zahavi (Zahavi 1975, Zahavi 1977) permet d'expliquer le maintien d'un signal honnête par le coût de production du signal. En effet, un individu ne peut produire un signal qu'en respect de ses capacités personnelles. Un individu de bonne condition peut supporter le coût de production d'un signal intense, et donc le transfert d'une information honnête. Un signal honnête, profondément étudié du point évolutif et physiologique, concerne les couleurs basées sur les caroténoïdes. Les caroténoïdes sont les pigments à l'origine des couleurs jaunes à rouges de nombreuses espèces. Pour expliquer la variabilité de la coloration due aux caroténoïdes, une expression dépendante de la condition de l'individu est proposée (Olson et Owens 1998). Plusieurs mécanismes pourraient permettre cette expression liée à la qualité de l'individu (Hill et Montgomerie 1994, Tschirren *et col.* 2003). Ainsi les processus d'utilisation des pigments (absorption, transport, métabolisme), la capacité d'acquisition des caroténoïdes lors du nourrissage (Kodric-Brown 1989, Hill 1994) et les propriétés, négatives

ou bénéfiques, des caroténoïdes (Nowak 1994, Olson et Owens 1998, von Schantz *et col.* 1999), conduiraient à la condition-dépendance du signal. Par exemple, le compromis entre l'utilisation des caroténoïdes pour des propriétés positives (*e.g.* activation du système immunitaire, réduction de la quantité de radicaux libres) et pour l'expression de la couleur illustre bien les mécanismes d'honnêteté de ce signal (Olson et Owens 1998, von Schantz *et col.* 1999). L'honnêteté des signaux, permettant le transfert efficace de l'information, reflète l'intention de l'émetteur de renseigner sur son état. Cependant, ces émetteurs produisent également des signaux, ou indices, par inadvertance au cours de leurs activités et de leurs interactions. L'émission de ces 'sous-produits' informatifs associée à l'émission de signaux constitue la seconde approche du transfert d'information, le point de vue du récepteur.

## *L'écologie de l'utilisation de l'information*

Du point de vue du récepteur, acquérir et utiliser des informations est une nécessité. Accepter de se reproduire avec tel partenaire, changer de lieu de vie, chercher de la nourriture : toutes ces questions, essentielles dans la vie d'un individu, possèdent de nombreuses réponses potentielles, et donc amènent à un choix. Comment un individu peut-il prendre la meilleure décision ? Comment peut-il réduire l'incertitude intrinsèque du monde environnant ? La méthode est simple et valable pour toutes les décisions à prendre : « Observer » le monde qui l'entoure ! En effet, le monde environnant est riche de signaux et d'indices qui constituent autant de sources d'information sur l'état de l'habitat, la santé et la qualité de ses voisins, et même sur la prédictibilité de cet environnement. L'utilisation de l'information a stimulé de nombreuses études de la part des écologues du comportement (Valone et Templeton 2002, Danchin *et col.* 2004, Giraldeau 1997, Dall *et col.* 2005). Ces études ont permis de cerner les implications écologiques et évolutives de l'utilisation de l'information, ainsi que d'établir un classement précis des types d'information utilisée (Fig. 2, Danchin *et col.* 2004, Dall *et col.* 2005). La dichotomie majeure dans ce classement concerne la séparation entre informations personnelles et informations socialement acquises.

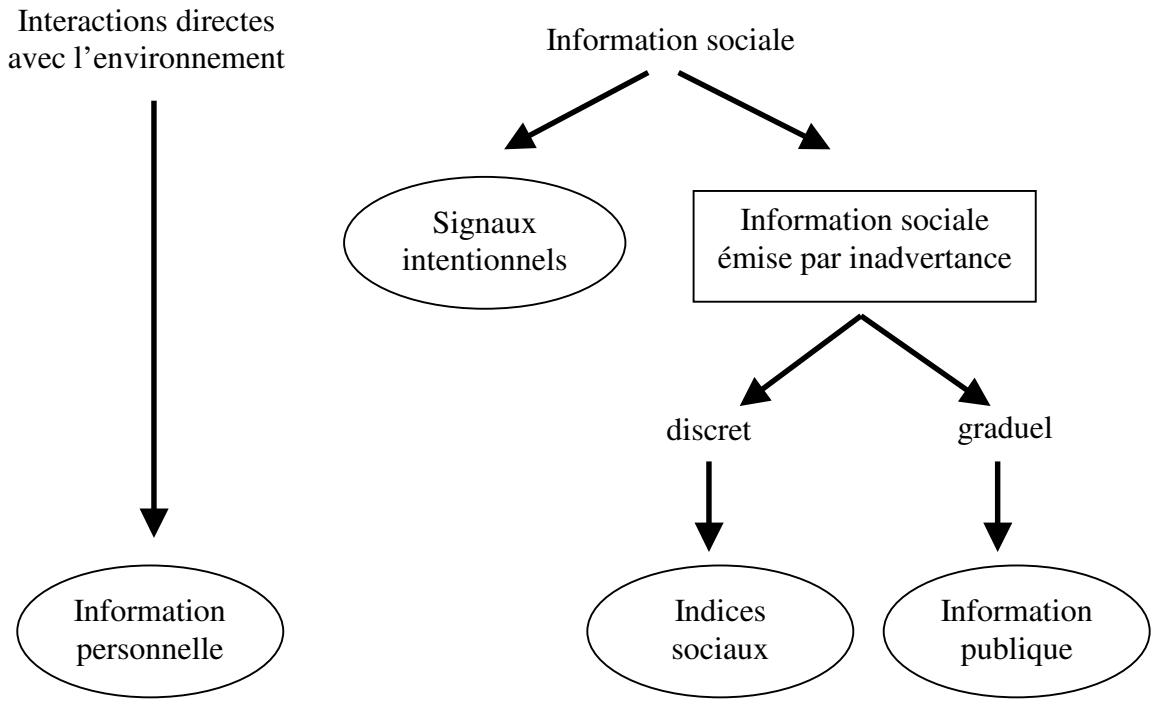


**Figure 2 :** Classification des sources d'information (Dall *et col.* 2005, Danchin *et col.* 2004)

Les interactions directes avec l'environnement génèrent des informations importantes sur les conditions et les ressources d'un habitat. Un individu est constamment en interaction avec son environnement. Cette source d'information est donc permanente et inévitable. Ainsi, ces informations personnellement acquises ont été intégrées dans l'étude de nombreux comportements. Le domaine d'application le plus évident est l'orientation spatiale et la navigation des individus dans leur environnement. Pour s'orienter un animal utilise divers indices environnementaux stimulant ses sens visuel, olfactif, auditif et tactile. Ainsi, les odeurs spécifiques, la lumière, les repères du paysage ou encore les bruits divers créent une carte spatiale activant certaines zones cérébrales et leur ensemble de neurones spécifiques. Par exemple, chez le rat, l'hippocampe et le noyau thalamique antérodorsal sont des zones cérébrales où se situent les cellules de lieu et les cellules de direction de la tête (Knierim *et col.* 1995, Taube 1995). Ces deux types de neurones ont des taux d'activation maximaux respectivement pour une position précise du corps et pour une direction de la tête donnée. Cela permet ainsi à l'animal de s'orienter et de naviguer dans son espace (Bures *et col.* 1997, Knierim *et col.* 1995). Cependant, l'activité de ces deux types de neurones, et ainsi l'orientation de l'animal, dépend fortement de la présence mais aussi de la stabilité des indices visuels, olfactifs et tactiles (e.g. Knierim *et col.* 1995, Bures *et col.* 1997, Zugaro *et col.*

2001). L'utilisation des informations personnelles pour la navigation est ainsi bien cernée du point de vue des mécanismes, mais reste faiblement étudiée du point de vue évolutif.

Du point de vue adaptatif, l'information personnelle a un rôle important dans de nombreux comportements, tels que la recherche de nourriture, le choix de partenaire, et l'évitement des prédateurs. En effet, un individu peut baser ses décisions futures sur ses expériences vécues dans un environnement donné. Il peut ainsi prendre des décisions plus sûres en 'estimant' les coûts et les bénéfices selon ses précédentes expériences. Un animal ayant recherché de la nourriture dans un patch donné possède plusieurs informations sur ce patch (Olsson et Holmgren 1998). A partir du temps passé à rechercher de la nourriture et du nombre de proies trouvées pendant ce temps, l'animal peut ainsi estimer ses chances futures d'obtenir de nouvelles proies. Cette estimation est essentielle dans l'utilisation optimale de patchs de nourriture et dans les décisions de mouvements inter-patchs (Giraldeau 1997). De la même façon, les indices laissés par les prédateurs ou les interactions précédentes avec des prédateurs permettent à l'animal d'estimer son risque de mortalité dans un habitat donné. Cette estimation va également affecter profondément les décisions de dispersion et plus généralement de mouvements au sein d'un habitat. Cependant, ces informations personnelles sont coûteuses et parcellaires car elles nécessitent une interaction directe entre l'individu et son environnement. L'individu ne pouvant pas interagir avec son environnement dans sa globalité (spatiale et temporelle), l'échantillonnage des informations est souvent biaisé. Chaque individu possède donc son pool personnel d'informations, dépendant de son histoire de vie. Le principe de l'information socialement acquise est né de cette simple idée. Si un individu possède son pool d'informations personnelles, un autre individu peut-il accéder à ces informations et les utiliser en association avec ses propres informations ?

## L'information sociale ou comment apprendre avec les autres

*« Le désir est désir de l'Autre»*
Jacques Lacan

Dans certaines sociétés humaines, les individus pré-reproducteurs (*i.e.* adolescents) développent un important copiage comportemental. Ainsi, ils se vêtissent des mêmes vêtements, ils emploient le même langage, ils ont les mêmes attitudes, les mêmes comportements. A travers ce copiage, ils essaient de ressembler aux personnes à succès (*e.g.* vedette du collège, vedette du cinéma) en espérant, en retour, augmenter leur réussite.

Changer son comportement en observant les autres pour augmenter son succès est donc un principe complètement intégré aux sociétés humaines. De récentes études montrent que ce principe est également vrai chez de nombreuses autres espèces.

Plusieurs revues récentes (Valone et Templeton 2002, Danchin *et col.* 2004, Dall *et col.* 2005) ont synthétisé les connaissances et proposé une classification précise des informations sociales. La distinction entre 'information publique' et 'indices sociaux de localisation' correspond à la principale classification des informations sociales. Celle-ci semble séparer clairement les indices discrets des indices graduels (Fig. 2, Danchin *et col.* 2004, Dall *et col.* 2005).

***Indices sociaux de localisation***

Parmi les informations sociales émises par inadvertance, les indices sociaux de localisation correspondent aux informations 'discrètes' (Valone et Templeton 2002, Dall *et col.* 2005). Le terme discret signifie que l'information renseigne sur la présence et la localisation de caractéristiques de l'habitat et de la composition de la population. L'exemple le plus étudié correspond à la localisation d'un patch de nourriture. Rechercher de la nourriture est un processus coûteux en terme de consommation d'énergie et de temps, ainsi que d'augmentation du taux de prédation. Tout mécanisme permettant de limiter ces coûts devrait donc être sélectionné. Selon ce principe, observer un congénère se nourrissant permet à un chercheur de nourriture de localiser une ressource de nourriture (revue dans Galef et Giraldeau 2001). Chez de nombreuses espèces d'oiseaux et de mammifères, les individus choisissent leur site de nourrissage à l'endroit où d'autres individus se nourrissent (*e.g.* Galef 1982, Avery 1994, Judd et Sherman 1996, revu dans Galef et Giraldeau 2001). Cela conduit à une augmentation locale de la densité de congénères par simple attraction pour les individus se nourrissant (Thorpe 1963, Galef et Giraldeau 2001). Chez les rongeurs, le dépôt d'odeur persistante sur les sites de prise de nourriture et sur le trajet menant à ces sites permet, en plus, aux congénères d'exploiter la ressource en l'absence physique d'informateur (Galef et Beck 1985). D'autres ressources, telles que les partenaires sexuels ou les abris, peuvent être localisées à partir d'indices sociaux. Par exemple, certains reptiles et amphibiens utilisent les odeurs déposées par les congénères pour repérer un abri sécurisé (Aragon *et col.* sous presse, Gautier *et col.* 2006). Chez ces espèces, les abris diurnes ou nocturnes sont essentiels dans la protection contre les prédateurs et sont souvent le lieu d'interactions sociales. Trouver un abri

est une nécessité qui peut être difficilement réalisable. L'information déposée par les congénères permet une localisation plus facile et plus sûre de ces abris. En accord avec ces observations, l'information sociale est également très importante dans la réaction immédiate face aux prédateurs. Ainsi, la fuite d'un individu face à l'approche d'un prédateur conduit généralement à un départ en masse des congénères environnants. Ce type d'information permet une réaction plus rapide et un évitement de la prédation plus important. Même si le bénéfice est évident, le coût d'une mauvaise information est important, particulièrement à l'échelle du groupe ou de la population (Lima 1994, Giraldeau *et col.* 2002). En effet, la transmission d'une information erronée conduit à des cascades d'informations et de mauvaises décisions collectives coûteuses à l'échelle de l'individu et de la population (Giraldeau *et col.* 2002). Les informations sociales affectent ainsi la répartition des individus au sein des habitats sur une échelle spatiale et temporelle, et ont d'importantes conséquences sur la dynamique des populations.

***Information publique***

Valone (1989) définit l'information publique comme l'estimation de la qualité d'un patch obtenue en observant le succès du comportement de recherche de nourriture des autres. Ainsi, les individus recherchant de la nourriture peuvent combiner leurs informations personnelles avec les informations de réussites et d'échecs des autres pour estimer rapidement et correctement la qualité d'un patch (Galef et Giraldeau 2001, Valone et Templeton 2002). L'information publique ayant été définie dans un contexte de recherche de nourriture, les démonstrations empiriques se sont initialement axées sur cette activité. Nous pouvons regrouper les études en deux questions concernant la recherche de nourriture (Galef et Giraldeau 2001) : 1) Quand manger ? et 2) Que manger ?

Dans les conditions naturelles, les ressources ne sont jamais infinies. A un certain moment, le stock de la ressource est épuisé. Et après un certain temps, la ressource est de nouveau présente. L'individu doit donc se poser deux questions : Quand dois-je commencer à rechercher de la nourriture ? Quand dois-je changer de patch ? Sans information publique, les individus recherchant la nourriture avec le moins de succès devraient être ceux quittant le patch les premiers. L'information publique permet potentiellement à tous les membres d'un groupe d'avoir la même estimation de la quantité de ressource. Cela devrait permettre un départ du patch à des temps similaires pour tous les individus. Templeton et Giraldeau (1995),

entre autres, vérifièrent cette prédiction chez l'étourneau. Ainsi, chez cette espèce, les individus associent leurs informations personnelles sur la qualité du patch à l'information publique délivrée par les congénères pour entamer et accélérer leur départ d'un patch de mauvaise qualité. De la même façon, plus un groupe est composé d'individus plus l'information publique devrait conduire à un départ rapide des patchs vides. Ainsi, les groupes de trois bec-croisés des sapins passent significativement moins de temps sur un patch vide que les paires d'individus ou les individus seuls (Smith *et col.* 1999).

Dans la recherche de nourriture, trouver des proies est essentiel, mais celles-ci doivent également être de 'bonnes' proies (Galef et Giraldeau 2001). Connaître les type de proie à consommer et celles à ne pas consommer peut avoir d'importantes conséquences sur le succès d'un individu. Par exemple, certaines proies contenant des toxines entraînent des conséquences négatives pour le consommateur. Face à une proie nouvelle, le rat domestique (*Rattus norvegicus*) observe le comportement et la santé de ses congénères ayant consommé cette proie pour décider de la consommer ou non. De la même manière, le carouge à épaulette privilégie la nourriture colorée si ses congénères ont précédemment mangé des proies colorées (Mason et Reidinger 1981). Ces deux exemples illustrent bien l'utilisation de l'information publique dans le choix des proies à consommer.

Outre la nourriture, la notion d'information publique a été ultérieurement élargie à l'estimation de la qualité de différents paramètres environnementaux à partir de l'activité des autres. La définition première de l'information publique s'appuie sur l'estimation de la qualité d'un patch. Un patch de bonne qualité est un patch dans lequel les individus obtiennent un bon succès. Or, le succès d'un individu peut s'estimer par sa survie, relative à la quantité de ressources alimentaires, mais également par sa reproduction, mesure directe de sa valeur sélective. La qualité d'un patch peut ainsi s'estimer par le succès reproducteur prédit, en terme de probabilité d'accouplement, de nombre de petits produits et de qualité des petits produits. Ce succès de la reproduction est affecté par deux mesures de qualité du patch : 1) la qualité de l'habitat et son influence sur le succès reproducteur, et 2) la qualité de la ressource utilisée pour la reproduction (*i.e.* partenaire sexuel). Plusieurs études se sont intéressées au rôle de l'information publique dans l'estimation de la qualité de l'habitat de reproduction, notion plus proche de la définition première de l'information publique. Ainsi, de plus en plus d'études, expérimentales et corrélatives, soutiennent l'idée que les individus utilisent le succès reproducteur des autres comme information publique de la qualité des sites de reproduction (*e.g.* Doligez *et col.* 2002, revue dans Valone et Templeton 2002, Danchin *et col.* 2004). Les

individus peuvent alors estimer la qualité de leur propre patch mais aussi celle des patchs avoisinants en prospectant dans ces patchs (Boulinier et Danchin 1997). Cette double utilisation de cette information publique affecte évidemment les mouvements entre patchs, conduisant à un départ plus important des patchs avec un faible succès reproducteur des congénères et à une installation plus importante dans les patchs avec un fort succès reproducteur des congénères (Boulinier et Danchin 1997). Cela implique des mouvements dépendants du succès reproducteur des patchs d'un système multi-patchs, et, plus généralement, a des conséquences importantes sur la dynamique des méta-populations (Boulinier et Danchin 1997). Plusieurs études récentes illustrent l'utilisation de cette information dans la sélection de l'habitat (*e.g.* Danchin *et col.* 1998, Doligez *et col.* 2002). Par exemple, les décisions de dispersion d'un site de reproduction et la sélection de nouveaux sites de reproduction dépendent du succès reproducteur local chez le gobe-mouche à collier (*Ficedula albicollis*, Doligez *et col.* 2002, Doligez *et col.* 1999). L'information publique affecte ainsi le succès reproducteur d'un individu par le choix du site de reproduction.

De plus, l'information publique apparaît comme importante dans le choix de partenaires sexuels. A partir de l'observation du comportement des autres, les femelles changent leur décision d'accouplement. Nous pouvons distinguer deux moyens d'accéder à cette information : 1) observer les accouplements des autres et copier leur choix sexuel, et 2) observer les interactions entres mâles et/ou femelles pour estimer la qualité de sa future reproduction. Alors que l'idée paraît simple, les bénéfices de l'utilisation d'une telle information sont moins clairs. Pour choisir un mâle, les femelles ont habituellement accès à des signaux reflétant la qualité du mâle (voir la partie précédente). Si les signaux reflètent honnêtement la qualité des mâles, observer la reproduction de ces mâles avec d'autres femelles peut sembler coûteux en termes de temps d'attente, de diminution de la quantité de sperme, et de risque d'imitation d'une mauvaise stratégie (Gibson et Höglund 1992). Néanmoins, la discrimination entre les mâles peut être difficile dans certaines conditions, notamment pour des femelles peu expérimentées, ou lorsque les mâles sont de qualités similaires (Valone et Templeton 2002). Il paraît alors bénéfique d'associer les signaux émis par les mâles (*i.e.* information intentionnelle) à une information publique sur les accouplements. L'imitation de l'accouplement a été démontrée plusieurs fois (revu dans (Valone et Templeton 2002). Cependant, peu d'études se sont intéressées à l'association entre l'information publique et l'intensité des signaux émis. Les femelles guppy (*Poecilia reticulata*) montrent ainsi une imitation comportementale importante lorsque le degré de

similitude entre les mâles est important et lorsque les femelles sont jeunes (Dugatkin 1996). Lors du choix du partenaire, les femelles peuvent également observer les interactions entre les mâles pour estimer la qualité des mâles. Chez de nombreuses espèces, les femelles préfèrent se reproduire avec les mâles gagnant les interactions qu'avec les perdants (e.g. Otter *et col.* 1999, Oliveira *et col.* 1998). Le résultat d'une interaction mâle-mâle constitue également une source d'information publique pour les autres mâles (Johnstone 2001, Valone et Templeton 2002). Les interactions entre les mâles peuvent être coûteuses car elles nécessitent du temps, de l'énergie et sont sources de risque de blessures. Chez plusieurs espèces, avant d'entamer une interaction, les mâles estiment la capacité compétitrice de leur éventuel opposant en observant ses précédentes interactions (Freeman 1987, Oliveira *et col.* 1998). Grâce à cette information, les mâles réduisent les coûts de leur interaction et donc en retirent un bénéfice. Même si ces informations sont délivrées publiquement, il reste cependant plus difficile de séparer la part d'information publique de la part du signal. Particulièrement, ces estimations lors des interactions peuvent être à la base d'amplification des signaux émis par les mâles (*i.e.* effet audience) et ainsi que de l'évolution de nouveaux signaux (Lotem *et col.* 1999, Danchin *et col.* 2004).

Nous avons résumé les principales informations publiques observées couramment dans le règne animal (Valone et Templeton 2002, Danchin *et col.* 2004). Cependant, de nouvelles formes d'information publique dans des contextes variés sont mises en évidence régulièrement. L'information publique permet, par exemple, d'estimer le parasitisme au nid (Poysa 2006) ou la sécurité d'un abri (Gautier *et col.* 2006). Même si la notion d'information publique est ouverte à tout contexte, certains auteurs soulignent la confusion qu'il peut exister entre l'information publique et l'information sociale au sens large (Valone et Templeton 2002).

***Entre information publique et indice social de localisation***

Valone et Templeton (2001) soulignent, ainsi, l'utilisation abusive du terme d'information publique pour décrire toutes formes d'apprentissage social (*i.e.* information sociale). Les auteurs considèrent que cette confusion n'est pas consistante avec la définition initiale par Valone (1989) et qu'elle obscurcit l'aspect unique de l'information publique comme source supplémentaire d'information utilisée à la fois pour augmenter le taux d'estimation et de réduction de l'incertitude concernant la qualité d'une ressource

environnementale. Ils proposent donc que le terme ‘information publique’ soit restreint à l’information sur la qualité d’une ressource environnementale obtenue des autres. Toute autre information obtenue en observant le comportement des autres devrait être nommée ‘information sociale’, terme général englobant les indices sociaux et l’information publique.

Le classement de certaines informations peut, cependant, se révéler plus compliqué. Prenons l’exemple de la question relative à la recherche de nourriture : ‘quand et où manger ?’. Comme indiqué précédemment, cette question peut être subdivisée en deux sous-questions (Galef et Giraldeau 2001) : Quand dois-je commencer à rechercher de la nourriture ? Quand dois-je partir d’un patch pour un autre ? Pour commencer à rechercher de la nourriture, il est moins coûteux d’attendre qu’un patch contenant de la nourriture soit localisé par un congénère. La première question implique donc l’utilisation d’une information relative à la localisation d’un patch de nourriture. Selon la classification admise, ce type d’information correspond plus à des indices sociaux qu’à une information publique. Au contraire, la décision de départ d‘un patch de nourriture dépend de l’estimation de la quantité et de la qualité de ressource disponible. Cette estimation est facilitée par l’utilisation d’information publique. Un individu se nourrissant sur un patch contenant peu de nourriture peut ne pas changer de patch si aucun autre patch n’est localisé par un de ses congénères. L’aspect temporel de la recherche de nourriture imbrique donc des questions relatives aux indices sociaux et à l’information publique. Ainsi, il peut être difficile de distinguer expérimentalement ces deux formes d’informations sociales. Cet exemple souligne un problème méthodologique plus qu’un problème de définition. Cependant, classer une information sociale peut être plus compliqué. Gautier et col. (2006) démontrent que la salamandre de Luschan utilise les indices chimiques déposés par les congénères pour localiser un abri sûr. Les auteurs concluent que les individus estiment ainsi la disponibilité et la qualité des abris grâce à une information sociale. Comme nous l’avons indiqué, la localisation d’une ressource fait appel à des indices sociaux plus qu’à une information publique. Cependant, dans cette étude, les individus ne localisent pas uniquement un abri mais un abri sûr. En effet, localiser un abri n’est pas nécessairement coûteux et donc l’utilisation d’indices sociaux n’est pas fondamentale. Au contraire, localiser un abri avec de bonnes conditions environnementales est essentiel pour un ectotherme vivant dans un milieu aride. Chez cette espèce, l’abri est également un moyen d’éviter les prédateurs. Les indices déposés par les congénères sont donc le reflet de la présence d’un abri mais aussi de la sûreté de l’abri. Pour cet exemple, il n’existe pas de distinction nette entre présence et qualité d’une ressource, et

donc entre indices de localisation et information publique. Dans leur réponse à Danchin *et col.* (2004), Lotem et Winkler (2005) soulignent également la difficulté de distinguer l'information publique d'autres formes d'information sociale. Ils illustrent leur propos avec les informations multiples délivrées par le chant des mâles. Le chant permet de renseigner sur la présence, la qualité et la densité des mâles. L'information sur la localisation (*i.e.* présence de mâles) et la qualité des ressources (*i.e.* densité de mâles) implique parfois le même indice, et cet indice est parfois identique au signal de qualité du mâle. Danchin *et col.* (2005) répondent à cette critique par la nécessité de distinguer signaux et indices, même si les indices peuvent être à l'origine de l'évolution des signaux (*e.g.* compétition entre mâles dépendante de l'audience). En effet, la distinction entre les informations émises intentionnellement (*i.e.* signaux) et celles émises par inadvertance (*i.e.* indices) s'accorde mieux aux processus de sélection et aux conséquences évolutives de ces informations. A la vue des exemples précédents et en accord avec Danchin *et col.* (2005), nous pensons que la définition de l'information publique peut être trop restreinte dans certaines conditions, et devrait être englobée dans le terme 'informations sociales émises par inadvertance'. Pour chaque exemple développé dans cette thèse, nous discuterons ainsi de leur position au sein de la classification des informations socialement acquises.

### *De l'information personnelle à l'information sociale*

Comme nous l'avons indiqué, les informations personnelles sont biaisées par des échantillonnages restreints conditionnés aux expériences de l'individu. Les informations sociales permettent ainsi d'éviter ces coûts de l'information personnelle. Cependant, les informations sociales peuvent être indisponibles, mal informatives, ou même en contradiction avec les informations personnelles (Giraldeau *et col.* 2002). Les récepteurs ne devraient donc pas privilégier les mêmes types d'informations dans les mêmes situations, ou devraient associer leurs informations personnelles à celles délivrées par leurs congénères lorsque cela est possible (Giraldeau *et col.* 2002).

## Contexte de l'étude : l'information sociale chez le lézard vivipare

*« I am the Lizard King, I can do anything »*
Jim Morrison

Nous axerons cette thèse autour de trois parties. Chacune de ces parties permettra d'illustrer l'existence, les mécanismes et les implications d'une information socialement

acquise chez le lézard vivipare (*Lacerta vivipara*). Comment mettre en évidence l'existence d'une information ? L'information se caractérise par sa transmission. Ainsi, une information non transmise n'est pas une information. Montrer l'existence d'une information passe donc par montrer sa transmission. Nous avons, au cours de cette thèse, développé deux types d'approches expérimentales. La première, illustrée par deux articles, considère l'information au niveau de la population. Les protocoles consistent à modifier l'information présente dans une population et à observer les conséquences comportementales sur les résidents de cette population. Pour réaliser ces expériences, nous utilisons des populations semi-naturelles de lézards vivipares. Une population semi-naturelle correspond à un enclos contenant un patch d'habitat et connecté à un autre enclos par un corridor (voir manuscrit 1). Ce corridor, de longueur identique à la distance minimale de dispersion naturelle, est terminé par un piège à dispersion. Grâce à ce piège, les dispersants sont collectés quotidiennement. Après les avoir identifiés, pesés et mesurés, les dispersants sont relâchés dans une autre population. En contrastant des paramètres informatifs entre les populations initiales, nous pouvons tester le rôle de ces paramètres sur la dispersion des individus. Cette méthode a pour avantage d'explorer, par la suite, les implications démographiques de la transmission de cette information. En effet, chaque dispersant étant relâché dans une population, nous pouvons suivre des traits d'histoire de vie de ces dispersants ainsi que la dynamique de ces populations. La deuxième approche, développée dans la seconde partie, prend en compte une vision individu-centré. Elle consiste à confronter des individus potentiellement récepteurs à des individus potentiellement porteurs d'une information. Si les récepteurs modifient leur comportement en fonction de l'information portée, alors l'information est transmise et utilisée. Cette approche permet également d'explorer les signaux et les indices utilisés pour véhiculer et moduler cette information. Après avoir développé ces deux types d'approches, il paraît important de montrer l'étendue de ce type d'information. En effet, plusieurs conditions environnementales modifient le phénotype des individus les subissant. Bien que nous n'ayons pas eu la possibilité d'examiner le transfert d'information, ces conditions possèdent tout l'arsenal nécessaire pour véhiculer ce transfert. Nous illustrerons la possibilité d'un transfert d'information lié au stress, son utilité et ses conséquences pour les individus, ainsi que la possibilité de renseigner sur le sexe-ratio des populations voisines.

# II. L'INFORMATION SOCIALE EXISTE-T-ELLE CHEZ LE LEZARD VIVIPARE ?

Dès sa naissance, le jeune lézard vivipare est confronté à un des choix les plus déterminants de son devenir : rester ou partir de son lieu de naissance. Cette décision est lourde de conséquences. Partir lui-demande de l'énergie et du temps. Mais rester, c'est continuer à subir les éventuels problèmes présents dans son habitat natal. C'est aussi admettre qu'ailleurs, ce ne soit pas mieux. Toute information que le juvénile peut acquérir permet de réduire l'incertitude de son choix, et donc d'augmenter le succès de sa décision de départ. Ainsi, tout mécanisme permettant d'obtenir des informations sur la qualité de son habitat et des autres habitats devrait être sélectionné. Cependant, chez une espèce sans capacité particulière d'exploration (*e.g.* lézard vivipare), les jeunes connaissent uniquement leur site de naissance. Alors que l'acquisition d'information sur l'habitat natal paraît aisée, l'obtention des informations sur les habitats inconnus du jeune lézard nécessite des mécanismes moins évidents. Dans les deux expériences qui suivent, nous illustrerons la possibilité que les jeunes ont de s'informer sur les conditions environnementales 1) de leur population de naissance et 2) des populations avoisinantes, ainsi que les conséquences sur leurs décisions de dispersion.

La dispersion natale est affectée par plusieurs paramètres biotiques et abiotiques de l'environnement (Clobert *et col.* 2004). La dispersion a ainsi évolué pour répondre, par exemple, aux effets négatifs des interactions sociales. Cependant, il existe une diversité d'interactions sociales affectant différemment la dispersion. Nous pouvons distinguer deux classes majeures d'interactions sociales : les interactions avec les apparentés et les interactions avec les non-apparentés. Ces deux classes d'interactions sont distinctes par leurs conséquences sur les traits d'histoires de vie des individus et leurs mécanismes. Alors que les interactions avec les non-apparentés affectent la compétition locale et l'accessibilité aux ressources alimentaires et reproductrices, les interactions entre apparentés sont liés à la compétition et la coopération entre apparentés ainsi qu'à l'évitement de la consanguinité (Gandon et Michalakis 2001). Dans un contexte de sélection de l'habitat, ces deux classes d'interactions diffèrent également à une échelle spatiale. En effet, la population natale contient un plus haut niveau d'apparentés que les populations voisines. Les problèmes ou les avantages liés aux interactions entre apparentés devraient donc être plus prononcées dans la population natale que dans les populations avoisinantes. Il paraît alors probable que les

interactions entre apparentés affectent plus fortement les décisions de départ de la population natale que les décisions de sélection de nouveaux habitats. Au contraire, les interactions avec les non-apparentés devraient jouer un rôle à la fois dans les décisions de dispersion (Lambin *et col.* 2001) et de sélection d'habitat (Stamps 2001). L'utilisation des informations liées à ces deux paramètres devrait également suivre ce pattern. La première expérience présentée manipule ainsi les interactions entre apparentés dans la population natale, alors que la seconde expérimente l'influence de la densité des populations avoisinantes.

## II - A. Se renseigner sur ses voisins et leurs parents

Manuscrit No.1 p.71 (Kin competition promotes colonization success)

L'interaction entre apparentés est une force majeure de l'évolution de la dispersion (Hamilton et May 1977, Le Galliard *et col.* 2005b). Ainsi, les interactions entre les jeunes d'une même famille et les interactions enfants-parents devraient affecter la dispersion natale. Plusieurs études, empiriques et théoriques, confirment cette prédiction (voir Lambin *et col.* 2001, Gandon et Michalakis 2001). Chez le lézard vivipare, la dispersion natale est dépendante des interactions mère-enfants, celles-ci étant modulées par la présence effective, la condition et l'âge de la mère (de Fraipont *et col.* 2000, Le Galliard *et col.* 2003, Léna *et col.* 1998, Ronce *et col.* 1998). Les interactions entre apparentés, et particulièrement les interactions mère-enfants, sont donc essentielles chez cette espèce. Cependant, les décisions de dispersion et leurs conséquences ne dépendent pas uniquement de la décision individuelle face à des problèmes personnels, mais aussi de l'accumulation du même problème chez les congénères dans la population. En effet, une interaction négative avec sa mère ne reflète pas obligatoirement la qualité ou le statut de la population. L'accumulation d'interactions de plusieurs individus avec leur mère est, par exemple, le signe d'un niveau d'apparentement augmenté dans la population, ce qui est potentiellement négatif en termes de consanguinité. Les conséquences pour l'individu d'un problème au niveau de la population peuvent donc être tout aussi néfastes qu'un problème au niveau individuel. Si un individu peut se renseigner sur le niveau d'interactions entre apparentés des congénères au sein de sa population, son choix de dispersion devrait aussi bien dépendre du niveau d'interaction au sein de la population que de son niveau individuel. Pour tester cette hypothèse, nous avons manipulé le niveau d'interactions mère-enfant, une importante interaction entre apparentés, de huit populations semi-naturelles de lézards vivipares, et observé les effets sur la probabilité de disperser des individus. En accord avec notre hypothèse, nous avons manipulé les interactions entre

apparentés à deux échelles. Premièrement, à l'échelle individuelle, nous avons manipulé la présence de la mère en relâchant chaque famille de juvéniles avec leur mère ou avec une autre femelle. Deuxièmement, à l'échelle de la population, nous avons varié la proportion de familles, et donc de jeunes, lâchées avec leur mère dans la population (67% des jeunes avec leur mère versus 33% des jeunes avec leur mère). En augmentant le nombre de mères présentes dans la population, nous avons également créé un plus fort niveau d'apparentement dans la population.

Les résultats de cette étude ont montré que la probabilité de disperser n'est pas affectée par les interactions d'un individu avec sa mère, alors qu'un fort niveau d'interactions des congénères de la population avec leur mère augmente la dispersion natale en nombre et en qualité des dispersants (*i.e.* augmentation de la taille corporelle des dispersants). Cela montre que les jeunes lézards ont accès à une information relative aux interactions mère-enfant de leurs voisins. Ainsi, ils sont capables d'estimer, par exemple, le nombre de mères présentes ou le degré d'apparentement de la population, et de modifier, en réponse, leur comportement de dispersion. Dans cette expérience, nous ne pouvons pas déterminer précisément le mécanisme sous-jacent du transfert de cette information socialement acquise. Le phénotype du jeune peut être modifié sous plusieurs aspects par la présence de sa mère. La reconnaissance de la mère se fait, au moins en partie, par l'intermédiaire de signaux olfactifs (Léna *et col.* 1998). Cette reconnaissance semble déterminée dès les premiers jours de la vie, suggérant une détermination prénatale ou très tôt après la naissance. Le jeune lézard peut donc déterminer rapidement la présence de sa mère dans la population et s'en servir comme d'une information personnelle. Nous savons, par ailleurs, que la présence de la mère peut engendrer des réponses comportementales rapides (Léna *et col.* 1998, Léna et de Fraipont 1998). Ainsi, les voisins peuvent ensuite utiliser ces modifications comportementales pour estimer les interactions entre apparentés présents dans la population. Par exemple, notre étude révèle que les jeunes en présence de leur mère initient leur dispersion plus tôt que les jeunes en absence de leur mère, cela sans différence de probabilité de dispersion. Une dispersion avancée pourrait ainsi constituer une information sociale permettant aux autres juvéniles d'estimer le niveau d'apparentement de la population. Le niveau d'apparentement affectant la valeur sélective des individus de la population, il peut être considéré comme un indice de la qualité de la population. Cette information sociale pourrait ainsi s'approcher d'une information publique utilisée dans le choix de dispersion.

## II - B. Se renseigner sur les autres populations

Manuscrit No.2 p.90 (Social information and emigration : Lessons from immigrants)

Partir de sa population est une décision qui peut s'avérer coûteuse. Elle demande du temps et de l'énergie pour parcourir la distance séparant deux populations. Elle implique également une part de risque en termes de prédation mais aussi d'incertitude. Après quelques jours de vie, les jeunes connaissent leur population natale mais n'ont a priori aucune idée de la qualité de vie dans les autres populations. Il est parfois difficile de s'installer dans une nouvelle population et cela n'est pas obligatoirement bénéfique si la nouvelle population est de moins bonne qualité que la population natale (*e.g.* Belichon *et col.* 1996). Acquérir des informations sur les populations avoisinantes peut permettre de pallier ou de diminuer ce coût. Les études sur l'information publique et la sélection d'habitat proposent la prospection comme mécanisme d'estimation de la qualité des populations avoisinantes (voir sections précédentes, et aussi Stamps 2001, Valone et Templeton 2002, Danchin *et col.* 2004). Ainsi, chez de nombreuses espèces, les dispersants peuvent visiter plusieurs habitats avant de s'installer dans celui de meilleure qualité. Cependant, la prospection est impossible pour des espèces à capacités exploratoires limitées et inclut des coûts similaires à ceux de la dispersion (énergie, temps, et prédation). Pour de nombreuses espèces, comme le lézard vivipare, estimer la qualité des populations avoisinantes sans les visiter apparaît comme le mécanisme le moins coûteux. Dans cette étude, nous proposons un tel mécanisme. Nous faisons l'hypothèse que si un individu prospectant une population peut acquérir des informations, ce même individu peut également renseigner sur la qualité des autres populations. Les immigrants pourraient ainsi constituer une source d'information sur leur population d'origine. Pour tester cette hypothèse, nous avons donc manipulé l'information portée par les immigrants en variant la qualité de leur population d'origine. Si les immigrants portent l'information relative à la qualité de leur population d'origine, nous devrions observer, dans la population où ils arrivent, une dispersion dépendante de cette origine.

Pour varier la qualité des populations, nous avons manipulé la densité de ces populations. En effet, la densité est un paramètre décisif dans la sélection d'habitat car elle affecte directement la quantité de ressource et le degré de compétition mais elle est également le signe d'un habitat attractif (Reigh *et col.* 1982, Krebs 1971, Stenseth et Lomnicki 1990,

Stamps, 2001, Doligez *et col.* 2003, Doligez *et col.* 2004). La densité apparaît, ainsi, comme une source d'informations multiples sur la qualité d'une population.

Effectivement, les immigrants délivrent bien une information sur la densité de leur population d'origine. En réponse à cette information, le niveau d'émigration de la population est modifié. Ainsi, dans les populations recevant des immigrants originaires d'une population de faible densité, les juvéniles dispersent plus. Cette dispersion dépendante des immigrants est le signe d'un transfert d'information sur la population d'origine des immigrants. Quel type d'information est transféré et par quels mécanismes est-elle transférée ? Cette information varie avec la densité de la population d'origine des immigrants, cependant il est peu probable que l'information estimée soit la densité elle-même. Nous pouvons, par exemple, montrer que le nombre d'immigrant n'est pas le mécanisme du transfert d'information. Or une information sur la densité devrait, en partie, être modulée par le nombre d'émetteurs de l'information. L'information estimée reflète probablement plus la qualité globale de la population ou le niveau d'interactions sociales, paramètres dépendants de la densité. Dans une population de faible densité, les juvéniles ont accès à plus de ressources et sont soumis à moins d'interactions sociales. Le phénotype des immigrants peut être affecté par cette densité, entraînant une imprégnation du phénotype par les conditions de la population d'origine. La manipulation de la densité peut ainsi avoir induit un départ d'immigrants de phénotype particulier. En effet, il a été précédemment démontré que différentes conditions entraînent le départ de différents types de dispersants en termes de phénotype (*e.g.* Léna *et col.* 1998, de Fraipont *et col.* 2000, Clobert *et col.* 2004). Les immigrants de populations de différentes densités pourraient exhiber des phénotypes différents (traits morphologiques, physiologiques ou comportementaux). Dans notre expérience, les immigrants provenant de populations de forte et de faible densités ne différent pas en ce qui concerne leur taille ni leur condition corporelle. Chez le lézard vivipare, nous savons que la densité et les interactions sociales affectent l'activité, l'agressivité et l'odeur des individus (Lecomte *et col.* 1994, Aragon *et col.* sous presse). Nous proposons, donc, deux autres mécanismes pouvant expliquer le transfert d'information : le comportement et les indices olfactifs. Pour explorer ces mécanismes, nous avons réalisé une expérience complémentaire (voir partie III - A). En plus de cette imprégnation phénotypique, les récepteurs de l'information doivent distinguer un immigrant d'un résident. Nous savons que les dispersants (*i.e.* immigrants) possèdent un phénotype spécifique (*e.g.* comportement (Meylan et Clobert soumis) permettant aux résidents de les reconnaître pendant un minimum de 6 mois (Aragon *et col.* 2006)). Par la maintient d'un

phénotype dépendant des conditions natales, les conditions d'honnêteté de l'information semblent être remplies.

Notre étude révèle également deux principes du transfert d'information : l'utilisation de l'information dépendante du récepteur et des conditions environnementales. En effet, nous pouvons observer que l'information transférée par l'immigrant n'est pas utilisée de la même manière par tous les individus. Nous avons précédemment introduit le rôle du récepteur dans le transfert d'information (voir chapitre I). Celui-ci peut différer par sa capacité d'intégration de l'information mais aussi par une valeur informative dépendante des traits personnels de l'individu. Dans cette étude, l'information portée par les immigrants affecte la dispersion en interaction avec la taille corporelle. Ainsi, la probabilité de disperser est positivement corrélée à la taille de l'individu uniquement dans les populations recevant des immigrants provenant de populations de fortes densités. Chez le lézard vivipare, les juvéniles de grande taille dominent les interactions sociales par leurs fortes capacités compétitives. Une information signalant un fort niveau de compétition (*i.e.* forte densité) entraîne uniquement le départ d'individus à forte capacité compétitive (*i.e.* individus de grande taille). Lorsque la population avoisinante est de faible densité (*i.e.* à faible niveau de compétition), le succès lors de l'installation des dispersants dépendrait moins de leur compétitivité. Nous observons, ainsi, que les individus de tous phénotypes dispersent avec la même probabilité dans cette situation.

L'utilisation de l'information peut dépendre des conditions d'acquisition et de l'origine de cette information (voir chapitre I). Dans notre étude, l'utilisation de l'information portée par l'immigrant est dépendante de la densité de la population du récepteur. L'origine de l'immigrant induit une réponse comportementale plus importante dans les populations de faibles densités. Ce résultat peut paraître inattendu dans une vision négative de la densité de population. Cependant, l'information délivrée par la densité est multiple. Une forte densité correspond à un habitat avec plus de compétition pour le partage des ressources (*e.g.* alimentaires et spatiales), mais est également le signe d'un habitat attractif (revue dans Stamps 2001). La dispersion et la sélection d'habitat ont été ainsi observées comme étant positivement ou négativement dépendantes de la densité en congénères pour plusieurs espèces telles que le lézard vivipare (Denno et Peterson 1995, Lambin 1994, Lambin *et col.* 2001, Stamps 2001, Le Galliard *et col.* 2003). La densité peut donc engendrer une information dépendante de l'origine de la source informative. Une forte densité dans l'habitat où réside l'individu pourrait signaler de bonnes conditions pour cet individu, alors que l'information

relative à la densité des autres populations pourrait être inversée par les mécanismes de transmission de cette information. En effet, les immigrants pourraient transmettre une information relative à la quantité de ressource et au niveau de compétition des populations à faible densité, indépendamment d'une information sur la densité de congénères. Les dispersants potentiels utiliseraient, ainsi, la qualité des informateurs (*i.e.* immigrants) et non la densité de congénères des populations avoisinantes comme indice de qualité de ces populations. Cependant, d'autres hypothèses pourraient expliquer cette dépendance de l'information aux conditions de vie des récepteurs. Par exemple, la qualité de la transmission de l'information a pu être affectée par la densité de la population du récepteur. Dans une population de forte densité, l'interaction immigrant-résident apparaît avec une plus faible probabilité. L'efficacité de la transmission de l'information serait ainsi réduite par une dilution des interactions émetteur-récepteur. Néanmoins, sous cette hypothèse, l'effet de l'origine de l'immigrant devrait dépendre du nombre d'immigrants (*i.e.* nombre d'émetteurs), ce qui n'est pas le cas dans notre étude. Finalement, nous ne pouvons pas exclure que la valeur et la signification de l'information puissent dépendre des conditions d'acquisition de l'information. Le bénéfice et la signification d'une information pourraient dépendre de la qualité de l'habitat du récepteur. Par exemple, disperser sans information est plus coûteux si l'individu vit dans un habitat de bonne qualité. Or, la dispersion n'est pas uniquement la réponse à la qualité de l'habitat. Ainsi, un dispersant fuyant sa mère utiliserait plus l'information relative aux populations avoisinantes si sa population est de bonne qualité. L'information étant plus importante dans les populations de faible densité, cette hypothèse soutiendrait une qualité plus importante des populations de faible densité, entraînant une plus forte utilisation de cette information. Cependant, cette hypothèse est opposée à ce que nous avons énoncé précédemment. Notre étude ne nous permet pas d'explorer ces hypothèses, ni d'accéder aux mécanismes de transfert d'information.

Même si des expériences complémentaires sont nécessaires, notre étude montre un moyen d'acquérir de l'information sur les populations avoisinantes sans les visiter. Cette information permet aux dispersants potentiels de connaître l'existence de populations de bonne qualité dans leur voisinage. Même si les dispersants ont connaissance de ces populations, nos résultats ne montrent pas que les immigrants les informent de sa localisation. Informer sur la localisation est néanmoins possible. Comme chez la plupart des reptiles et des amphibiens, les indices olfactifs sont une source importante d'information chez le lézard vivipare (Léna *et col.* 1998, Aragon *et col.* sous presse). Cette espèce vivant dans une

végétation dense, les indices chimiques devraient être favorisés par rapport aux indices visuels (Aragon *et col.* sous presse). Certaines espèces peuvent ainsi localiser des abris ou des lieux grâce à ces indices olfactifs (e.g. Gautier *et col.* 2006). La reconnaissance des indices olfactifs laissés par les immigrants pourrait permettre de localiser l'habitat d'origine de ces immigrants. D'autres tests doivent évidemment être réalisés pour savoir 1) si la localisation d'un habitat est possible, et 2) si les indices olfactifs correspondent au mécanisme de localisation. Cependant, dans un contexte de populations fragmentées à patchs éloignés et peu nombreux, seule l'existence de patchs de qualité réduit les coûts importants d'une dispersion dans un milieu inter-patch souvent hostile (*e.g.* sans végétation, peu de nourriture, risque de prédation). L'information sociale portée par les immigrants renseigne à la fois sur la présence et la qualité des populations avoisinantes. Il nous paraît difficile de distinguer entre information publique et indices sociaux. Quel que soit son nom, cette information sociale permet de renforcer les connections entre les populations existantes et ainsi d'augmenter la viabilité des populations fragmentées.

# III. MECANISMES DU TRANFERT D'INFORMATION

Les deux études précédentes démontrent l'existence d'information sociale chez le lézard vivipare. Les mécanismes restent cependant obscurs et nécessitent des expériences complémentaires. Comme pour la plupart des reptiles, les signaux acoustiques sont absents chez le lézard vivipare. L'information doit employer d'autres indices ou signaux pour être émise. Les indices comportementaux, physiologiques (*i.e.* couleur et odeur), et morphologiques (*e.g.* taille corporelle, voir annexes) semblent très informatifs chez cette espèce. Entre autres, ils affectent les prises de décisions au cours des interactions inter- et intra-sexuelles (voir ci-dessous et en annexes, e.g. Léna *et col.* 1998, Aragon *et col.* sous presse). Dans cette partie, nous illustrerons différents mécanismes pouvant intervenir dans le transfert d'information. Pour réaliser cela, nous analyserons le transfert d'information d'un point de vue individuel (partie III – A), les modifications du phénotype (partie III – A et III – B), ainsi que des variations individuelles constantes (partie III – C) liées à la densité de la population.

## III - A. Le comportement, une source d'information

Manuscrit No.3 p.107 (Density, information and space use in common lizard)

L'immigration modifie le comportement des résidents au niveau de la population (Partie II – B) et au niveau individuel (Aragon *et col.* 2006). Aragon et col. (2006) montrent ainsi que l'arrivée d'un immigrant change l'utilisation de l'espace par le résident. Cette étude souligne une estimation du statut de dispersion. Un individu peut distinguer un dispersant d'un non-dispersant et change son comportement en réponse. Les résidents peuvent ainsi reconnaître les individus étrangers à la fois par une reconnaissance individuelle et par une reconnaissance du statut de dispersion. Au niveau de la population, nos résultats montrent que le comportement des résidents est affecté par la densité de la population d'origine de ces immigrants. La densité de la population modifie certains traits comportementaux tels que l'agressivité ou l'activité (*e.g.* Rose 1981, Lecomte *et col.* 1994, Aars et Ims 2000). Ces changements induits par la densité peuvent servir d'indices comportementaux renseignant sur la densité de la population. Nous avons donc mesuré, en laboratoire, le comportement des sub-adultes vivant dans des populations de densités différentes. Nous pouvons constater que la densité augmente le temps d'activité alors que les autres comportements mesurés ne

semblent pas affectés (*e.g.* thermorégulation). En population de forte densité, les ressources alimentaires et spatiales sont moins disponibles. Cela entraîne un fort niveau de compétition et d'interactions sociales (*e.g.* Simon 1975). La restriction alimentaire et le stress social augmentés par la densité sont deux paramètres de stress pour la plupart des espèces (Silverin, 1998, Jacobson 1999, Lanctot *et col.* 2003, Comendant *et col.* 2003). La réponse hormonale à ces stress, via l'élévation du taux de corticostérone, initie un ensemble de changements comportementaux permettant de réduire ou d'échapper à la source de ce stress. Parmi ces changements, une augmentation de l'activité locomotrice et journalière est observée chez plusieurs espèces incluant le lézard vivipare (Moore *et col.* 1984, Dufty et Belthoff 1997, de Fraipont *et col.* 2000, Cote *et col.* 2006). Ces changements dépendant du stress constituent une explication à l'augmentation d'activité des sub-adultes vivant dans des populations de forte densité.

Pour tester le transfert d'information relative à la densité, nous avons observé les changements comportementaux induits par une interaction avec un congénère d'une population de faible ou de forte densité. Ce test a été réalisé à l'échelle individuelle dans deux situations : soit le lézard ayant subi l'interaction avec un congénère pouvait changer de micro-habitat (*i.e.* abri et spot de thermorégulation), soit le lézard était contraint de rester dans ce même micro-habitat. Nous avons créé ces deux situations car elles représentent une alternative présente dans les situations naturelles. Ainsi, en milieu naturel, un individu répond à un élément stressant selon deux types de réaction : fuir ou se cacher (Wingfield et Ramenofsky 1999). Quand la dispersion est possible et peu coûteuse, des mouvements locaux permettent à l'individu de fuir la source de stress. Quand de tels mouvements sont risqués (*e.g.* prédation) ou que la source de stress est temporaire (*e.g.* conditions climatiques), les individus préféreront se cacher et attendre de meilleures conditions. Dans notre étude, l'interaction avec un individu d'une population de forte densité entraîne ces deux types de réaction. Après une interaction avec un individu d'une population de forte densité, les sub-adultes, de nouveau seuls, passent plus de temps cachés s'ils ne peuvent pas fuir. Au contraire, ces individus changent plus d'habitat lorsque cette possibilité leur est donnée. Ces résultats montrent donc que les lézards peuvent percevoir la densité d'origine d'un congénère au cours d'une interaction. Ceux-ci modifient leur utilisation de l'espace en réponse à cette information, ce qui soutient les résultats observés au niveau de la population. Par quel mécanisme cette information est-elle transmise ?

Les individus utilisés comme informateurs (sous-échantillon des populations expérimentales) ne présentaient pas, dans cette expérience, de différences de condition, ni de couleur selon la densité de leur population. Il existait une différence de taille corporelle mais celle-ci n'affectait ni le comportement ni le transfert d'information. Nous n'avons observé aucune morsure entre les sub-adultes durant notre expérience, éliminant l'agression directe comme source potentielle d'information. Une étude précédente et une expérience complémentaire, non présentée dans cette thèse, montrent que les indices olfactifs de populations de forte ou de faible densité ne semblent pas affecter le comportement des sub-adultes (Meylan et Clobert soumis). Ainsi, le transfert d'information dépend plus probablement des changements comportementaux. Particulièrement, l'augmentation de l'activité d'un lézard interagissant peut entraîner une information pour le receveur. Comme nous l'avons observé, cela le conduirait à adopter des réponses comportementales stéréotypées du stress. Bien que d'autres tests soient nécessaires pour manipuler directement le transfert d'information, l'utilisation de l'espace dépendant de cette information a des conséquences importantes sur la sélection d'habitat.

## III - B. Autres sources d'information : indices et signaux multiples

Manuscrit en préparation (Multiple traits of sexual dimorphism: disentangling between selective pressures)

En variant la disponibilité des ressources alimentaires et sexuelles, la densité en congénères modifie les pressions de sélection agissant sur le développement phénotypique des nouveau-nés (Stamps et Krishnan 1997, LeBlanc *et col.* 2001). Certains traits du phénotype peuvent ainsi être affectés par un changement de la densité de la population. De plus, les pressions de sélection n'affectant pas de façon symétrique le développement des jeunes femelles et des jeunes mâles, le dimorphisme sexuel peut être profondément modifié par la densité (Stamps et Krishnan 1997, LeBlanc *et col.* 2001). Nous avons donc mesuré les conséquences de la densité sur deux traits phénotypiques du dimorphisme sexuel : la taille corporelle et la couleur ventrale. Le dimorphisme sexuel de cette espèce comprend une différence de taille corporelle, de condition corporelle et de couleur ventrale (Bauwens et Verheyen 1985, Pilorge *et col.* 1987). Les femelles sont plus grandes que les mâles alors que ceux-ci sont plus corpulents (Pilorge *et col.* 1987). La couleur ventrale, présente de la gorge à la base de la queue, varie du jaune au rouge pour les mâles et du jaune clair à l'orange chez les femelles (Vercken *et col.* sous presse). La couleur ventrale apparaît dès l'âge d'un an, la

reproduction débutant vers l'âge de 2 ans dans les populations naturelles (Bauwens et Verheyen 1985, Pilorge *et col.* 1987). Pour ces raisons, nous avons mesuré ces traits phénotypiques sur des sub-adultes de populations expérimentales de forte et de faible densité. Pour réaliser cela, nous avons relâché 402 nouveau-nés dans des populations semi-naturelles en créant deux densités différentes. L'année suivante, nous avons capturé les survivants (61 femelles et 47 mâles) pour les peser, les mesurer et prendre leurs spectres de couleur (manuscrit en préparation).

La densité de la population affecte différemment les mâles et les femelles, conduisant à un dimorphisme sexuel dépendant de la densité. Les individus vivant dans une population de faible densité sont plus grands ($F_{1,14} = 8.96$, $P = 0.0097$) et de meilleure condition corporelle ($F_{1,14} = 4.95$, $P = 0.043$). L'effet négatif de la densité sur la taille corporelle est dépendant du sexe ($F_{1,33} = 4.38$, $P = 0.0440$) et significatif uniquement pour les mâles (femelles : $F_{1,14} = 0.55$, $P = 0.47$, mâles : $F_{1,14} = 16.72$, $P = 0.0013$). Au contraire, l'effet de la densité sur la condition corporelle ne dépend pas du sexe ($F_{1,33} = 0.00$, $P = 0.96$). Cela résulte en une différence de taille corporelle entre les sexes (*i.e.* dimorphisme sexuel) uniquement significative dans les populations de forte densité (forte densité : $F_{1,22} = 16.41$, $P = 0.0005$, faible densité : $F_{1,9} = 0.38$, $P = 0.55$). Au niveau de la couleur, la densité a également des effets différents sur les femelles et les mâles (densité*sexe: $F_{1,28} = 4.39$, $P = 0.04$). Dans les populations de faible densité, les mâles sont significativement plus colorés alors que la couleur n'est pas affectée chez les femelles (femelles : $F_{1,14} = 1.63$, $P = 0.22$, mâles : $F_{1,14} = 4.77$, $P = 0.048$). Au contraire de la taille, le dimorphisme sexuel de couleur est uniquement significatif dans les populations de faible densité (forte densité : $F_{1,19} = 3.27$, $P = 0.09$, faible densité : $F_{1,10} = 13.89$, $P = 0.0039$). Nous pouvons expliquer ces résultats par un effet de la densité sur les pressions de sélection subies ou sur l'ontogénie du dimorphisme sexuel. Dans les populations de forte densité, la compétition pour la nourriture est augmentée alors que les sub-adultes sont trop petits pour accéder à la reproduction dès leur première année. Au contraire, dans les populations de faible densité, la compétition pour la nourriture est réduite alors que l'accès à la reproduction pour les sub-adultes est augmentée. Ainsi, les femelles jeunes et adultes ont une probabilité d'être gravide plus élevée dans les populations de faible densité ($F_{1,14} = 4.68$, $P = 0.048$). Cet accès à la reproduction pourrait conduire à la sélection de sub-adultes à caractères sexuels secondaires plus prononcés. Nous observerions alors des mâles plus colorés dans les populations de faible densité. Cependant, un développement des caractères sexuels dépendant de la densité pourrait expliquer ces résultats. Certaines études

prédisent que les membres de chaque sexe doivent atteindre une taille corporelle minimale pour produire le développement de caractères sexuels secondaires (Stamps et Krishnan 1997). Ceci est en accord avec une croissance plus rapide dans les populations de faible densité. La taille corporelle minimale pour accéder à la reproduction serait donc atteinte plus rapidement, permettant aux mâles de développer leurs couleurs vives. Une faible densité en congénères conduirait ainsi à des mâles plus grands et plus colorés à l'âge d'un an. Bien que la taille corporelle est corrélée positivement avec la couleur ($F_{1,28}$ = 18.74, $P$ = 0.0002), l'effet de la densité sur le dimorphisme sexuel de couleur est toujours présent lorsque nous ajoutons la taille corporelle dans les modèles statistiques. Ce résultat est en opposition avec un effet de la densité sur l'ontogénie des dimorphismes sexuels. Même si une sélection dépendante de la densité semble plus probable, d'autres analyses restent nécessaires pour déterminer précisément le mécanisme.

D'un point de vue informatif, la densité de la population affecte donc la taille et la couleur des mâles. Ces deux traits phénotypiques peuvent alors être utilisés comme signaux dans les interactions intra- et inter-sexuelles. Par exemple, ces deux traits semblent signaler la qualité des individus dans les compétitions pour les ressources sexuelles et alimentaires (voir manuscrits 9 et 10 des annexes et données non publiées pour la compétition pour la nourriture). Ces traits peuvent donc être utilisés à la fois comme des signaux de qualité individuelle et des indices reflétant la qualité des populations avoisinantes. Bien que dans notre précédente étude (voir partie II – B) la taille et la couleur des jeunes immigrants n'étaient pas encore affectées par la densité, ces indices pourraient être émis par les sub-adultes. A partir d'un an, ces traits phénotypiques pourraient jouer le rôle d'indices dans la sélection d'habitat et de signaux dans la sélection intra- et inter-sexuelle. Lors d'une interaction intra- ou inter-sexuelle, le récepteur évaluerait la qualité de son partenaire grâce à ces traits phénotypiques alors que ces traits permettraient au récepteur d'estimer la qualité de populations lors d'un choix d'habitat. Ces traits du phénotype pourraient ainsi avoir alternativement le rôle d'indices émis par inadvertance et de signaux intentionnels selon l'utilisation faite par le récepteur.

## III - C. Différences individuelles dans l'utilisation de l'information

Manuscrit No.4 p.136 (Social personalities influence natal dispersal in a lizard)

L'intégration et l'utilisation d'une information dépendent des capacités sensorielles et de l'avantage des récepteurs à l'utiliser (voir chapitre I). En d'autres termes, l'information n'a pas la même valeur ni la même utilité pour tous les individus. Nous avons montré que l'utilisation de certaines informations peut varier selon la capacité compétitrice des individus (voir partie II – B). Un individu à faible capacité compétitrice peut être plus sensible à une information relative à la densité de congénères. Cette information devrait être plus utilisée dans ses décisions comportementales. Plusieurs études récentes démontrent l'existence de traits comportementaux constants au cours de la vie d'un individu et à travers les contextes environnementaux (revue dans Sih *et col.* 2004 et Dall *et col.* 2004). Cette notion de personnalités, ou de syndromes comportementaux, permet d'expliquer pourquoi tous les individus ne réagissent pas identiquement à une même condition environnementale. En accord avec cette théorie, tous les individus ne devraient pas utiliser les mêmes informations ni développer la même réponse comportementale pour une information donnée. (Marchetti et Drent 2000) montrent, par exemple, que l'utilisation de l'information sociale dépend de la personnalité exploratrice des mésanges charbonnières.

L'information relative à la densité apparaît comme un bon candidat à une utilisation dépendante de la personnalité. Chez de nombreuses espèces, certains individus évitent constamment les interactions sociales tandis que d'autres les recherchent (Gosling et John 1999). Ce trait comportemental, nommé sociabilité ou tolérance sociale, devrait affecter la réaction à une augmentation de la densité. En effet, un individu 'asocial' devrait réagir négativement à un fort niveau d'interactions sociales lié à une forte densité, alors que cela ne devrait pas être le cas pour des individus 'sociaux'. Chez le lézard vivipare, nous pouvons montrer une attraction variable vis à vis d'indices olfactifs laissés par les congénères. Cette différence individuelle de tolérance sociale est, au minimum, présente de la naissance à l'âge d'un an. L'information relative à la présence de congénères entraîne donc des réponses comportementales dépendantes des différences individuelles de 'sociabilité'. La personnalité 'sociale' influe également sur la réaction comportementale à la densité. Ainsi, les individus fortement attirés par l'odeur de congénères dispersent plus des populations de faible densité, alors que les individus faiblement attirés tendent à disperser plus des populations de forte

densité. Les individus montrant une attraction sociale à la naissance semblent donc rechercher des populations plus denses lorsqu'ils vivent dans des populations de faible densité. Le contraire tend à être vrai pour les individus à faible attraction sociale à la naissance. Ces résultats sont corroborés par la réaction des individus dans leurs nouvelles populations. Un individu dispersant d'une population de faible densité, et donc supposé rechercher une population plus dense, s'installe plus souvent dans une population de forte densité que dans une population de faible densité.

Nos résultats suggèrent fortement que les personnalités sociales existent et qu'elles affectent les décisions de dispersion. Dans cette étude, nous n'avons pas pu tester une utilisation dépendante de la personnalité des informations relatives aux populations avoisinantes. Cependant, nous démontrons que l'utilisation des informations relatives à la présence de congénères ainsi que la réaction à une augmentation de la densité dépend des personnalités sociales des lézards vivipares.

# IV. D'AUTRES SOURCES D'INFORMATION ?

Nous avons illustré l'existence et les mécanismes de quelques informations socialement acquises chez le lézard vivipare. Cependant, d'autres conditions environnementales peuvent induire des indices ou signaux permettant de renseigner sur la qualité d'un individu et d'une population. Dans ce chapitre, nous développerons deux informations : une relative à la qualité d'un individu, l'état de stress, et l'autre relative à la population, le sexe-ratio. Nous n'avons pas eu la possibilité de tester le transfert de ces informations, mais nous présenterons les signaux et indices émis ainsi que l'utilité potentielle de telles informations.

## IV - A. Renseigner sur son niveau de stress et sur l'état de la population

Manuscrit No.5 p.146 (Blood corticosterone levels but not carotenoid-ingestion affect the ventral coloration of the common lizard *Lacerta vivipara*)
Manuscript No.6 p.169 (Experimental enhancement of corticosterone levels positively affects subsequent male survival)

Dans leur milieu naturel, les animaux sont soumis à de nombreux facteurs stressants tel que la prédation, les conditions climatiques ou la disponibilité des ressources. Ces facteurs stressants sont souvent les signes de mauvaises conditions environnementales. Face à ces stress, les individus répondent par la modification de paramètres comportementaux et physiologiques permettant de limiter les effets négatifs de ces mauvaises conditions (Wingfield et Ramenofsky 1999). En modifiant son comportement et sa physiologie, un individu stressé produit des indices reflétant son état de stress. Ces indices peuvent ainsi être une source d'information relative à la qualité de l'individu (*i.e.* état de stress) mais également à la qualité des conditions environnementales. Parmi les réponses physiologiques au stress, la production de glucocorticoïdes est une réponse commune à de nombreux facteurs de stress (Axelrod et Reisine 1984, Romero *et col.* 2000, Harvey *et col.* 1984, Breuner et Hahn 2003). Chez de nombreuses espèces, la libération de corticostérone, la principale glucocorticoïde, engendre des modifications comportementales et physiologiques. Cette hormone permet de mobiliser l'énergie en augmentant des processus de catalyse qui aboutissent, entre autre, à la dégradation des protéines musculaires (Holmes et Phillips 1976). Cette mobilisation d'énergie engendrée par la corticostérone va permettre la mise en place d'une réponse comportementale permettant d'échapper aux effets négatifs du stress ou au stress lui-même (revue dans Wingfield et Ramenofsky 1999, e.g. Dufty et Belthoff 1997, Brotto *et col.* 2001, Breuner *et*

*col.* 1998, Astheimer *et col.* 1992, DeNardo et Sinervo 1994). Chez le lézard vivipare, la corticostérone induit bien une mobilisation de l'énergie qui se reflète dans une consommation de nourriture plus importante associée à une forte perte de masse par gramme de nourriture ingérée (manuscrit 6). La corticostérone conduit également à une durée et un taux d'activité journalière plus importants (manuscrit 6, de Fraipont *et col.* 2000). L'augmentation de l'activité et de la prise alimentaire est concordante avec d'autres études montrant une activité et une recherche de nourriture plus importantes (Gross *et col.* 1980, Silverin 1986, Wingfield et Silverin 1986, Dufty et Belthoff 1997, Brotto *et col.* 2001, Breuner *et col.* 1998, Astheimer *et col.* 1992, DeNardo et Sinervo 1994). Cette modification de l'activité pourrait constituer un indicateur de réponse au stress perceptible par les congénères. Les interactions sociales sont également affectées par la corticostérone. En effet, la corticostérone induit la ré-allocation de l'énergie utilisée dans la reproduction et les interactions agressives dans la réponse au stress (Greenberg et Wingfield 1987, DeNardo et Licht 1993, Breuner *et col.* 1998). Chez le lézard vivipare, la corticostérone augmente la tolérance sociale pour l'exploitation des ressources spatiales et augmente ainsi le partage des ressources des individus traités à la corticostérone (données non publiées). Cette proximité plus importante pourrait permettre un transfert plus important de l'information. En plus de ces indices comportementaux, la corticostérone affecte profondément la couleur des individus (manuscrit 5 et données non publiées). Même si le mécanisme demeure inconnu, notre étude montre que la corticostérone rend les individus plus colorés (*i.e.* plus orange). Plusieurs études complémentaires révèlent que cet effet est rapide (i.e. dès 4 jours de traitement) et existe pour les deux sexes, dès l'âge d'un an, et pour différentes situations (*e.g.* statuts reproducteurs, régimes alimentaires). La théorie de l'honnêteté des signaux dépendant des caroténoïdes prédirait une couleur réduite par le stress. Bien que la couleur ventrale des lézards vivipares soit déterminée par les caroténoïdes (manuscrit 5), la disponibilité des caroténoïdes n'est pas un facteur limitant de la couleur de cette espèce. En appliquant directement la corticostérone et non le facteur stressant, nous avons simulé une plus grande capacité à répondre au stress, et non un stress plus important. La couleur ventrale plus orange, également corrélée à la condition corporelle, signalerait honnêtement la capacité d'un individu à répondre au stress. Nos études prédisent également que pour un stress donné un mâle produisant plus de corticostérone survivrait mieux, alors qu'un tel effet n'existe pas chez les femelles. En utilisant la couleur comme signal de la capacité à répondre au stress, les lézards pourraient estimer un paramètre de la qualité des mâles, le succès des mâles dans des conditions stressantes. Les indices comportementaux renseigneraient sur l'état de stress des individus tandis que les signaux colorés refléteraient un

paramètre de qualité de l'individu, sa capacité à répondre au stress. Toutefois, les indices comportementaux pourraient également être perçus comme des indicateurs de la qualité de l'habitat.

Au niveau de la population, le niveau de corticostérone est un indicateur des conditions environnementales (Marra et Holberton 1998, Romero et Wikelski 2001, Lanctot *et col.* 2003). Dans des conditions stressantes, les individus vont produire de la corticostérone. Dans nos études, l'application de corticostérone sans la source de stress représente la réponse adaptative au stress. Cependant, mesuré à un instant donné, le niveau de corticostérone sanguin reflète la quantité de stress induite par de mauvaises conditions environnementales tels que le manque de ressources alimentaires, la prédation et le climat (Marra et Holberton 1998, Romero et Wikelski 2001, Lanctot *et col.* 2003). Grâce aux effets maternels, ce type d'information est également utilisé à travers les générations (Meylan *et col.* 2002). Chez le lézard vivipare, le niveau de corticostérone maternel constituerait une sorte d'information sur la qualité des conditions environnementales ou sur la santé de la mère dépendant de l'âge de cette mère (Meylan *et col.* 2002). En réponse, les jeunes modifient leur décision de dispersion pour éventuellement fuir les mauvaises conditions (Meylan *et col.* 2002). Cependant, les individus adultes n'ont pas directement accès au niveau sanguin de corticostérone de leurs congénères. L'existence d'indices, par exemple comportementaux, permettrait aux individus d'estimer le niveau de stress et ainsi la qualité d'une population. D'autres informations pourraient également être estimées à partir de ces indices. Par exemple, chez la paruline flamboyante, les niveaux de corticostérone sanguins sont affectés par le sexe-ratio adulte lors de la saison de reproduction (Marra et Holberton 1998). A partir des indices produits lors d'un stress, d'autres informations, telles que le sexe-ratio, pourraient être estimées. Le sexe-ratio futur de la population étant un paramètre important de la valeur sélective des individus (voir partie IV - B), l'acquisition de toute information relative au sexe-ratio est essentielle.

## IV - B. Renseigner sur le sexe-ratio des autres populations

Manuscrit en préparation (Sex-ratio of immigrants affects dispersal in Commom lizard)
Manuscrit No.7 p.178 (Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio)
Manuscrit No.8 p.187 (Direct and delayed effects of multiple mating attempts on females: can females compensate for a bad start?)

Le sexe-ratio adulte est un facteur essentiel de la dynamique des populations et de la sélection sexuelle (*e.g.* Legendre *et col.* 1999, Jirotkul 1999, Le Galliard *et col.* 2005). Chez le lézard vivipare, un excès de mâles adultes conduit à une augmentation des agressions sexuelles (Le Galliard *et col.* 2005). Un sexe-ratio biaisé vers les mâles a ainsi des conséquences dramatiques sur la viabilité des populations par l'intermédiaire de coûts importants pour les femelles (Le Galliard *et col.* 2005). Ainsi, un haut niveau d'agression des mâles réduit la survie et la reproduction immédiates des femelles adultes (Le Galliard *et col.* 2005, manuscrits 7 et 8). Tout mécanisme permettant d'estimer le sexe-ratio d'une population avant de s'y installer devrait donc être sélectionné. La prospection n'existant pas chez le lézard vivipare (partie II – B), nous faisons l'hypothèse que les immigrants pourraient être de nouveau la source d'information. Pour que cette hypothèse soit juste, les immigrants doivent exhiber des indices informatifs du sexe-ratio de leur population d'origine. Plusieurs indices pourraient être le support de cette information. Une expérience manipulant le sexe-ratio adulte sur une année a montré que la couleur ventrale des femelles adultes est moins prononcée dans les populations à sexe-ratio biaisé vers les mâles. Cette modification du signal coloré semble être le sous-produit d'un taux élevé d'agressions des mâles. L'entièreté des résultats sur les coûts pour les femelles suggère que ce signal reflèterait une mauvaise condition des femelles dans les populations à sexe-ratio biaisé vers les mâles. En tant qu'information portée par les immigrants femelles, cette couleur réduite pourrait être un indice de la qualité de leur population d'origine. La couleur des mâles restant inchangée, cet indice serait uniquement porté par les immigrants femelles. Nous pourrions ainsi prédire que les récepteurs mâles et femelles ne prendraient pas les mêmes décisions en réponse à cette information.

Cependant, la majeure partie des immigrants est représentée par les jeunes lézards. La couleur ventrale des jeunes n'étant pas affectée par le sexe-ratio, la quantité d'information semble faible. Néanmoins, un second paramètre de l'immigration peut être à l'origine d'un transfert d'information. Le Galliard et col. (2005) montrent que le sexe-ratio adulte ne modifie pas différemment la probabilité de disperser des jeunes mâles et des jeunes femelles. En

d'autres termes, une population biaisée vers les mâles produirait un pool de dispersants également biaisé vers les mâles. Le sexe-ratio des immigrants dépendrait ainsi du sexe-ratio des populations extérieures mélangées. Bien que cette information ne permette pas obligatoirement de prédire le sexe-ratio de chaque population (voir localisation des habitats, partie II – B), elle permet à l'éventuel dispersant de 'comparer' le sexe-ratio de sa population à celui du monde extérieur. Pour tester cette hypothèse, nous avons analysé l'effet du sexe-ratio des immigrants sur la dispersion natale. Au cours des deux dernières expériences (partie II – B et une autre expérience), les immigrants étaient lâchés aléatoirement dans les populations. Il en résulte une variation du sexe-ratio final des immigrants pour chaque population. Ainsi, le sexe-ratio moyen des immigrants était de 0.48 ± 0.23 (sexe-ratio femelle, 0.61 ± 0.30 en 2004 et 0.39 ± 0.10 en 2005) et variait de 0 à 1. Chaque année, l'expérience se déroulait sur un ensemble de 16 populations. Au cours de la saison d'activité et après le lâcher des nouveau-nés, nous avons pu mesurer la dispersion provenant de ces populations. Nous faisons l'hypothèse que le sexe-ratio des immigrants affecte la dispersion des résidents. Nous pouvons ainsi étudier l'impact du sexe-ratio des immigrants sur un total de 32 populations (manuscrit en préparation). Les deux expériences s'étant déroulées sur deux années consécutives, nous pouvons également tester la dépendance de nos effets au contexte. La probabilité de disperser tend à être positivement liée à la proportion de femelles au sein des immigrants ($F_{1,511} = 3.14$, $P = 0.08$). Cependant, l'interaction entre le sexe du jeune et le sexe-ratio des immigrants est significative ($F_{1,511} = 4.34$, $P = 0.0378$). Les femelles dispersent plus lorsque le sexe-ratio des immigrants est biaisé vers les femelles alors qu'aucun effet n'est présent chez les mâles (contrastes, femelles $F_{1,511} = 8.19$, $P = 0.0044$, mâles $F_{1,511} = 0.01$, $P = 0.90$). Ces effets ne sont pas significativement différents entre les années (année*sexe-ratio: $F_{1,510} = 1.75$, $P = 0.19$, année*sexe-ratio*sexe :$F_{1,510} = 1.19$, $P = 0.27$), suggérant un effet du sexe-ratio indépendant de l'année. Enfin, plus le sexe-ratio est biaisé vers les femelles, plus la taille corporelle des dispersants des deux sexes est grande ($F_{1,43} = 6.26$, $P = 0.0163$). Cet effet est significatif pour les deux années de l'étude (sexe-ratio*année: $F_{1,43} = 5.68$, $P = 0.0217$; Contrastes, 2004: $F_{1,43} = 4.42$, $P = 0.0415$, 2005: $F_{1,43} = 6.64$, $P = 0.0135$). Ces résultats montrent que 1) le sexe-ratio affecte la dispersion dépendante du sexe chez les jeunes lézards, et 2) qu'elle affecte le phénotype des dispersants. La question du mécanisme par lequel le sexe-ratio des immigrants affecte la dispersion reste présente. Nos résultats montrent que les résidents subissent différemment l'arrivée d'une femelle ou d'un mâle. Plusieurs différences phénotypiques liées au sexe peuvent expliquer cette réaction différente. Dans nos expériences, la dispersion survient dans les premières semaines de vie des nouveau-nés. Aucune de nos

expériences ne montre de comportement dépendant du sexe pour les juvéniles (manuscrits 3, 5, 7). Le temps d'activité, de thermorégulation, le nombre d'interactions sociales, et la probabilité de disperser ne semblent pas différentes au cours de la première année. En effet, la différentiation sexuelle de certains comportements semble survenir avec l'accès à la reproduction (*i.e.* entre 1 et 2 ans). Le comportement n'est donc pas une explication probable de l'effet du sexe-ratio des immigrants. Chez le lézard vivipare, les femelles diffèrent des mâles par leur taille corporelle et leur couleur ventrale. Alors que la couleur ventrale n'est pas exprimée durant la première année, le dimorphisme de taille corporelle est présent dès la naissance et s'amplifie au cours de la première année. Cependant, nous pouvons montrer que la taille moyenne des immigrants n'affecte pas la probabilité de disperser (taille moyenne : $F_{1,512} = 0.00$, $P = 0.96$, taille moyenne*sexe : $F_{1,512} = 6.26$, $P = 0.64$), et qu'un modèle incluant la taille moyenne des immigrants mène aux mêmes effets du sexe-ratio. Le dimorphisme sexuel de taille corporelle et de couleur ventrale n'est donc pas non plus la bonne explication à l'effet du sexe-ratio des immigrants. Il existe un autre mécanisme possible, les indices olfactifs. Léna *et col.* (1998) montrent, en effet, que la réaction à l'odeur d'un mâle adulte est différente pour un juvénile mâle et un juvénile femelle. Les indices olfactifs laissés par les immigrants des deux sexes pourraient constituer des indices sur le sexe des immigrants. Néanmoins, Léna *et col.* (1998) montrent aussi que l'odeur des nouveau-nés n'affecte pas le comportement d'autres nouveau-nés. Les immigrants de notre étude sont, cependant, plus âgés que dans l'étude de Léna *et col.* (1998). La maturation des individus peut avoir ainsi permis une modification ou une construction des indices olfactifs. Jusqu'à présent, les études sur l'odeur des juvéniles n'ont pas distingué l'odeur des mâles et des femelles. La différentiation sexuelle de l'odeur pourrait, néanmoins, exister dès les premiers jours de vie. Ce mécanisme, non testé actuellement, reste un mécanisme possible et réaliste pour expliquer le rôle du sexe-ratio des immigrants dans la décision de dispersion.

L'effet du sexe-ratio des immigrants peut être vu de deux façons. Premièrement, une arrivée de plus de jeunes femelles, ou de moins de jeunes mâles, peut représenter le potentiel reproducteur futur de la population. Les immigrants (*i.e.* dispersants) survivant souvent mieux dans leur population d'arrivée, le sexe-ratio adulte futur pourrait dépendre assez fortement du sexe des arrivants. En conséquence, une femelle pourrait avoir intérêt à disperser d'une population où le sexe-ratio futur sera biaisé vers les femelles. Deuxièmement, le sexe-ratio des immigrants peut informer sur le sexe-ratio moyen des populations avoisinantes. Sous cette hypothèse, on prédirait une dispersion plus importante des mâles pour un sexe-ratio

immigrant biaisé vers les femelles. Nous observons le résultat inverse. Cependant, au vu des coûts qu'une femelle subit dans une population où le sexe-ratio est biaisé vers les mâles, une jeune femelle réduirait ces coûts futurs en s'installant dans des populations peu biaisée vers les mâles. En milieu naturel, le sexe-ratio adulte sur toute la population est biaisé vers les femelles. Un sexe-ratio immigrant biaisé vers les mâles refléterait un taux anormal de mâles dans les populations avoisinantes, potentiellement coûteux pour les femelles. Les femelles devraient, en réponse, rester plus souvent dans leur population face à un sexe-ratio immigrant biaisé vers les mâles. Ces deux interprétations restent très possibles. Pour mieux distinguer entre les alternatives, il est nécessaire de réaliser une meilleure estimation des différences sexuelles chez les juvéniles ainsi qu'une mesure précise de l'impact des immigrants sur la dynamique des populations et sur la valeur sélective des résidents.

# CONCLUSION ET PERSPECTIVES

## Synthèses des principaux résultats

Au cours de cette thèse, nous avons démontré l'existence de plusieurs types d'informations sociales. Les lézards vivipares peuvent ainsi renseigner leurs congénères sur plusieurs traits relatifs à la qualité de leur population. A la vue de l'ensemble de ces résultats, nous pouvons nous interroger sur l'avantage de ces informations. Particulièrement, de nombreux traits peuvent être interprétés comme de l'information sans que ceux-ci ne soient utilisés. Ainsi, la plupart des traits phénotypiques sont 1) gouvernés par les conditions internes et externes de l'individu et 2) perçus par la plupart de ses congénères. Le potentiel informatif est donc présent dans tous ces traits. Mais cela n'induit pas obligatoirement leur utilisation comme outil informatif. En effet, l'utilisation efficace d'une information est contrainte par plusieurs nécessités. Premièrement, l'information doit être utilisée par un ou plusieurs récepteurs. Pour répondre à cette nécessité, nous avons testé le transfert de l'information dans plusieurs études (manuscrits 1, 2 et 3). Observer la réponse comportementale (*e.g.* dispersion) d'individus recevant l'information permet de tester l'utilisation et les implications de cette information. Cependant, la voie du signalement impliquée dans ce transfert reste souvent inconnue. Mesurer uniquement le signal induit par un 'état donné' permet ainsi de connaître les mécanismes de transfert d'information. Les études présentées dans les manuscrits 3 – 8 illustrent la deuxième nécessité pour une efficacité de l'information : à partir d'un signal ou d'un indice, un récepteur doit être capable d'acquérir une information honnête et distincte d'autres informations. Or, certains signaux sont induits par plusieurs conditions environnementales. Par exemple, la couleur ventrale des lézards vivipares est dépendante de plusieurs conditions internes et externes. Une forte densité ralentit le développement de la couleur des jeunes mâles. De même, un sexe-ratio biaisé vers les mâles induit des femelles moins oranges. Et finalement, la couleur ventrale des femelles et des mâles change positivement lors d'une réponse au stress. Ces trois résultats soulignent des conditions multiples affectant la couleur ventrale. De façon plus générale, un signal commun pour des conditions diverses ne permet pas à l'individu de décider de façon adéquate. Par exemple, le sexe-ratio et la densité n'ayant pas les mêmes conséquences sur la valeur sélective des femelles, une mauvaise traduction du signal peut être coûteuse. Partir ou rester dans sa

population ne devrait donc pas dépendre de cet unique signal. D'autres moyens permettent de réceptionner la bonne information dans ces situations. L'existence de signaux multiples correspond à un de ces moyens (Møller et Pomiankowski 1993, Johnstone 1997). Effectivement, une condition environnementale donnée affecte rarement un seul trait phénotypique. Particulièrement, le comportement, une composante multiple du phénotype, est modifié par la plupart des conditions environnementales. Chez le lézard vivipare, le comportement de thermorégulation et l'activité sont modifiés en réponse au stress (manuscrit 6), alors que la densité affecte uniquement l'activité (manuscrit 3). L'association d'indices comportementaux à d'autres traits phénotypiques modifiés permet ainsi de distinguer entre plusieurs sources d'informations pour prendre une décision plus circonstanciée. La réception de signaux ou d'indices émis par plusieurs signaleurs est également un moyen de s'assurer de la nature de l'information transférée. L'émission d'un même signal par plusieurs individus reflète une information sur un groupe d'individus. Le récepteur peut ainsi interpréter ce signal en fonction des caractéristiques communes des individus de ce groupe (*e.g.* même sexe, même origine, même âge). Dans cette thèse, nous avons montré que les immigrants peuvent être une source d'information sur la qualité des populations avoisinantes. L'utilisation de cette information nécessite l'association de deux sources d'information : une source renseignant sur le statut de dispersion de l'individu (de la même population versus pas de la même population) et une source renseignant sur la qualité de la population de l'immigrant (*e.g.* densité). Pour récupérer ces deux informations, le récepteur doit 'comparer' les indices de différents individus émetteurs pour distinguer les résidents des immigrants. Après cette distinction, l'émetteur peut estimer la qualité des populations avoisinantes. Cette double estimation permet ainsi au récepteur d'acquérir avec plus de certitude la bonne information. En plus de l'association de différentes sources d'information, la redondance d'un signal peut permettre une meilleure estimation (voir chapitre I). En effet, un récepteur observant plusieurs femelles étrangères émettant un signal peu coloré pourrait distinguer une information relative au sexe-ratio des populations extérieures d'autres informations affectant similairement les deux sexes.

Nous venons de préciser qu'un récepteur doit être capable de reconnaître si un individu est originaire d'une autre population. L'existence de phénotypes 'dispersants' a été démontrée chez plusieurs espèces (*e.g.* Dixon 1985, O'Riain *et col.* 1996). Le phénotype 'dispersants' comprend des traits morphologiques (*e.g.* Dixon 1985, Venable *et col.* 1998, O'Riain *et col.* 1996), des traits physiologiques (Dufty et Belthoff 2001) et des traits

comportementaux (O'Riain *et col.* 1996, Meylan et Clobert soumis). Particulièrement, chez le lézard vivipare, les dispersants se caractérisent par une association de traits comportementaux constituant un syndrome comportemental (Meylan et Clobert soumis). Ces syndromes phénotypiques (*i.e.* physiologie, morphologie, comportement) ne diffèrent pas uniquement entre les dispersants et les non-dispersants. En effet, tous les dispersants ne possèdent pas les même spécificités du phénotype. Ainsi, les caractéristiques phénotypiques des dispersants dépendent du facteur induisant leur départ (*e.g.* densité, apparentement). Par exemple, les résultats du manuscrit 1 montrent qu'un fort taux d'apparentement produit des dispersants de plus grande taille et de meilleure capacité à coloniser (résultats du manuscrit 1 non développés dans la thèse). Les individus réagissant à l'augmentation de l'apparentement sont donc de meilleurs colonisateurs. Cette capacité à coloniser est probablement le signe d'une préférence de ces individus pour des habitats vides, en accord avec une étude précédente (Le Galliard *et col.* 2005a). Cette dispersion dépendante de l'apparentement révèle ainsi un syndrome phénotypique 'colonisateur' constitué par des différences morphologiques (*e.g.* taille corporelle) et sûrement comportementales (*e.g.* préférence pour les habitats vides, néophilie). De façon similaire, le manuscrit 5 démontre l'existence de personnalités sociales correspondant aux deux réactions observées face à la densité de congénères : l'attraction sociale et la répulsion sociale. Il est probable que ces personnalités soient le signe de syndromes phénotypiques plus importants comprenant d'autres différences comportementales et physiologiques. L'existence de tels syndromes phénotypiques pourrait permettre de caractériser le statut ou la personnalité d'un individu. Certains traits du phénotype reflèteraient le statut 'intrinsèque' d'un individu alors que d'autres traits correspondraient à des signaux dépendants des conditions environnementales. Avoir simultanément accès à ces différents traits phénotypiques permettrait une estimation précise et efficace de l'information, ainsi que l'utilisation d'informations plus complexes.

L'existence d'une information socialement acquise ainsi que celle de syndromes comportementaux affecte profondément notre compréhension de l'évolution de la dispersion et de la dynamique des populations. En effet, l'évolution de la dispersion est la conséquence d'une balance entre les coûts de la dispersion et ses bénéfices (*e.g.* diminution d'une compétition intra-spécifique pour les ressources, évitement de la compétition entre apparentés, évitement de la consanguinité ; Clobert *et col.* 2001). L'information sociale permet d'augmenter les bénéfices et de réduire les coûts de la dispersion. Par exemple, nos résultats démontrent clairement que l'information sociale permet une estimation de

l'apparentement d'une population. Cette estimation permet ainsi de fuir sa population natale en réponse à un niveau d'apparentement élevé. Il est généralement considéré que l'évitement de la compétition entre apparentés et l'évitement de la consanguinité dépendraient d'une estimation personnelle de sa compétition avec des apparentés (Lambin *et col.* 2001). Cette estimation personnelle peut être une source d'erreurs importantes car un degré personnel ne correspond pas nécessairement à la qualité de la population globale en termes d'apparentement. L'utilisation d'une information sociale constitue un mécanisme d'estimation de l'apparentement à l'échelle de la population et permet ainsi de prendre une décision basée sur la qualité et le devenir potentiel de sa population. Le même avantage existerait pour une information dépendante du niveau de stress. La réponse au stress est généralement considérée comme la réponse individuelle à une dégradation des conditions environnementales (Wingfield et Ramenofsky 1999). Cependant, une baisse de la condition individuelle ou une rencontre avec un prédateur sont de mauvais signaux de la qualité d'un habitat. Ces sources de stress individuel ne devraient donc pas induire les mêmes réponses comportementales que la réaction à une mauvaise qualité d'habitat. Par exemple, se déplacer localement ou se cacher dans un abri apparaissent comme des réponses plus adaptées et moins coûteuses qu'une dispersion vers d'autres habitats. La dispersion devrait donc correspondre à la réponse à un stress global de la population plus qu'à un stress individuel. L'information sociale serait ainsi un moyen d'estimer ce stress global et de moduler sa réponse en conséquence. Sans coût à la dispersion, un individu pourrait idéalement visiter toutes les populations pour estimer personnellement la qualité des différents habitats. Seulement, la dispersion demande du temps et de l'énergie pour une finalité incertaine en termes d'aboutissement du déplacement (*e.g.* prédation), de succès d'installation et de qualité de la future population. Nos études démontrent que ces coûts peuvent être réduits avant le départ des individus. A partir des indices émis par les immigrants, les éventuels dispersants pourraient ainsi estimer plusieurs paramètres qualitatifs des populations avoisinantes (*e.g.* densité, sexe-ratio). Ces individus pourraient alors comparer 'virtuellement' la qualité de leur population natale à celle des populations avoisinantes, ce qui permettrait aux éventuels dispersant de 'prédire' le succès de leur dispersion et leur valeur sélective dans la population future. En contribuant à l'estimation des coûts et des bénéfices, l'information sociale augmenterait le succès d'une dispersion. Cependant, le succès d'une dispersion dépend également de l'adéquation entre le type de dispersant et le type d'habitat d'arrivée. Nos études démontrent que certains dispersants connaissent un succès plus important dans la colonisation d'un habitat vide. D'autres dispersants semblent au contraire préférer des habitats à fortes ou à faible densité en

congénères. Même si aucune mesure de valeur sélective n'a été effectuée, nous pouvons fortement prédire que les dispersants de syndromes phénotypiques différents réussiraient mieux dans leur habitat 'préférentiel'. L'information sociale permettrait aux individus de syndromes différents de baser leur dispersion sur l'existence de leur habitat préféré plus que sur l'existence d'un habitat de bonne qualité. Cela résulterait en la réduction des coûts de la dispersion dépendant de l'adéquation syndrome-habitat.

Finalement, il existe d'importantes conséquences sur la dynamique des populations fragmentées. Une approche de dynamique des méta-populations nous permet de discuter des implications pour les populations fragmentées et l'invasions de nouveaux habitats (Levins 1969, Enbenhard 1991, Hanski et Gaggiotti 2004). La notion classique des méta-populations considère un ensemble d'habitats variant du statut vide à occupé, sous une dynamique d'extinctions et de colonisations (Levins 1969). La dispersion vient complexifier cette vision classique (Clobert *et col.* 2004) par son double rôle : le renforcement des habitats déjà occupés versus la colonisation des habitats vides. Nos études démontrent que ces deux processus ne sont pas réalisés par les mêmes types de dispersants. La colonisation serait effectuée par des dispersants à phénotype colonisateur en réponse à une information sur l'apparentement natal, alors que le renforcement serait la conséquence de dispersants tolérants socialement, répondant à une information sur la densité des populations avoisinantes. Cette dispersion à phénotypes 'spécialisés' affecterait fortement la composition de la population. En effet, un habitat vide devrait être colonisé par une classe particulière d'individus. En conséquence, les populations colonisées seraient composées d'individus à phénotype particulier, voir à génotype particulier. Néanmoins, il est nécessaire d'ajouter une échelle temporelle à cette dispersion à phénotypes particuliers. Supposons trois syndromes phénotypiques de dispersants : 1) les individus évitant complètement les congénères (i.e. colonisateurs), 2) les individus peu tolérants socialement (i.e. syndrome intermédiaire), et 3) les individus recherchant les congénères (*i.e.* individus sociaux). Les individus de la première catégorie quitteront leur habitat natal en réponse à un fort niveau d'apparentement pour s'installer préférentiellement dans un habitat vide. Après l'arrivée de quelques colonisateurs et leurs reproductions, cet habitat sera faiblement dense. En réponse à cette augmentation de la densité, quelques individus quitteront cet habitat pour immigrer dans un autre habitat. Ces immigrants porteront ainsi l'information sur l'existence d'habitats faiblement denses lorsqu'ils visiteront de nouvelles populations. Cette information entraînera, en conséquence, le renforcement de ces habitats colonisés par les dispersants à syndrome intermédiaire.

Comme son nom l'indique, le renforcement augmentera la densité des habitats colonisés. De la même manière que précédemment, les individus quittant ces habitats (*i.e.* dispersants 'colonisateurs' et 'à syndrome intermédiaire') porteront l'information d'habitats denses aux habitats voisins. Finalement, cela résultera en un départ des dispersants recherchant les congénères pour s'installer dans ces habitats. L'utilisation différentielle de l'information créerait ainsi une fluctuation spatiale et temporelle de la composition en individus de syndromes spécifiques des habitats d'une méta-population. Nous avons distingué trois classes de dispersants à syndrome phénotypique bien distinct. Cependant, nous pouvons envisager la possibilité d'une gradation plus continue de ces syndromes à déterminismes génétiques et maternels complexes. En conséquence, la fluctuation de la structuration génétique et phénotypique devrait profondément affecter la dynamique de ces populations. Finalement, nos études montrent que les immigrants constituent une source d'information fiable sur les connections d'une méta-population. Une dispersion basée sur cette information sociale renforcerait les connexions entre les populations existantes, résultant en une homogénéisation des tailles de populations (Doncaster *et col.* 1997, Hanski et Gaggiotti 2004). Par conséquent, la probabilité d'extinction des patchs d'une méta-population devrait être réduite et ainsi la viabilité des populations fragmentées augmentée.

# Perspectives

Bien que nos études démontrent l'existence d'informations socialement acquises chez le lézard vivipare, la compréhension du système informatif souffre de plusieurs lacunes. Ainsi, le lien entre le mécanisme de transfert et l'utilisation de l'information reste souvent mal compris. Dans nos études, nous prédisons un effet positif de l'information sur la dynamique des populations et des méta-populations, notamment via un effet sur la dispersion. Cependant, les modalités et les conséquences de l'utilisation de l'information manquent toujours de tests expérimentaux. Pour répondre à ces manques, plusieurs études sont nécessaires. Nous pouvons les regrouper en cinq catégories.

### *Mieux comprendre les signaux et les indices*

Dans notre première étude, nous avons démontré l'existence de transfert d'information sur les interactions entre apparentés. Cependant, le mécanisme de ce transfert demeure inconnu. Par ailleurs, nous savons que les jeunes lézards dispersant en réponse à la présence de la mère ont une taille corporelle et une couleur ventrale différente à l'âge d'un an (données non publiées). Ces résultats soulignent l'impact important de la présence de la mère sur le

phénotype de ses jeunes. Une série d'expériences devrait être réalisée pour connaître le rôle de la présence de la mère sur les indices comportementaux et olfactifs des jeunes. Même si plusieurs hypothèses existent, des études plus poussées sont également nécessaires pour tester les indices impliqués dans le transfert d'information par les immigrants. Par exemple, une mesure de l'impact de la densité sur les indices olfactifs permettrait de distinguer entre plusieurs hypothèses. Nous avons récemment mis en place des méthodes moléculaires d'identification de l'odeur pour notre espèce. Désormais, nous pouvons associer des réactions comportementales à des mesures moléculaires pour déterminer précisément le rôle de l'environnement dans le développement de l'odeur. Finalement, nous ne connaissons pas les mécanismes de modification de la couleur par la corticostérone (voir manuscrit 6). Cette modification, confirmée par cinq expériences et une étude corrélative en population naturelle, n'est pas en accord avec les théories classiques concernant les couleurs basées sur les caroténoïdes. Pour mieux cerner ce problème, nous avons récemment étudié les effets complémentaires de la corticostérone (enzymes antioxydantes, réponse immunitaire et métabolisme basal, données non publiées). Alors que la corticostérone modifie ces paramètres, ces effets n'expliquent qu'en partie le changement de couleur. Comprendre la détermination et la variabilité de la couleur ventrale nécessite donc des expériences complémentaires sur la physiologie de la couleur.

***Cerner les modalités de l'utilisation de l'information***

Dans notre discussion, nous concluons que toutes les informations ne devraient pas être utilisées par tous les individus dans tous les contextes. En effet, utiliser une information peut être coûteux et inutile dans certains contextes. Une première série d'expériences devrait permettre de comprendre les facteurs individuels déterminant l'utilisation d'une information. En proposant plusieurs informations à un groupe d'individus, il est possible de savoir quel type d'informations est utilisé par quel type d'individus et ainsi de pouvoir corréler cette utilisation aux traits phénotypiques des individus. Dans certaines conditions environnementales, l'utilisation d'une information sociale paraît également inappropriée. Ainsi, l'utilisation de l'information devrait être développée uniquement dans un contexte où elle présente un avantage. Par exemple, un individu vivant dans un milieu changeant régulièrement recevrait un faible avantage à utiliser l'information délivrée par les congénères de sa population actuelle. Des expériences au niveau de la population pourraient permettre d'estimer les conditions d'utilisation des différentes informations sociales.

***Manipuler l'information***

Comprendre les signaux et les indices nous permettrait de manipuler l'information et son transfert. Pour mesurer l'utilisation de l'information, l'étape suivante consiste en la manipulation du signal au lieu de la source d'information. Par exemple, nous pouvons collecter les odeurs d'individus de différentes conditions environnementales et manipuler directement les indices olfactifs présents dans une population. De façon plus générale, d'autres informations sociales existent sûrement chez le lézard vivipare. En considérant les immigrants comme support d'information, nous pouvons faire varier d'autres caractéristiques de la population d'origine telles que le sexe-ratio ou la densité d'une seule des classes d'âge. Par exemple, la proportion de juvéniles dans une population serait un indice important du succès reproducteur de la population. Enfin, il faudrait mesurer réellement le transfert d'information sur le niveau de stress d'une population. En appliquant le même protocole que pour l'apparentement, nous pourrions faire varier la proportion d'individus à fort niveau de corticostérone et mesurer la dispersion provenant de cette population. Si un individu peut renseigner sur son état de stress, un niveau plus élevé de corticostérone devrait induire un fort niveau de dispersion.

***Développer la notion de syndrome phénotypique***

Pour démontrer l'existence de syndromes phénotypiques, des suivis comportementaux et physiologiques de dispersants devraient être réalisés sur de longues périodes. Le protocole nécessaire est assez simple et similaire à celui présenté dans le manuscrit 5. Il faut mesurer un certain nombre de traits phénotypiques dès la naissance et au cours de la vie des individus. Ces mesures comprennent, par exemple, des dosages hormonaux, des mesures d'activité et d'interactions sociales. Ces individus devraient ensuite être placés dans des conditions environnementales variées avec la possibilité de disperser. Il suffirait ensuite de corréler le statut de dispersion et les conditions environnementales à la valeur des traits phénotypiques mesurés. Une nouvelle étape dans la compréhension de ces syndromes est de passer de l'observation à la compréhension des mécanismes sous-jacents de ces syndromes (*e.g.* génétique, effet maternel). Par exemple, le niveau de corticostérone maternel affecte profondément le phénotype des jeunes (e.g. de Fraipont *et col.* 2000, Meylan *et col.* 2002). La réponse au stress modifie la réaction des individus face à leur milieu naturel. La réponse au stress maternel devrait amener, par les effets maternels, à la production de jeunes à syndromes phénotypiques spécifiques. La compréhension de ces syndromes nécessite également la distinction entre facteurs génétiques et effets maternels. Plusieurs expériences permettraient

de distinguer ces deux mécanismes. Deux étapes seraient particulièrement utiles pour répondre à cette question. La première consiste à la transplantation d'œufs entre des femelles de syndromes différents. Cette manipulation, utilisée dans d'autres espèces de reptiles, devrait être mise en place chez le lézard vivipare. En observant le syndrome phénotypique des juvéniles transplantés, il est ainsi possible de distinguer certains effets maternels de facteurs génétiques. Pour tester expérimentalement les facteurs génétiques, la seconde étape consisterait en une série d'accouplements contrôlés entre des individus de syndromes différents. L'association de toutes ces expériences permettrait de comprendre les origines et les implications des syndromes phénotypiques.

***Conséquences sur la dynamique des populations***

Nous avons réalisé nos expériences sur une échelle temporelle assez courte du point de vue de la population (*i.e.* 1 an). Cependant, notre système expérimental permet un suivi à long terme de la dynamique des populations. Plusieurs axes de recherche apparaissent alors importants. Une étude relativement simple est l'observation de la dispersion et de la dynamique de la population sur plusieurs années. En effet, certaines études prédisent que l'information sociale devrait être différemment utilisée après un certain temps (*e.g.* Boudjemadi *et col.* 1999, Le Galliard *et col.* 2003). Les nouveau-nés ne connaissant pas encore la qualité de leur population, ils utiliseraient plus l'information amenée par les autres que leur information personnelle. Le développement de l'information personnelle devrait en conséquence pondérer ou moduler l'utilisation de l'information sociale. Un suivi du comportement des jeunes sur plusieurs années permettrait de quantifier la part relative de l'information personnelle et sociale au cours de la vie. Une expérience à plus long terme nous permettrait également d'accéder aux conséquences des différents syndromes comportementaux sur la valeur sélective des individus et leurs conséquences sur la population. Finalement, nous avons conclut précédemment sur la structuration de la population en syndromes phénotypiques dépendante de l'information transmise. Il paraît évident que l'observation de cette structuration et de son évolution temporelle est nécessaire. Pour effectuer cette expérience, il serait essentiel de développer notre système pour l'adapter plus précisément à un modèle de méta-population. La création de connexions multiples entre des populations de statut différent (*e.g.* vides, faiblement denses, fortement denses) permettrait de manipuler les diverses sources d'informations et leurs conséquences sur la dynamique et la structuration des populations fragmentées.

L'association d'études au niveau de la population et d'études au niveau de l'individu apparaît aujourd'hui nécessaire afin de cerner à la fois les mécanismes par lesquels les conditions environnementales influent sur le comportement animal et la conséquence de ces effets sur la dynamique de la population. La possibilité de suivre la dynamique d'une population permet, en particulier, d'accéder aux conséquences de ces informations socialement acquises sur le devenir des populations fragmentées et d'étudier la dynamique d'acquisition de l'information dans un environnement social changeant.

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# MANUSCRITS

# MANUSCRIT 1

## Kin competition promotes colonization success

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**Biological Sciences**

**Ecology**

# Kin competition promotes colonization success

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## Summary

Colonization is the crucial process underlying range expansions, biological invasions, and meta-population dynamics. Therefore, identifying the tenets of a successful colonization represents a major challenge. Which individuals leave their natal population to colonize empty habitats is one of the most exciting questions in the study of species spatial organization and evolution, and is presently unresolved. Dispersal underpins colonisation. However not all dispersing individuals are necessarily good colonizers. Indeed, the phenotype of dispersers differs depending on the selective pressures that induce dispersal. In particular, kin-based dispersal, at the root of social evolution, should induce the different social response profiles displayed by non-dispersing and dispersing individuals. Kin competition, the competition between family members (here parents and offspring), may be expected to produce dispersers with the best colonizing ability. Despite the evidence for the importance of kin competition for dispersal decisions, the hypothesis that kin competition promotes colonization success has never been tested. Using the common lizard (*Lacerta vivipara*), we conducted a multi-population experiment to study the effect of kin competition on colonization success. We manipulated parent-offspring interaction, the most important component of kin competition, at the family and population levels, and measured its consequences on colonization success. We demonstrate that kin competition at the population level significantly influences colonization success, by enhancing the colonization rate and the growth and survival of colonizers. Based on these results, we calculated that kin-induced colonization halves the extinction probability of a newly initiated population. Kin competition is therefore likely to affect a species' ability to track habitat modifications due to global warming, and to have important implications for understanding invasion dynamics and meta-population functioning.

## Introduction

One of the best examples of successful range expansion has been humans colonizing the Earth. Beginning in Africa, humans have subsequently colonized all continents, islands and habitats (1). However, other species were enabled to track habitat change and had since disappeared. Rather than a simple diffusion process, colonization seems thus to correspond to an endogenous necessity, reflecting an active process (1). For example, in Polynesian island societies, a tradition was to send out young and robust people in the expectation that they would find other islands on which to settle (2, 3). The rapid re-colonization of the habitats made available by the retraction of glaciers (4, 5) also shows that many species have had the capacity to expand their distribution, when environmental conditions offer them the possibility (5). The species northern range expansion due to global warming (6) demonstrates the importance of colonizing processes which allows a species to track environmental changes (6, 7). Similarly, biological invasions are an extreme example of range expansion that demonstrates the advantages of such a process (8).

Colonization is movement from a natal or breeding population followed by settlement in an area where no individuals of the same species are currently present (9). Colonization has been most often viewed as a random process, where some individuals end up in a suitable new habitat by chance (10). It has recently been suggested that not all dispersers from a source population display the same colonization success, and that successful colonizers might display particular phenotypic profiles(11), that enhance their colonization success (12). In which circumstances or in response to which factor(s) inducing dispersal are such phenotypes produced? Dispersal, as the first step leading to successful colonization, is promoted by many different biotic and abiotic factors (12). Among these factors, kin interactions, at the root of social evolution(13, 14), are

involved in the evolution of dispersal (10, 14-18). Kin competition does not only affect the decision to stay or leave, but it also promotes the dispersal of morphologically and/or behaviorally different individuals (17, 19, 20). Since kin competition is involved in the evolution of both dispersal and sociality, and promotes the departure of individuals with specific morphological (e.g. higher body condition, higher body size (12, 17, 19-22)) and behavioral attributes (less stressed by new environments (23), less social-dependent individuals (15)), we hypothesize that individuals dispersing for kin-based reasons will display the best colonizing capacities. In this work, we experimentally tested whether individuals leaving a population with high levels of kin competition, have a higher colonization success.

The common lizard has all attributes needed to test such a hypothesis. First, it has been demonstrated that offspring dispersal is strongly shaped by mother-offspring interactions, a component of kin competition (17, 22). Second, the mother's presence, condition and age, which reflect the expected risk of a mother-offspring interaction, are cues used by offspring to initiate dispersal (17, 19, 24). Finally, offspring leaving their natal population in response to the presence of their mother have specific morphological and behavioral profiles both in terms of morphology and behavior (17, 19, 22, 24).

To investigate whether kin-based dispersal enhances colonization success, we performed a replicated experiment by creating eight pairs of connected patches with semi-natural substrate (25). A replicate consisted of a lizard population in one patch connected by a 20m long dispersal corridor to a similar sized patch containing no lizards. The enclosure dimensions correspond to the average size of a natural home range (in this non-territorial species many individuals share the same home range) and the length of corridors corresponds to the mean dispersal distance observed in natural populations (25). The experiment mimics a situation where potential colonizers of a source population would first have to emigrate through unsuitable habitat (the

corridor), before encountering a new suitable place to settle. Dispersing individuals were identified by capture in pitfall traps before they entered the new population. To assess survival and growth, individuals were recaptured in all patches (for further details see materials and methods). We manipulated kin competition at two levels: first, at the individual scale by manipulating the presence and absence of the mother and second, at the population scale, by varying the proportion of individuals which was in presence or absence of their mother (67% or high population relatedness treatment, or 33% or low population relatedness treatment). We then use the term 'kin competition' for examining the effect of the mother presence at the individual scale and the term 'population relatedness' to examine the effect of the proportion of individuals in presence of their mother within a population. Offspring were released either with their mother or with a surrogate female to keep the age- and sex- structure constant across treatments and populations.

## Results and discussion

Kin competition at the individual scale had no effect on the dispersal probability (Fig. 1A), whereas at the population scale, higher population relatedness significantly increased offspring dispersal (Table 1). This strongly suggests that at birth, an offspring is able to perceive the level of relatedness present in its population. Indeed, the response to the mother's presence is partly determined at the prenatal stage(18), while density (competition with congeners) appears to be assessed at the post-natal stage(16). In other words, the information about potential mother-offspring conflict is gathered before the information about potential conflict among congeners. Consequently, offspring escaping potential competition with their mother should initiate dispersal earlier than those escaping competition with their congeners. In our study, kin competition advanced offspring departure time at the individual scale ($F_{1,51}$ = 4.09, $P$ = 0.0483, presence of

the mother: 3.88 days ± 0.07 SE, absence of the mother: 4.07 days ± 0.06 SE), but not at the population scale ($F_{1,6}$ = 0.31, $P$ = 0.5992). The timing of dispersal movements then constitutes a sort of public information for non-kin who would be able to assess the relative importance of kin competition in the population. This in turn might explain the higher dispersal probability found in populations with a high level of relatedness. The actual mechanisms underlying increased dispersal in populations with high relatedness remains to be more thoroughly examined.

As expected from laboratory experiments(16), offspring dispersing from populations with high population relatedness had significantly bigger body size at birth than non-dispersing offspring, and no differences were observed in populations with low population relatedness (Table 1, independent contrast high population relatedness: $F_{1,790}$ = 9.65, $P$ = 0.0022, low population relatedness: $F_{1,790}$ = 0.57, $P$ = 0.4506). As a consequence, offspring dispersing from populations with high population relatedness have significantly bigger body size at dispersal time than offspring dispersing from populations with low population relatedness ($F_{1,6}$ = 11.51, $P$ = 0.0046, high population relatedness: 40.69 mm ± 0.75 SE, low population relatedness: 37.43 mm ± 0.85 SE). Since body size positively predicts competitive ability, reproduction and survival in the common lizard (25, 26), dispersers from high relatedness populations should display increased colonization success compared to dispersers from low relatedness populations*(9)*. Indeed, colonizers (i.e. dispersers settled in an empty patch) from populations with high relatedness survived better (Fig. 1B) and their body growth rate in the newly colonized patches was significantly greater than for individuals originating from populations with a low level of relatedness ($F_{1,5}$ = 11.36, $P$ = 0.0199, high population relatedness: 18.86 mm/year ± 1.69 SE, low population relatedness: 10.87 mm/year ± 1.83 SE). In squamate reptiles, sexual maturity is body size-dependent(26). Individuals which are bigger at birth or which grow faster should reach

sexual maturity sooner. Indeed our results show that independent of the treatments, bigger one-year old females (body size: $F_{1,123} = 4335.26$, $P < 0.0001$) and colonizers ($F_{1,123} = 10.41$, $P = 0.0016$) were more likely to reproduce. We did not find any treatment effect ($F_{1,4} = 0.13$, $P = 0.7347$). In this species, females start to reproduce in their second and only occasionally in their first year(27). The absence of differences is thus not surprising as all individuals manipulated were in their first year at the end of the experiment, i.e. were in their majority not sexually mature. However, the increased body size should affect reproduction in the following years, because bigger females have a higher probability of reproduction and lay bigger clutches(27). Differences in colonization, survival and growth rates resulted in higher population size of initially empty patches when individuals came from a population with high relatedness compared to population with low relatedness (Fig. 1C). To measure the impact of the above results on the probability of a successful establishment, we constructed stochastic two-sex models of structured populations where the means and standard errors of the dispersal probability, survival and fecundity characteristics of the low versus high kin population treatments were based on results from this experiment (additional details see methods). The probability of failing to colonies an empty patch for individuals originating from a population with high relatedness was half that of individuals from low relatedness populations (extinction risk (Pe), high relatedness: Pe=0.23, low relatedness: Pe=0.46).

To our knowledge, our results provide the first experimental demonstration that kin competition affects colonization success. We demonstrated that offspring leaving a population due to a high level of kin competition are more numerous, and of bigger body size than offspring leaving a population with low level of kin competition. In the newly colonized habitats, these individuals display higher growth rate and survival probability, and newly founded populations are less likely to go extinct. This clearly demonstrates that an offspring's colonization ability

depends on the level of kin competition experienced in its natal population. In an earlier experiment, we additionally found that individuals of bigger body size preferentially colonized empty habitats (29). This result is similar to the one reported in the present study, and suggests that not only is the success of colonization enhanced, but also the likelihood that the colonization of empty habitats will be achieved by individuals of bigger body size. All together, these results implicate kin competition is a key factor in the colonization processes. In particular, in situations where individuals leave their natal populations because they have no other choice but settle in empty patches (e.g. isolated or introduced populations), those leaving the population for reasons of kin competition will have better colonizing success.

The above results are likely to have important implications for the study of invasion, range expansion and meta-population processes where colonization is a driving force of the population's dynamics. Whenever the level of kin interactions within a population increases, it can be predicted that the capacity of this population to produce good colonizers will be highly modified. For example, small, introduced populations, which are likely to rapidly build-up high levels of relatedness (30) should export a greater number of good colonizers. The repetition of such situations could potentially lead to an invasion (31). In the same way, range expansions due to global warming could be accelerated or decelerated depending on kin structure along the habitat margins. As kin interactions are a widespread phenomenon that all species have to deal with, our findings are likely to be quite general. Species might however vary in the extent to which dispersal evolution has been driven by kin interaction or in the way they can assess population relatedness, and further studies comparing species with different mode of habitat occupation (such as sedentary versus vagrant species) will help assessing the generality of our results. It remains that evaluating the role of kin interactions in dynamical processes is likely to be an important issue that may be as important as its role in the evolution of dispersal and

sociality. Our results further stress that accounting for kin structure and kin competition into conservation policies and reintroduction programs may have important consequences for the conservation of animal species.

## Materials and Methods

**Experimental system.** The experiment was conducted in 2003 at the Ecological Research Station of Foljuif (Seine-et-Marne, 48°17'N, 2°41'E). Lizards were maintained in eight enclosed patches (10 m × 10 m) containing natural habitat, which offered semi-natural conditions. The enclosure size corresponds to the female's home-range size under natural conditions (25) and pairs of enclosures were connected by two one-way corridors (20 m). The length of the dispersal corridors corresponds to the minimal dispersal distance observed in natural populations (25). A pitfall trap at the end of each corridor served for the daily capture of dispersing lizards. Lizards captured in pitfall traps are referred to as dispersers, while lizards that stayed in their populations are referred to as residents.

**Kin competition treatments.** In June 2003, we established lizard populations in eight enclosures (a lizard population in one enclosure of each enclosure pair). Populations were initiated with 10 adult males, 18 adult females, 12 yearlings (6 males and 6 females) and 103.3 ± 3.08 SE juveniles. These ratios correspond to the age and sex structure of natural populations from which the introduced individuals originate (28). All lizards used in this experiment had been housed for at least one year in semi-natural populations located at the Ecological Research Station of Foljuif. At the start of the experiment all lizards were collected over two consecutive days. Females were maintained in the laboratory until they gave birth (22) and males were released into the empty populations a few days after capture. Two days after birth, all offspring of a family were released with their mother or with a surrogate female to manipulate kin competition at the individual

scale. To manipulate kin competition at the population level, we either released 6 families with their mother and 12 with a surrogate female in four of the eight populations, or 12 (67%) families with their mother and 6 with a surrogate female in the remaining four populations. Families were randomly selected to be released with or without their mothers and populations were similarly randomly distributed among treatments. Family characteristics (i.e. body length of the female released, number and body length of offspring) were not significantly different in the two kin competition treatments (individual and population scale) nor by their interaction ($P > 0.1$). This shows that the starting conditions were indeed random with respect to the treatments.

**Field monitoring.** Lizards were individually marked by toe clipping and both snout-vent length and body mass were measured prior to release. Body condition was defined as body mass relative to snout-vent length, by adding snout-vent length as a covariate in our analyses. Pitfall traps were checked daily to monitor dispersal. Dispersers were identified, measured for snout-vent length and body mass and immediately released into the enclosures of arrival. Some dispersers attempt a secondary dispersal from arrival enclosures. These secondary dispersal attempts were not dependent on population relatedness ($F_{1,6} = 1.47$, $P = 0.2709$) and these dispersers were then released in non-experimental enclosures. In order to measure survival probability and growth rate, we recaptured all surviving individuals in May 2004, almost one year after release. To ascertain that no individuals were left in the enclosure, we conducted 10 successive recapture sessions. Immediately after capture, lizards were brought to the laboratory where they were measured and housed until the end of the tenth capture session. The escape-proof enclosure and the absence of living lizards during the last six recapture sessions allowed us to ascertain that all survivors were recaptured.

**Statistics.** Dispersal probability, colonizer survival and reproduction probability were modeled with mixed effects logistic regressions using the GLIMMIX macro in SAS (32). Body size,

offspring age at dispersal and average growth rate of colonizers were modeled using the MIXED procedure in SAS (32). The initial model included the effects of experimental treatments (at the familial and population level), sex and body size at birth as fixed factors as well as the random effects of enclosures nested within the population treatment and family nested within both enclosures and individual treatment. For the analyses on the colonizer's characteristics the date of dispersal was added as a covariate. The final model was obtained by backward elimination, dropping in a stepwise process all non-significant effects. Statistical tests are type III F tests for fixed effects.

**Population model.** Stochastic two-sex model (33, 34) were used to compare the overall colonization success across treatments. We only modeled the population growth rate in the colonized patch during the first year of the colonization process (from establishment of the source population in August year t to the last recapture session in June of year t+1). The post-breeding census life cycle graph (34) described only the juveniles class which is the colonizing age class in our experiment. The demographic parameters characterizing the newly founded populations are the means over replicates of survival, fecundity and immigration rate split by sex and treatments (high versus low relatedness). The model included demographic stochasticity on survival probability with a binomial distribution and on fecundity with a Poisson distribution. Environmental stochasticity was included for the survival using means and standard errors at the replicate level. For each combination of parameters, 100 population trajectories of one-year length were drawn using Monte Carlo simulations. Extinction probabilities were computed as the number of extinct trajectories over the total number of simulated trajectories (35). Simulations were performed with the ULM computer program (36).

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# Tables

**Table 1.** Kin competition, at familial and population level, on the natal dispersal probability.

| | Test statistic | P |
|---|---|---|
| Family kin competition | $F_{1,792} = 1.45$ | 0.23 |
| Relatedness | $F_{1,6} = 6.90$ | 0.039 |
| Initial body length | $F_{1,792} = 0.92$ | 0.34 |
| Initial body length*Relatedness | $F_{1,792} = 7.53$ | 0.0062 |

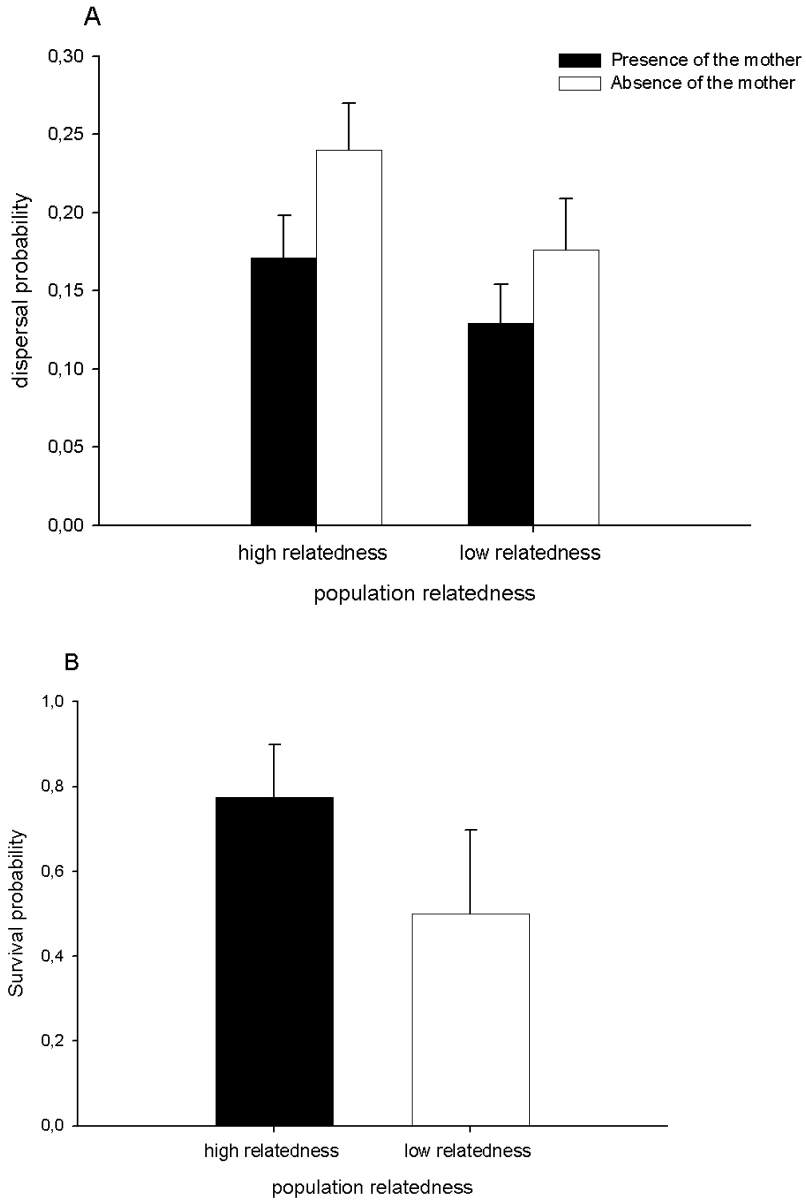
Dispersal probability was modelled with mixed effects logistic regressions using the GLIMMIX macro in SAS. The initial model included the effects of experimental treatments (at the familial and population level), sex and body size at birth as fixed factors as well as the random effects of enclosure nested within the population treatment and family nested within both enclosure and family treatment. The final model was obtained by backward elimination, dropping in a stepwise process all non-significant effects. Statistical tests are type III F tests for fixed effects.

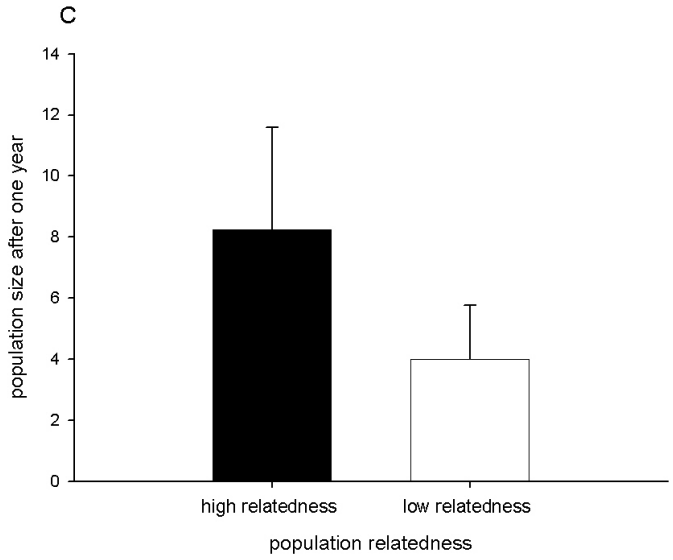
## Figures legends

**Figure1.** Effect of average relatedness on parameters of colonization success. (A) Offspring dispersal probability from the source population. In populations of high kin competition (high average relatedness) 67% of the offspring were released with their proper mother, while in populations of low kin competition (low average relatedness) 33% of offspring were released with their mother. Offspring exposed to more or less kin competition at the familial scale showed a similar dispersal probability ($F_{1,790} = 1.90$, $P = 0.1686$), while offspring living in populations of higher relatedness, dispersed more ($F_{1,6} = 7.58$, $P = 0.0332$, for more statistical details see methods). There was no interaction between the two levels of kin competition ($F_{1,789} = 2.69$, $P = 0.1017$). Values are least square means ± 1 sd. (B) Offspring survival of colonizers in relation to average relatedness of the source population. Colonizers from high kin competition populations survived better than individuals originating from populations with a low level of kin competition ($F_{1,6} = 7.96$, $P = 0.0303$). Values are least square means ± 1 sd. (C) Population size in relation to the average relatedness of the source population. The population size of the empty patches was significantly higher when individuals originated from a population with high kin competition compared to low kin competition (logistic regression with Poisson distribution, Proc GENMOD: $\chi_1 = 6.02$, $P = 0.014$). Values are means ± 1 se.

**Figure 2.** Experimental design. Grey indicates enclosures where 67% of the offspring were released with their proper mother (i.e. populations of high kin competition), while black indicates enclosures where 33% of the offspring were released with their proper mother (i.e. populations of low kin competition). White indicates enclosures that were initially empty. Pitfall traps at the end of each one-way corridor are represented in black. Scale bar, 20 m.

**Figure1**


A
Presence of the mother
Absence of the mother
dispersal probability
0,30
0,25
0,20
0,15
0,10
0,05
0,00
high relatedness
low relatedness
population relatedness
B
Survival probability
1,0
0,8
0,6
0,4
0,2
0,0
high relatedness
low relatedness
population relatedness


C
14
12
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4
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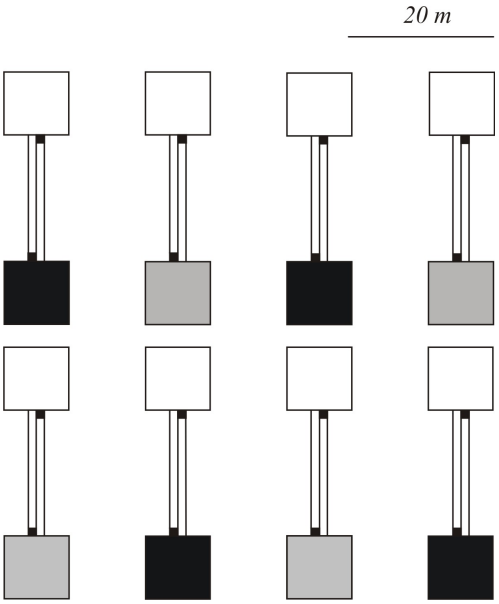
population size after one year
high relatedness
low relatedness
population relatedness

**Figure 2**



# MANUSCRIT 2

## Social information and emigration: lessons from immigrants

Soumis à *Ecology Letters*

**Letter**

# Social information and emigration : lessons from immigrants

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References : 29

Tables: 1

Figures: 2

Keywords: Socially acquire information; dispersal; common lizard; immigration

Short running title: Immigrants mediate social information

## Summary

"Should I stay or should I go?" is the fundamental question that faces any candidate for emigration, as emigrating without any outside information has major costs. Up to now, most studies have concentrated on cost-reducing strategies (e.g. exploration) developed after leaving the natal habitat. None have proposed or investigated the idea that information can be acquired before leaving. One simple way to acquire this information, before leaving one's habitat, is through immigrants who potentially carry information about their origins. Here, we manipulated the density of the immigrants' population of origin to test the idea that immigrants of the common lizard (*Lacerta vivipara*) transmit such information. Emigration of residents was clearly dependent on immigrant origin. This study demonstrates that immigrant characteristics serve as cues about surrounding population densities. Immigrants therefore constitute a source of information, which should deeply affect the evolution of dispersal and species persistence in a fragmented habitat.

## Introduction

Emigrating without any information about the surroundings represents one of the major costs of dispersal (Clobert *et al.* 2001; Stamps 2001; Dall *et al.* 2005). In humans, the cost of leaving one's native country to settle abroad is decreased by the accessibility of various sources of information (e.g. media, books) regarding the quality of life elsewhere in the world. Such sources of information were not available to human in ancient time, and a fortiori are unavailable for all other species. A potential way to decrease emigration costs is to reduce uncertainty about the 'outside world' by gathering information about the surroundings and to allow candidate emigrants to make dispersal decisions based on an assessment of their potential success in another population (Valone & Templeton 2002; Doligez *et al.* 2004; Dall *et al.* 2005). Species should therefore reduce the level of uncertainty about the existence and quality of surrounding populations by gathering appropriate information whenever possible (Danchin *et al.* 1998; Stamps 2001; Dall & Johnstone 2002; Doligez *et al.* 2004; Dall *et al.* 2005). While, in human populations, communication media convey such information, only recently have studies demonstrated that non-human species are also adept information gatherers (Valone 1989; Templeton & Giraldeau 1995; Doligez *et al.* 2002; Schjorring 2002; Valone & Templeton 2002; Danchin *et al.* 2004; Dall *et al.* 2005; Aragon *et al.* in press). Various parameters of the physical and social environment can potentially serve as sources of information for emigrants as they represent valuable cues about the state of the future environment (Danchin *et al.* 2004). It has been demonstrated that individuals can assess environmental quality through socially acquired information like presence or absence of conspecifics, their activities and their performances (Danchin *et al.* 2004; Doligez *et al.* 2004; Dall *et al.* 2005). For example, settling individuals assess the quality of an area by observing the density (Doligez *et al.* 2004), reproductive success (Doligez *et al.* 2002) or foraging capacities (Templeton & Giraldeau 1995) of residents. At first sight, this information should

only be available when visiting new populations (e.g. prospecting), after the decision to leave the natal environment has been made. Prospecting is, however, impossible for species with limited exploratory capacities and induces costs in term of energy, time, and predation. If visitors to a population could gather information through local individuals, one might hypothesize that residents could also gather information about the outside through visitors. We hypothesize that immigrants can supply residents with information about surrounding populations. Residents might then potentially have access to information regarding aspects of quality from several other patches. For example, the density of conspecifics in new habitats is a key factor of future fitness outcome, and thus in the selection of a new habitat (Stamps 2001). Potential emigrants therefore have the possibility to base their dispersal decisions on comparisons between their current population and other populations without the need for prospecting.

To test this hypothesis, we used the common lizard as model system and manipulated population density. The sensorial capacity of the common lizard has been well studied, and this species shows a marked ability to detect relatives (Léna & de Fraipont 1998), conspecific density (Aragon *et al.* in press), and to recall previous interactions among conspecifics (Aragon *et al.* in press) based on odour cues. Therefore, the common lizard frequently uses social information for behavioural decisions. Furthermore, recent studies strongly suggested that individuals knew about the existence of other populations (Boudjemadi *et al.* 1999; Lecomte *et al.* 2004). To experimentally investigate the possibility for immigrants to be sources of information, we used 16 semi-natural populations of the common lizard in which we manipulated population density both in resident's patches and in departure patches of young immigrants in a full factorial crossed design (see materials and methods). Using pitfall traps, any juvenile attempting to disperse was identified. These dispersers were then released as immigrants in another enclosure according to our factorial treatment. This protocol allowed

us to test for effects of immigrants' origin (high-density or low-density) in interaction with the density in the residents' population.

# Materials and Methods

## *Experimental system*

The experiment was conducted in 2004 at the Ecological Research Station of Foljuif (Seine-et-Marne, 48°17'N, 2°41'E). Lizards were maintained in sixteen enclosed patches (10 × 10 m) containing natural habitat, which offered semi-natural conditions. That enclosure size corresponded to the female's home-range size under natural conditions and pairs of enclosures were connected by two one-way corridors (20 m). The length of the dispersal corridors corresponded to the minimal dispersal distance observed in natural populations (Lecomte & Clobert 1996). A pitfall trap at the end of each corridor served for the daily capture of dispersing lizards. Lizards captured in pitfall traps were referred to as dispersers, while lizards that stayed in their populations were referred to as residents.

## *Density treatments*

In June 2004, we established lizard populations such that treatments were randomly distributed among enclosures. Eight populations were initiated with 8 adult males, 12 adult females, 20 yearlings (10 males and 10 females) and 34 ± 3.7 SE juveniles (i.e. high density populations) and eight populations were initiated with 4 adult males, 6 adult females, 10 yearlings (5 males and 5 females) and 17 ± 2.5 SE juveniles (i.e. low density populations). These ratios correspond to the age and sex structure of natural populations from which the introduced individuals originated (Massot *et al.* 1992). All lizards used in this experiment had been housed for at least two years in semi-natural populations located at the Ecological Research Station of Foljuif. At the start of the experiment, all lizards were collected over two consecutive days. Females were maintained in the laboratory until they gave birth and males were released into the empty populations a few days after capture. Two days after birth, all

offspring of a family were released with their mother. Families were randomly selected to be released in a given density treatment and family characteristics (i.e. mother body size, number and body size of offspring) did not significantly different between density treatments ($P > 0.5$).

## *Field monitoring and manipulation of immigrants' origin*

Lizards were individually marked by toe-clipping and both snout-vent length and body mass were measured prior to release. Body condition was defined as body mass relative to snout-vent length, by adding snout-vent length as a covariate in our analyses. Pitfall traps were checked daily to monitor dispersal. Dispersers were identified, measured for snout-vent length and body mass and immediately released into an enclosure. To manipulate the origin of immigrants, we specifically selected dispersing juveniles originating from either a low-density population or a high-density population. Half of the 16 populations received only immigrants from high-density populations whereas the other half received immigrants from low density populations. To disentangle the effect of the origin of immigrants from the number of immigrants, we also applied a gradient of the number of immigrants within the two treatments.

## *Statistics*

Dispersal probability was modelled with mixed effects logistic regressions using the GLIMMIX macro in SAS (Littell *et al.* 1996). The initial model included the effects of experimental treatments (arrival patch density and origin of immigrants), the number of immigrants, sex, the body size and interactions as fixed factors as well as the random effects of enclosures nested within treatments and the family effect nested within the population. The final model was obtained by backward elimination, dropping in a stepwise process all non-significant effects. Statistical tests are type III F tests for fixed effects.

## Results

Emigration rate strongly depended on the origin of the immigrants received (departure patch density of immigrants: $F_{1,12} = 6.79$, $P = 0.0230$, Fig. 1, effect nested in population) and was completely independent of the number of immigrants ($F_{1,301} = 0.62$, $P = 0.4324$). In populations receiving immigrants from low-density populations, juveniles dispersed more frequently following arrival of immigrants (Fig. 1).

The sensitivity to immigrant origin also depended upon both the residents' phenotype and the density at the residents' patch. First, the effect of immigrants' origin on dispersal of residents varied with resident's body size (resident initial body size × immigrant's departure patch density: $F_{1,301} = 6.26$, $P = 0.0129$, Fig. 2). In populations receiving immigrants from high-density populations, there was a positive correlation between body size of residents and the probability to emigrate ($F_{1,148} = 4.27$, $P = 0.0405$, Fig. 2). This relationship was non-significant in populations receiving low-density immigrants ($F_{1,156} = 0.01$, $P = 0.97$, Fig. 2). Second, immigrants' origin affected emigration rate depending on the density in the residents' patch (residents patch density × immigrant's departure patch density: $F_{1,12} = 5.77$, $P = 0.0333$, Fig.1). Separate analyses for each residents patch density revealed that only resident lizards of low-density patches reacted towards the immigrants' population of origin (Table 1).

## Discussion

Our results show that residents changed their emigration behaviour depending on immigrants' origin. Immigrants therefore supplied information about other populations' status. Emigration was not significantly related to the number of immigrants received. Thus, the transfer of information did not involve immigration rate, but was more likely related to immigrants' phenotype. At the start of the experiment, individuals were randomly distributed in the two density treatments with regard to their morphological characteristics and previous

history (see materials and methods). Manipulation of population density thus appears to have induced the departure of immigrants of particular phenotypes in term of morphology, physiology or behaviour. It has been demonstrated in an earlier experiment that different conditions induce the departure of dispersers with different phenotypes (Léna *et al.* 1998). In this experiment, immigrants did not exhibit particular morphology ($P > 0.5$ for body size and body condition). Thus, differences in behaviour or in physiology (e.g. odor) between immigrants are good candidates as cues providing information about immigrants' origin.

The dispersal reaction towards immigrants in the residents patch was also phenotype-dependent. This was not entirely unexpected as, in a few species including ours, dispersal has been demonstrated to be phenotype-dependent (O'Rian *et al.* 1996; Clobert *et al.* 2004). Furthermore, the sensitivity of juveniles to the presence of conspecifics has also been shown to be phenotype-dependent, especially with respect to conspecific density (Léna *et al.* 1998). We can thus sketch the following scenario to explain our results. Large juvenile lizards are highly competitive and dominate most social interactions. Encountering an immigrant from a high-density population should signal to residents that only highly competitive residents (i.e. large) should disperse, because they are going to encounter high densities elsewhere. This will be less of a concern for residents emigrating to a low-density population (when receiving immigrants from a low-density population) such that individuals of all phenotypes are likely to emigrate to low-density populations.

However, only resident lizards of low-density patches reacted towards the immigrants' population of origin. This result pleads for an even more complicated scenario. Population density has dual information content: the existence of potential competitors and the quality of the habitat (Clobert *et al.* 2004). The presence of conspecifics has been demonstrated to attract rather than repulse other individuals, and, at the population level, emigration has been sometimes found to be negatively, rather than positively related to density in some species

including common lizards (Stamps 2001; Le Galliard *et al.* 2003). It is therefore possible that in our experiment a high density indicates a good quality habitat rather than a crowded habitat. This might then explain why residents of high-density populations (i.e. good quality habitat) did not react to the information brought by immigrants while those in low-density population (i.e. poor quality habitat) did react. Those individuals leaving the high-density population probably had other reasons for dispersing than the quality of the habitat, such as, for example, kin competition (Ronce *et al.* 1998; Léna *et al.* 2000), which partly shapes dispersal independently from density in this species (Le Galliard *et al.* 2003). However, other scenarios are equally likely such as better information transmission at low densities, or a density-dependent message delivery by immigrants. Whatever the exact explanations, the results clearly demonstrate that the use of immigrants as a source of information from surrounding populations is context-dependent as well as phenotype-dependent. This plasticity is probably required to optimise an individual's dispersal strategy with respect to the numerous and potentially inconsistent pieces of information that can be gathered about the physical and social environment at a meta-population level. Understanding the exact influence of density and social information on dispersal strategy will obviously require additional work.

To our knowledge this is the first study that demonstrates the use of immigrants as a cue to assess the quality of surrounding populations without visiting them. This form of social information should allow dispersers to reduce the risks of settlement without any costs of prospecting. To be of value, this information should be reliable. Indeed it is likely that when reaching a new population, immigrants would have difficulty to hide their status and therefore should be expected to deliver an honest signal. First, immigrants are imprinted by their population of origin (e.g. food, crowding). Second, most dispersing individuals have a dedicated phenotype, which is essential to increase their success as dispersers. We previously showed that resident and dispersing juveniles still recognized each other 6 months after the

dispersal phase (Aragon *et al.* 2006). Immigrants are therefore likely to constitute a reliable source of social information on the connections in a fragmented habitat. Basing dispersal decisions on information brought by immigrants will re-enforce connections among extant populations and will help homogenize population sizes and converging towards an ideal free distribution (Doncaster *et al.* 1997; Holt & Barfield 2001). Therefore, this will help decreasing the overall probability of extinction (Hanski & Gaggiotti 2004) and thus increasing the viability of fragmented population. Evidence that immigrants are a cue to assess the quality of surrounding populations should deeply change our view on evolution, persistence and functioning of meta-populations, and should have profound consequences for how to deal with the conservation of species leaving in fragmented habitats.

## Acknowledgments

We are grateful to Ryan Calsbeek, Etienne Danchin, Jean-François Le Galliard, Manuel Massot, Sandrine Meylan and Murielle Richard, for comments, and to L. Carlier and C. Lamotte for field assistance. Financial support was received from the French Ministry of Education and Research (ORE program) and the French Ministry of Environment.

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**Table 1. Natal dispersal probability depended on the origin of immigrants and the density in the residents' patch.**

| | High density populations | Low density populations |
|---|---|---|
| Initial body size | $F_{1,203} = 1.90$ $P = 0.1695$ | $F_{1,98} = 0.21$ $P = 0.6507$ |
| Origin of immigrants | $F_{1,5} = 0.00$ $P = 0.9719$ | $F_{1,5} = 13.53$ $P = 0.0143$ |
| Number of immigrants | $F_{1,203} = 0.05$ $P = 0.8256$ | $F_{1,98} = 1.09$ $P = 0.2990$ |
| Body size × Origin | $F_{1,203} = 0.02$ $P = 0.8999$ | $F_{1,98} = 12.99$ $P = 0.0005$ |

Dispersal probability was modelled with mixed effects logistic regressions using the GLIMMIX macro in SAS. The initial model included the effects of experimental treatments (origin of immigrants and number of immigrants) sex and body size at birth as fixed factors as well as the random effects of enclosure nested within the origin of immigrants and family nested within enclosure. The final model was obtained by backward elimination, dropping in a stepwise process all non-significant effects. Statistical tests were type III F tests for fixed effects.

## Figures legends

**Figure 1. Effects of origin of immigrants and the density of residents' population on the dispersal probability.** Offspring exposed to immigrants from low-density populations dispersed more than offspring exposed to immigrants from high-density populations and this effect depended on the density in residents patch. Values are least square means ± IC. The number of individuals for each group is represented.

**Figure 2. Phenotype-dependence of the effect of immigrants on natal dispersal probability.** The sensitivity to the origin of immigrants depended on the body size of residents. Body size of juveniles in the residents patch was positively correlated to their probability of emigration in populations receiving high-density immigrants, while no correlation was found in populations receiving low-density immigrants. Values are predicted values by the final model and the regression line is shown.

Figure 1

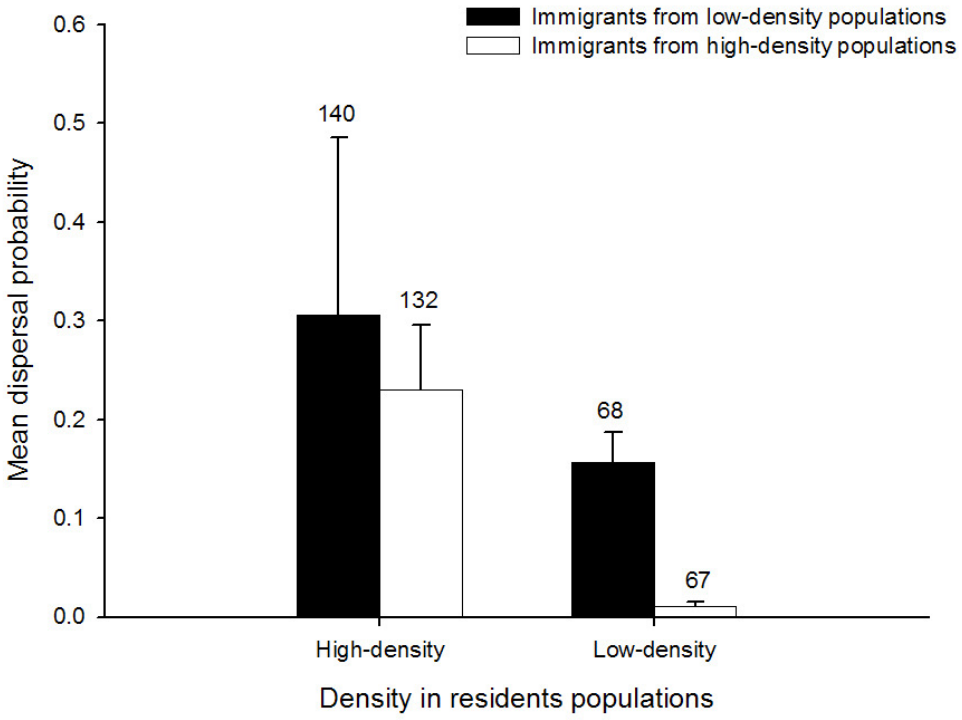
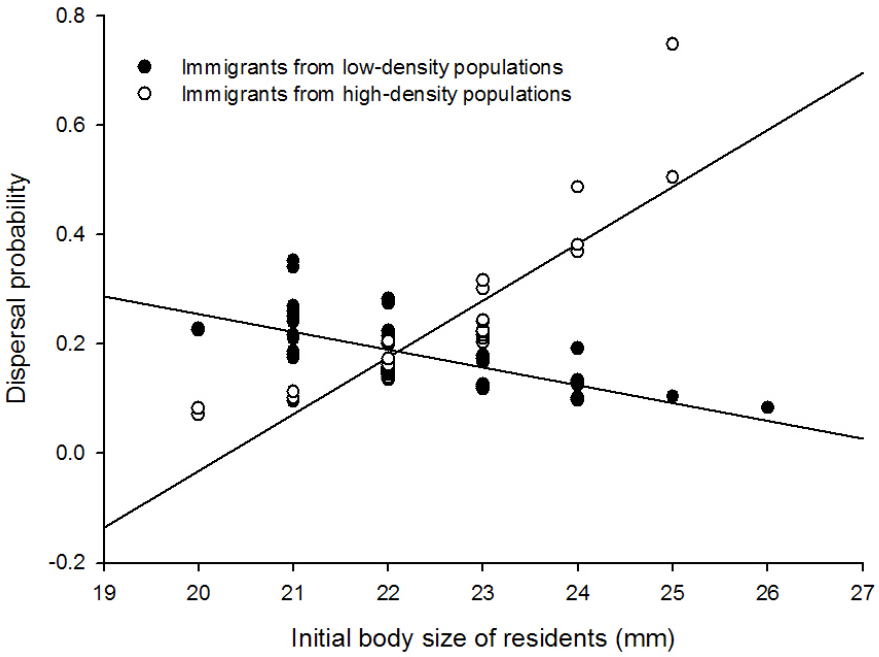

Immigrants from low-density populations
Immigrants from high-density populations
Mean dispersal probability
0.6
0.5
0.4
0.3
0.2
0.1
0.0
140
132
68
67
High-density
Low-density
Density in residents populations

Figure2


Immigrants from low-density populations
Immigrants from high-density populations
Dispersal probability
Initial body size of residents (mm)
0.8
0.6
0.4
0.2
0.0
-0.2
19
20
21
22
23
24
25
26
27

# MANUSCRIT 3

## Density, information and space use in the common lizard

En preparation

# Density, information and space use in the common lizard (*Lacerta vivipara*)

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## Abstract

Animals monitor others' interactions and activities, and take many behavioral decisions based on this social information. In this way, individuals may decide to leave their habitat and to select a new one using social information about habitat quality. Few studies investigated the role of density-related information, a cue about habitat quality, in movements across populations. However, a direct measurement of the transfer of density-related information among individuals is still needed. Here, we test for the possibility that common lizards (*Lacerta vivipara*) transfer information about their population density during interaction. Our results strongly suggest that some transfer of information about the population density of the lizard encountered is possible. Thereby, conspecifics use interactions to acquire appropriate information and change accordingly their space use. Density-related information, influencing space use, should have important consequences in dispersal decisions and in population dynamic.

Keywords: social information; dispersal; population density; interaction; common lizard

## Introduction

Animals are constantly using personal and/or environmental information to take decisions for reproduction, foraging, and habitat selection (reviewed in Giraldeau 1997; Dall et al. 2005). However, in many situations, personal and/or environmental information is biased or difficult to collect (Giraldeau 1997; Dall et al. 2005). Not surprisingly then numerous studies have recently focused on the role of socially acquired information as fitness indicators (reviewed in Danchin et al. 2004; Dall et al. 2005). Animals acquire information on the suitability of habitats by monitoring others' interactions and activities, and take decisions about staying or moving elsewhere based on this information (e.g. Doligez et al. 1999; Boulinier et al. 2002; Pärt and Doligez 2003; reviewed in Danchin et al. 2004). Among cues of habitat quality, conspecific density is key information about present and future fitness outcomes. Indeed, fitness and population density are interconnected by several ways (e.g. Lidicker 1978; Eckman 1984; Sinclair 1989; Massot et al. 1992). Many fitness-related traits such as fecundity, behaviour and dispersal are found to be density-dependent (e.g. Hassel and May 1985; Crespi & Taylor 1990; Massot et al. 1992; Lecomte et al. 1994). For example, high-density often induces higher aggressiveness and lower accession to food and mate (e.g. Reigh et al. 1982; Krebs 1971; Stenseth & Lomnicki 1990; Lecomte et al. 1994). Therefore, numerous studies emphasized the key role of density-related information in habitat selection and dispersal decision (Crespi & Taylor 1990; Lambin et al. 2001; Stamps 2001; Clobert et al. 2004; Doligez et al. 2004).

Potential dispersers are therefore likely to acquire information on densities in both their actual population and the surrounding ones. Although density in populations of residence is supposed to be directly assessed, the density in surrounding populations is hardly attainable by direct assessment while it constitutes an important cue on which to base a dispersal decision. The suitability of surroundings populations might then be assessed when prospecting (Doligez et al. 2004) or by using immigrants as a source of density-related

information (Cote and Clobert submitted). As habitat quality and social environment imprints individuals' physiology, morphology and behaviour (e.g. Reigh et al. 1982; Krebs 1971; Stenseth & Lomnicki, 1990; Clobert et al. 2004; Meylan et al. in press), density-dependant phenotype might serve as indirect and/or complementary source of information. Candidate emigrants might then base their dispersal decision on this social information by comparing habitat characteristics of their resident to surroundings populations. Since few studies investigated the role of density-related information at the population scale (e.g. Doligez et al., 2004; Cote and Clobert submitted), a direct measurement of the transfer of density-related information among individuals appear as a priority to understand more deeply how density-related information is affecting dispersal decision.

Here, we test for density-related information in the common lizard (*Lacerta vivipara*) and discuss the role of density-dependant phenotype as source of information to other individuals. We fist manipulated population density and then used lizards from these populations as sources of information. We measured the behavioral and morphological differences between lizards from high- and low-density populations. We also tested the behavioral reaction of individuals from high- or low-density population to an interaction with another individual from high- or low-density population. As behavioral responses are often context-dependent, two situations have been explored: 1) lizards had no possibility to escape the place of interaction; 2) lizards had the choice either to stay or leave the place of interaction. As dispersers can differ from philopatric individuals in morphology (Dixon 1985; Venable 1998; O'Rian, 1996), physiology (de Fraipont et al. 2000; Dufty and Belthoff, 2001) and behavior (O'Rian 1996; Fraser et al. 2001; Meylan et al. in press), the dispersal status might influence the transfer of density-related information. We also used individuals of which the dispersal status was known.

# Methods

## *Species and study site*

The common lizard (*Lacerta vivipara* Jacquin 1787) is a small lacertid (adult snout-vent length: males 40-60mm, females 45-75mm) inhabiting humid habitats in Eurasia (Avery 1962). Lizards emerge from hibernation between late March and early April. Females produce offspring once a year and laying occurs in June-July. Juveniles are independent of their mother immediately after birth and disperse after 10 days of age on average. Hibernation begins late October.

This experiment was conducted using lizards which has been living in semi-natural populations at the Ecological Research Station of Foljuif (Seine-et-Marne, 48°17'N, 2°41'E, (Le Galliard et al. 2003). Semi-natural populations are enclosures (10 m × 10 m) protected from avian and mammal predation which are prolonged by a one-way 20 m dispersal corridor. The enclosure size is equivalent to a natural home range size (home ranges are overlapping in this species) and the length of the corridor corresponds to the minimal dispersal distance observed in natural populations (Boudjemadi et al. 1999). A trap is located at the extremity of each corridor to catch dispersing lizards.

## *Density treatments*

In June 2004, we established lizard populations such that treatments were randomly distributed among enclosures. Eight populations were initiated with 8 adult males, 12 adult females, 20 yearlings (10 males and 10 females) and 34 ± 3.7 SE juveniles (i.e. high density populations) and eight populations were initiated with 4 adult males, 6 adult females, 10 yearlings (5 males and 5 females) and 17 ± 2.5 SE juveniles (i.e. low density populations). These ratios correspond to the age and sex structure of natural populations from which the introduced individuals originated (Massot et al. 1992). All lizards used in this experiment had

been housed for at least two years in semi-natural populations located at the Ecological Research Station of Foljuif. At the start of the experiment, all lizards were collected over two consecutive days. Females were maintained in the laboratory until they gave birth and males were released into the empty populations a few days after capture. Two days after birth, offspring were released with their mother. Families were randomly selected to be released in a given density treatment, and family characteristics (i.e. mother body size, number and body size of offspring) did not significantly differ between density treatments (all $P > 0.5$). Lizards caught in the corridor trap while attempting to leave their enclosure were considered as 'dispersers' and were randomly released in another enclosure either of high or low density. As juveniles disperse on average after 10 days of age (Massot et al. 2002), dispersers mostly experienced the population density of their release enclosures.

## *Reaction to interaction*

### First experiment: Without the possibility to escape

In April 2005, 64 one-year old lizards (i.e. two females and two males per enclosure) were captured during a four-day session. All lizards were measured for body length (nearest mm) and body mass (nearest mg). Among lizards captured in these enclosures, 18 were dispersers (see above). To provide each individual with the same standardized environment (e.g. food, water, heat, social interactions), lizards were individually housed in plastic terrariums (25 x 15.5 x 15 cm, containing a 3 cm of litter (Le Galliard et al. 2003). In one corner of the terrarium a bulb provided heat for thermoregulation and light from 9:00 a.m. to 12:00 p.m., and from 1:00 p.m. to 5:00 p.m.. A piece of carton and a plastic tube were provided to allow the lizards to hide. The experimental test was conducted the day after the capture to avoid potential effects of stress due to capture.

Behavioral measurements were performed in plastic terrariums of the same dimensions as living terrariums. A piece of carton (shelter) was added in the center of the

terrarium allowing the lizards to hide and a bulb provided heat for thermoregulation. First, the behavior of lizards alone was recorded. In particular, the lizard could choose between staying inactive under the shelter or leaving the shelter and being exposed (basking or moving). During 10 minutes, we quantified the time spent under the shelter, the time spent moving and the time spent basking with the software "The Observer". We excluded the time where the lizards scratch the floor and the wall for two reasons. First, this behavior is rather a sign of experimental stress than an exploratory behavior (de Fraipont et al. 2000). Second, the time of scratching is always small (<2% of time). Then, lizards were transferred in another terrarium with a second lizard of the same sex and of a similar body length. The second lizard was issued from whether high- or low- density populations. The two lizards were associated in a full-crossed design according to population densities. Lizards were maintained in this terrarium during 10 minutes, and were then removed and isolated. With the same procedure than above, we observed again the behavior of each lizard alone to test for behavioral modifications induced by the interaction. The same observer performed all the tests without knowing the lizard treatment of origin. All lizards were then released in their original populations.

### Second experiment: With the possibility to escape

40 one-year old lizards (i.e. 20 females and 20 males) were captured 10 days later than for the first experiment. As above, we measured the body length and the body mass of lizards. Among these lizards, 8 were dispersers. Lizards were individually maintained as described previously and experiments started one day after capture. Behavioral measurements were performed in woody terrarium (50 x 30 x 20 cm) separated in 2 identical parts (25 x 30 x 20 cm) by a mobile wall. In each part, a piece of carton (shelter) was added in the center of the terrarium allowing the lizards to hide and a bulb provided heat for basking behavior. The

distance between the two shelters, and thus between the two heat sources (35 cm) produced 2 basking spots separated by a zone preventing any basking behavior.

First a lizard from high- or low-density populations was introduced in one part of the terrarium, the other part remaining not accessible to the lizard. The lizard was left exploring the terrarium and the basking spot for 10 minutes, which has been demonstrated to be sufficient for this lizard to behave as a resident (Aragon et al. 2006). Then, another lizard matched for sex and size (interacting lizard), originating either from a high- or low-density population, was added. The two lizards interacted for 10 minutes. Then, we removed the second lizard (interacting lizard) as well as the mobile wall, rending the second part of the terrarium accessible. After 10 minutes of habituation to the two parts of the terrarium, we recorded the part of the terrarium that the lizard was in (always under one of the two spots provided) to analyze the choice of the thermoregulation spot. The experiments were performed on two days. 20 lizards were tested the first day and the 20 others were used as interacting lizards. The day after, we tested the 20 lizards being used as interacting lizards on the first day with the first day 20 tested lizards as interacting lizards. Two same lizards were never used in a pair, and neither the day of experiment nor the first day experiment outcome (choice of the thermoregulation spot) did not influence the results (all $p>0.30$).

## *Statistical analyses*

We estimated the individual activity, using the time spent in the three described behaviour (hidden, moving, basking) before the interaction in the first experiment (i.e. without the possibility to escape). The duration of these behaviours, the body length and the body condition (body mass with body length as covariate) were analysed with a MIXED procedure in SAS v. 8.02 (Littell et al. 1996). The behavioural modifications induced by the interaction was analysed with the differences of time spent (after interaction – before

interaction) for the three behaviours as dependent variables. For the second experiment (i.e. with the possibility to escape), the choice of the shelter was coded as 0 and 1. This variable was analysed using the GLIMMIX procedure in SAS v. 8.02 (Littell et al. 1996) with a logit link function and a binomial error term. These procedures (GLMMs, MIXED and GLIMMIX) account for the presence of both fixed and random effects. The fixed effects were the population densities and the dispersal status of the tested and interacting lizards, the sex, the body length and interactions. As all the results obtained were sex independent ($P > 0.30$ for simple effects and interactions), we therefore did not present the sex effects in our analyses. We also added a random factor controlling for the pair of interacting lizards (Quinn and Keough 2002). For the analysis of the shelter choice, we added a random factor accounting for spatial differences in experimental system. Indeed, thermal differences in the experimental room might be crucial in the choice of basking spots. The assumptions of theses models were verified on residuals. Likelihood ratios were used to test the significance of each factor or interaction. Simplification of all models was made using backward elimination of the non-significant interactions. Significance level was set at $p=0.05$. In all analyses, we have two kinds of density treatments: the population density of the lizard tested, named 'density', and the population density of the lizard interacting with the tested lizard, named 'density-interact'.

# Results

## Morphological and behavioral traits

In the first experiment, one-year old lizards from high-density populations were longer than in low density populations, but not in the second experiment (Table 1). The body length was not significantly affected by the dispersal status in the first and second experiment (Table 1). Body condition was not affected by density treatments and dispersal status in the first and second experiment (Table 1).

We analyzed the individual activity before the interaction in the first experiment (i.e. without the possibility to escape). The body length had no effect on the time spent in each behavior (i.e. $P > 0.26$ for all). As found in other studies (Clobert et al. 1994; Aragon et al. 2006a and b), the dispersal status significantly influenced individual basic activities in the terrarium (here the time spent basking, see table 2). However, population density significantly affected the difference of activities between non-dispersing and dispersing individuals (significant interaction between population density and dispersal status on time spent moving, see table 2). While non-dispersing lizards from high-density populations moved more than non-dispersing lizards from low-density populations, the time spent moving did not depend on population density in dispersers (contrasts, non-dispersing individuals: $F_{1,60} = 20.29$, $P < 0.0001$, dispersers: $F_{1,60} = 1.16$, $P = 0.29$). Finally, the time spent hidden did not depend on the population density and on the dispersal status (Table 2).

## Behavioral modification induced by the interaction

The change in time spent hidden was significantly affected by the population density of the lizard interacting with the tested lizard (density-interact, $F_{1,30} = 5.46$, $P = 0.03$) but not by the population density of the tested lizard (density, $F_{1,30} = 1.24$, $P = 0.27$). After an interaction with an individual from high-density populations, lizards increased their time spent hidden (change = 132.28 ± 51.6 s.e., $P = 0.0156$ ; figure 5) while there was no significant change for interaction with a lizard from low-density populations (change = - 4.89 ± 42.03 s.e., $P = 0.91$ ; figure 5). The dispersal status of the tested and interacting lizards affected the change in time spent hidden (dispersal-interact, $F_{1,30} = 1.34$, $P = 0.26$, dispersal status, $F_{1,30} = 4.26$, $P = 0.05$, dispersal*dispersal-interact status, $F_{1,30} = 6.47$, $P = 0.02$) but the interactions between the dispersal status and the density treatments were not significant ($P > 0.20$ for all interaction between the dispersal status and the density treatments). Dispersers spent generally more time hidden after an interaction but this effect was only significant when

the interacting lizard was another disperser (contrasts, dispersing interacting lizards: $F_{1,30}$ = 4.44, $P$ = 0.04, non-dispersing interacting individuals: $F_{1,30}$ = 1.77, $P$ = 0.19). The changes in time spent moving and basking after an interaction were independent from the population densities and the dispersal status of the tested and interacting lizards ($P > 0.20$ for all simple effects and interactions). The body length of tested and interacting lizards did not affect behavioral modifications ($P > 0.68$ for the three behaviors observed) and the other effects remain the same when we added these covariates.

### Choice of thermoregulation spot

Lizards did not significantly choose a given spot depending on their population density (density: $F_{1,33}$ = 1.09, $P$ = 0.3047), but their choices were significantly affected by the population density of the interacting lizard (density-interact : $F_{1,33}$ = 5.18, $P$ = 0.0294). Lizards interacting with lizards from high-density populations changed more often of basking spot (high-density: 0.5 ± 0.11 ; low-density : 0.3 ± 0.10 ). The probability to change was also positively affected by the body length of the tested lizard ($F_{1,33}$ = 4.93, $P$ = 0.0333) but not affected by the body length of the interacting lizard ($F_{1,32}$ = 0.00, $P$ = 0.95). The dispersal status of the tested and interacting lizards did not affect the probability to change ($P > 0.10$ for all simple effects and interactions with the density treatments).

## Discussion

### Conspecific as a cue about habitat quality of surrounding areas

Conspecifics have been demonstrated to be a source of information for many behavioral decisions including mate choice, foraging activities and habitat selection (Galef and Giraldeau 2001; Doligez et al. 2002; reviewed in Valone and Templeton 2002; Danchin et al. 2004). For example, habitat quality is often assessed through the reproductive success of conspecifics during the exploration of new sites of reproduction (Boulinier and Danchin 1997;

Doligez et al. 1999). For species with restricted exploratory capacities, this strategy of information gathering is not available, and other mechanisms enabling access to this information should be favoured by natural selection. It has been therefore suggested that immigrants to a population might serve as sources of information on local conditions elsewhere through their morphology and behavior (Clobert et al. 2004; Aragon et al. 2006; Cote and Clobert submitted). This gives indirect information to residents about the suitability of other areas through information carried by conspecifics. Our results indeed showed that an individual modified its behavior depending on the dispersal status and on the population density of the conspecific encountered. This strongly suggests that some transfer of information about the population density of the lizard encountered is possible. Conspecifics might thus use interactions to acquire appropriate information and change accordingly their behavior as it has been demonstrated in other contexts (Aragon et al. 2006). Here, we observed two different behavioral responses depending on the experimental situation encountered.

After an interaction with a lizard from high-density populations, the time spent hidden is increased in the first experiment whereas lizards left more their basking spot in the second experiment. This difference in behavioral response probably reflects the offered possibility that individuals have to leave the place of interaction in the second experiment. Usually, high densities should induce high competition levels for food and space. Individuals leaving in such situations should have developed behaviors and/or physiology that might act as signals of population density. The high-density information carried by encounters from high-density populations might thus signal high level of social and nutritional stressors. When encountering such competitive individuals, two behavioral stress responses are predicted: to leave or to hide (Wingfield and Ramenofsky 1999). When moving is possible and not costly, as in our experimental set up, individuals should escape stressors and/or bad conditions (e.g.

high competition levels) by changing of location. Although the exact significance of the behaviors displayed in our experiments might be questioned, our results clearly revealed that the nature of the conspecific encountered, and especially the density of its population of origin, has some important effect on space use even after the physical presence of the conspecific encountered. Thereafter, space use, even when the encounter disappeared, is influenced by this information. The question of how the information is transmitted remains however open.

## Conspecifics' phenotype as cues about habitat quality?

Potentially, any particular feature of an individual can serve as a cue about the internal or external environment of this individual. For example, odor in mammals, insects and reptiles serve to mark territory and path to foraging or to signal sex while visual displays serve to advertise for dominance. These features can be observed by interacting and non-interacting individuals to make further choice (e.g. Deutsch and Nefdtz 1992; Gautier et al. 2006; Aragon et al. 2006a). Individuals living in high-density populations display particular morphological characteristics such as reduced body size or body condition (e.g. Massot et al. 1992; LeBlanc et al. 2001; Le Galliard et al. 2006) and could thus serve as cues about population density. While density treatment did not affect body condition in our study, it led to reduced body size. Although being significantly different between density treatments, body size is still largely overlapping such that assessing population density based on this simple criterion will often lead to erroneous decision. Moreover, body size of interacting individuals was not related to behavioral modifications. Morphological traits do not thus appear to be good candidates for a transfer of information in this species. Furthermore, as we did not observe any wounds or aggressive displays during the interactions, we could also discard aggressiveness as a source of information on density, at least in sub-adults. On the contrary, density-dependent behaviors constitute the best candidate as sources of information. Indeed,

individuals issued from high-density populations are more active. Previous studies on several species, including the common lizard, showed an increased activity induced by high-density (Rose 1981; McPeek and Crowley 1984; Lecomte et al. 1994; Ars et al. 2000). In high-density populations, resources (e.g. food, basking sites) are less available. These constraints often lead to high competition and/or interaction among conspecifics (e.g. Simon 1975; Morpurgo et al. 1993; Hansen et al. 1999). Decreased food availability and increased social interactions are considered as stressors in most species (Silverin 1998; Jacobson 1999; Lanctot et al. 2003; Commendant et al. 2003). It often entails an increased activity either to escape stressors or to increase foraging (Moore et al. 1987; Dufty and Belthoff 1997; Breuner et al. 1998; Cote et al. 2006). Indeed, food restriction and social stress is inducing the production of corticosterone, a stress hormone (Silverin 1998; Jacobson 1999; Lanctot et al. 2003; Comendant et al. 2003). Corticosterone elevation has been demonstrated to increase locomotion, daily activities and foraging in several species, including the common lizard (Moore et al. 1984; Dufty and Belthoff 1997; Breuner et al. 1998; Cote et al. 2006). In other words, an increased activity might be the cue by which other individuals assess the population density of conspecifics. However, this species inhabits a dense vegetation habitat such that relying on chemical cues rather than visual ones should be favored to acquired social information (Aragon et al. 2006). Indeed, as in most reptiles (Mason 1992; Cooper 1994) olfactory cues have been shown to be a crucial support of social information in the common lizard (Aragon et al. 2006; Léna et al. 2000). We cannot therefore exclude that olfactory cues might have been the support of information about population density. Further experiments are needed to better describe the exact nature of the information transfer.

## Dispersal and density of surrounding populations

The likelihood that individuals living in a population access to information about surrounding populations depends on the fact that residents are able to discriminate individuals visiting its population from other residents. As found in a previous study (Aragon et al. 2006), our results show that individuals distinguish and display a different behavior faced to a disperser than to a philopatric encountered. The assessment of dispersal status associated with a potential individual identification (e.g. through olfactory cues) allow residents to discriminate lizards from another population. Moreover, density-dependent information does not depend on the dispersal status of informants. In other words, a disperser induces the same behavioral modification related to its population density than a philopatric, and thus seems to carry similar density-related information. Furthermore, immigrants are expected to deliver an honest signal on their population of origin. We previously showed that resident and dispersing juveniles still recognized each other 6 months after the dispersal phase (Aragon et al. 2006) and that immigrants are imprinted by their population of origin (e.g. food, crowding, e.g. Meylan et al. submitted). Immigrants are therefore likely to constitute a reliable source of information on their population of origin. However, dispersers from high-density populations do not display increased activity in our study. The density-related information mediated by increased activity, previously proposed, sounds more questionable. Nevertheless, the number of dispersers used in our experiments might be too low to reveal such behavioral modifications.

While further experiments are needed to assess more deeply the role of conspecifics and immigrants in transferring information on surrounding population densities, our study illustrates that the transfer of density-related information at small spatial scales is existing. This density-related information is likely to influence space use and dispersal (Cote and Clobert submitted), and thus might have profound consequences on habitat selection theory.

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## TABLES

Table 1. Effects of population density and dispersal status on lizards' morphology after one year.

| | First Experiment | | Second experiment | |
|---|---|---|---|---|
| Factor | Body size | Body condition | Body size | Body condition |
| Density | **$F_{1,62} = 14.21$**** | $F_{1,61} = 2.23$ | $F_{1,38} = 0.17$ | $F_{1,37} = 3.39$† |
| Dispersal status | $F_{1,61} = 0.03$ | $F_{1,60} = 0.06$ | $F_{1,37} = 0.99$ | $F_{1,36} = 1.37$ |
| Density × dispersal | $F_{1,60} = 1.95$ | $F_{1,59} = 3.25$† | $F_{1,36} = 0.10$ | $F_{1,35} = 1.47$ |

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$

Table 2. Effects of population density and dispersal status on activities time after one year. Estimates are given for low-density populations ($D^-$) and non-dispersing (ND) lizard.

| | Time spent moving | | Time spent basking | | Time spent inactive | |
|---|---|---|---|---|---|---|
| Factors | Estimates ± s.e | Test statistics | Estimates ± s.e | Test statistics | Estimates ± s.e | Test statistics |
| Density ($D^-$) | -22.9 ± 21.33 | $F_{1,60} = 1.67$ | 15.6 ± 61.3 | $F_{1,61} = 0.06$ | 25.2 ± 40.5 | $F_{1,61} = 0.39$ |
| Dispersal status (ND) | -32.6 ± 14.6 | $F_{1,60} = 0.26$ | **-130.4 ± 64.9** | **$F_{1,62} = 4.03$*** | 47.8 ± 43.0 | $F_{1,62} = 1.23$ |
| Density × dispersal | **77.7 ± 24.6** | **$F_{1,60} = 10.01$**** | 25.8 ± 143.7 | $F_{1,60} = 0.03$ | -55.7 ± 94.7 | $F_{1,60} = 0.35$ |

† P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.0001

## Figures legends:

Figure 1. Time spent moving and density treatment. Mean time spent moving (seconds ± s.e.) depending on the density of the population where the lizard lives.

Figure 2. Time spent hidden and density-dependent interaction. Mean time spent hidden (seconds ± s.e) before and after an interaction depending on the population density of the lizard which were interacting with the tested lizard.

Figure 3. Probability of changing of basking spot after an interaction and density treatment. Mean Probability of changing of basking spot (± s.e) after an interaction depending on the population density of the lizard which were interacting with the tested lizard.

**Figure 1**

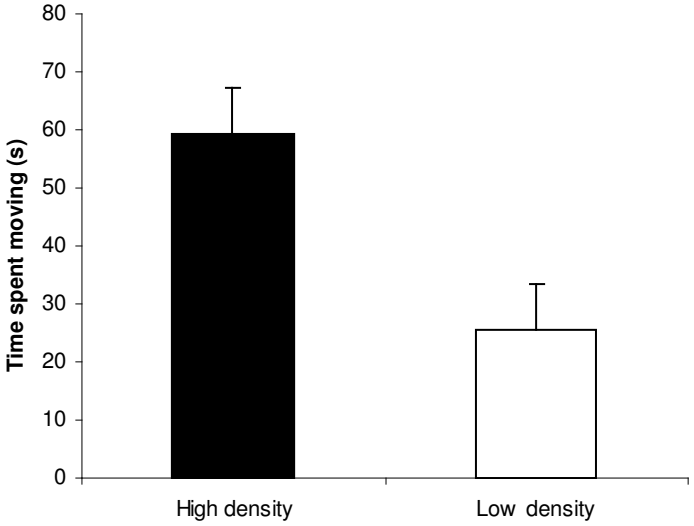



**Figure 2**

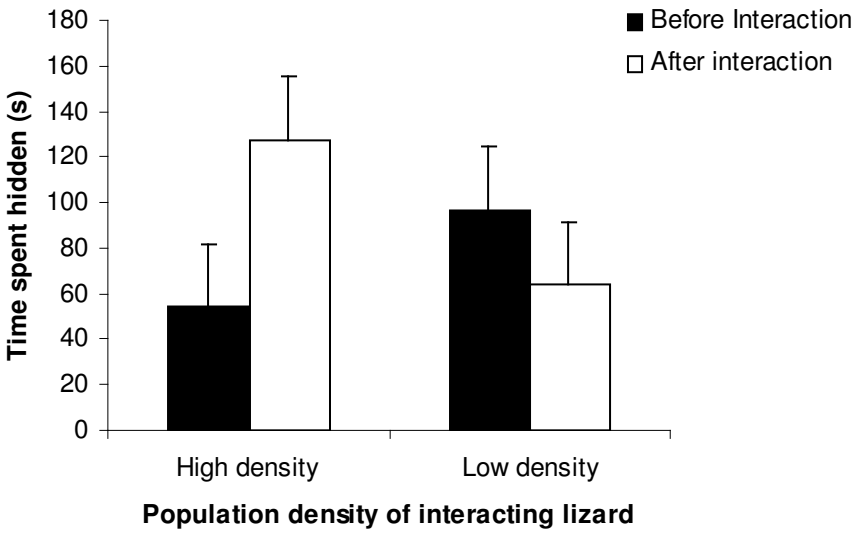
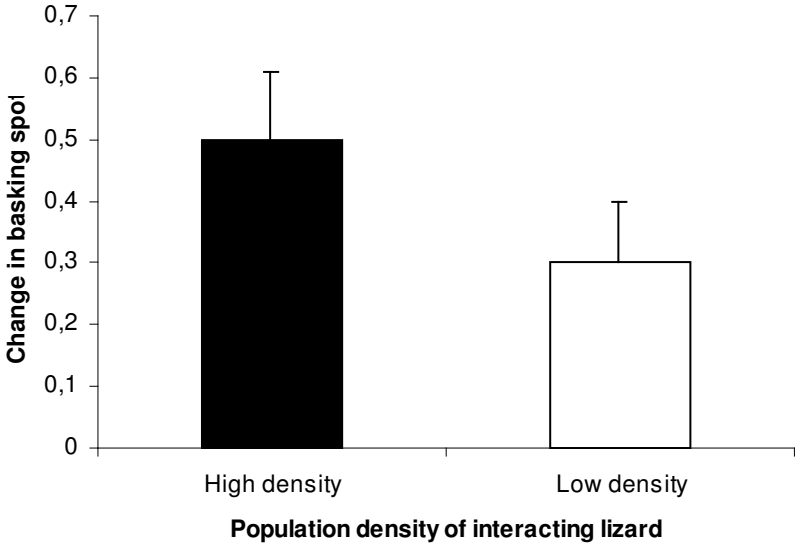


**Figure 3**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Change in basking spot
High density
Low density
Population density of interacting lizard

# MANUSCRIT 4

## Social personalities influence natal dispersal in a lizard

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# Social personalities influence natal dispersal in a lizard

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Animal personalities are common across taxa and have important evolutionary and ecological implications. Such consistent individual differences correlate with important life-history traits such as dispersal. Indeed, some environmental conditions are supposed to determine dispersers with a specific personality. For example, an increased density should promote the departure of individuals with less social tolerance. Therefore, we hypothesized that dispersers from high-density populations should primarily be asocial individuals, whereas dispersers from low-density populations should be social individuals. In the common lizard (*Lacerta vivipara*), we measured attraction towards the odour of conspecifics on juveniles at birth as a metric of social tolerance. We then released these juveniles into populations of different densities and measured dispersal and settlement behaviours with regard to social tolerance. One year later, we again measured the social tolerance of surviving individuals. The social tolerance is constant across time and strongly reflects the individual's dispersal and settlement patterns with respect to population density. These results strongly suggest that social personalities exist and influence dispersal decisions. Further studies will help to elucidate the proximate and ultimate determinants of social personalities.

**Keywords:** behavioural differences; personality; dispersal; sociability; habitat selection; common lizard

## 1. INTRODUCTION

The ecology of personality is a fast-growing field in animal behaviour (Dall *et al.* 2004; Sih *et al.* 2004). For several decades, psychologists have explored the considerable range of human and non-human personalities (reviewed in Gosling & John 1999; Gosling 2001), primarily in reference to a deviation from a norm. While such studies aimed to find a common origin of personalities to resolve human psychological problems (Gosling 2001), behavioural ecologists propose an adaptive framework to these presumed non-adaptive individual differences (Dall *et al.* 2004; Sih *et al.* 2004). 'Personality differences', defined as consistent individual differences across time and contexts, have been observed in numerous behaviours (Clobert *et al.* 1994; Verbeek *et al.* 1994; Marchetti & Drent 2000; Dingemanse *et al.* 2003*b*, 2004; Sih *et al.* 2004; Dall *et al.* 2004; Aragon *et al.* 2006). Personality differences have been found in exploration, aggressiveness, reactivity and boldness, and are observed across taxa and in both vertebrates and invertebrates (Dingemanse *et al.* 2003*b*; Sinn & Moltschaniwskyj 2005). While in many species some individuals avoid social interactions and others search for conspecifics (Gosling & John 1999), social personality, or sociability, has been rarely studied in non-human species and particularly with an ecological perspective (Gosling & John 1999).

Differences in personalities have been found to correlate with important life-history traits such as reproduction and dispersal (Fraser *et al.* 2001; Dingemanse *et al.* 2003*a*; Both *et al.* 2005). For instance, recent studies on Trinidad killifish and great tits revealed that natal dispersal distance is positively correlated to boldness (Fraser *et al.* 2001; Dingemanse *et al.* 2003*a*). Dispersal is a typical response to locally degrading conditions (Clobert *et al.* 2001). However, all individuals do not disperse with respect to the same environmental factor (Clobert *et al.* 2001). For example, competition among conspecifics or among kin can lead to the departure of particular phenotypes (Léna *et al.* 1998; Le Galliard *et al.* 2003; Moore *et al.* 2006), and dispersal has been shown to correlate with social behaviours such as cooperation (Sinervo & Clobert 2003; Le Galliard *et al.* 2005*b*). Recent theoretical and empirical work on the evolution of altruism, sociality and dispersal suggest links between dispersal and sociality (Sinervo & Clobert 2003; Le Galliard *et al.* 2005*b*; Sinervo *et al.* 2006*a*). For a long time, dispersal has been seen as a mean to avoid negative effects of intraspecific competition (Lambin *et al.* 2001; Clobert *et al.* 2004). Meanwhile, behavioural ecologists were demonstrating that settlement (i.e. habitat selection) probability was increased in the presence of conspecifics (Crespi & Taylor 1990; Lambin *et al.* 2001; Stamps 2001; Doligez *et al.* 2004). Two opposite responses to increasing density have presently been documented: a higher dispersal rate (reviewed in Lambin *et al.* 2001) and a higher settlement rate (Stamps 1991; Lambin 1994; Denno & Peterson 1995; Le Galliard *et al.* 2003). Various interpretations have been given to explain such varying responses of dispersal to density (reviewed in Lambin *et al.* 2001), but none have attempted to integrate findings from ecologists and behaviouralists. If density informs on both crowding and habitat suitability, then the sign of the relationship between dispersal and

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density is likely to be a function of the balance between increased competition and conspecific attraction (Clobert *et al.* 2004). As dispersal has either a genetic or a strong maternal determinism (Sinervo *et al.* 2006*a*), the above hypothesis militates for the existence of an individual variability in the responses to density, for example, along a trade-off between sociability (attraction towards conspecific) and associability (sensitivity to crowding). Several recent empirical findings militate for such a scenario. Individuals leaving a high-density population have been found to be phenotypically different from those leaving a low-density population (Léna *et al.* 1998). In a population density manipulation experiment, dispersers were found to have long-lasting behavioural differences with residents (Aragon *et al.* 2006). Similarly, in a colonization experiment, individuals colonizing empty habitats were found to display different phenotypes to those in adjacent occupied habitats (Le Galliard *et al.* 2005*a*). Therefore, we hypothesized that the phenotypic differences between resident and dispersing individuals might be associated with differences in social personalities and that dispersers from high-density populations should primarily be asocial individuals, whereas dispersers from low-density populations should be social individuals.

To test this hypothesis, we used the common lizard as our model system. This species has a density-dependent dispersal probability, which can be either positive or negative (Massot *et al.* 1992; Le Galliard *et al.* 2003). Dispersers have been shown to have particular phenotypes different from non-dispersers in term of morphology (e.g. body size and body condition), physiology (stress response) and reaction to olfactory cues (Clobert *et al.* 1994; Léna *et al.* 1998; de Fraipont *et al.* 2000; Le Galliard *et al.* 2003; Meylan & Clobert 2004; Meylan *et al.* 2004). These particular phenotypes could be associated with documented variability in the sensitivity of individuals to changes in social contexts like density of conspecifics (Aragon *et al.* 2006). Thus, the presence of both positive and negative reactions to these social contexts might reflect different social personalities. The results from these previous studies allow us to predict the existence of social personalities associated with dispersal decisions in the common lizard. To characterize social personalities, we measured the attraction of individuals towards the odour of conspecifics at birth, a metric of social tolerance. We then released these individuals as juveniles into semi-natural populations of different densities and measured juvenile dispersal attempts and the settlement success of these individuals during the following year. Finally, the social tolerance of surviving individuals was again measured after 1 year to estimate the stability of the social personality type across time and contexts.

## 2. MATERIAL AND METHODS

### (a) *Species, study site and rearing conditions*

The common lizard (*Lacerta vivipara*; Jacquin 1787) is a small Lacertidae (adult snout–vent length: males, 40–60 mm; females, 45–75 mm) inhabiting humid habitats in Eurasia (Avery 1962). Lizards become active between late March and the beginning of April (Massot *et al.* 1992) and begin hibernation in late September. Females produce offspring once a year and laying occurs in June–July. Juveniles are independent of their mother immediately after birth and disperse after 10 days of age on average (Massot *et al.* 2002).

This experiment was conducted using lizards living for the previous 3 years in semi-natural populations at the Ecological Research Station of Foljuif (Seine-et-Marne, 48°17′ N, 2°41′ E; Le Galliard *et al.* 2003). These semi-natural populations occur in enclosures (10 m × 10 m) protected from avian and mammalian predation, which are connected to a one-way 20 m dispersal corridor. The enclosure size is equivalent to the individual's core home range size and the length of the corridor corresponds to the minimal dispersal distance observed in natural populations (Boudjemadi *et al.* 1999). A trap is located at the extremity of each corridor to catch dispersing lizards. The lizards caught in the corridor trap while leaving their enclosure were considered 'dispersers'.

In June 2004, we captured all lizards maintained in the enclosures. Males were released a few days after the capture, whereas females were maintained in laboratory until they gave birth. To provide each lizard with the same standardized environment (e.g. food, water, heat, social interactions), pregnant females were individually housed in plastic terrariums (25 × 15.5 × 15 cm, containing a 3 cm litter; Le Galliard *et al.* 2003). In one corner of the terrarium, a bulb provided heat for thermoregulation and light from 9.00 to 12.00 and 13.00 to 17.00 h. A piece of cardboard and a plastic tube were provided to allow the lizards to hide. Female lizards gave birth in the terrariums and all offspring were thereafter released into semi-natural populations as described in §2*c*. On the day of birth, all offspring were measured for body length (nearest millimetre), tail length (nearest millimetre) and body mass (nearest milligram), and their sex was determined by counting ventral scales (Lecomte *et al.* 1992). For later identification, juveniles were individually marked by toe-clipping.

### (b) *Reaction to conspecific odours*

Adult males were selected as the source of odour for two reasons. Previous studies showed that juvenile philopatry was increased in the presence of an adult male odour while it was reduced in the presence of adult female odour (Léna *et al.* 1998), suggesting that adult male odours are socially attractive to juveniles. Second, while juveniles are sensitive to the odour of adult males when selecting a shelter (i.e. juveniles prefer a shelter with or without an odour depending on their origin and morphology), they are indifferent to the odour of other categories of individuals (Aragon *et al.* in press); thus, the important social context again appears to be based on male odour. To obtain olfactory cues, six different pairs of adult males were maintained in the same terrarium for the whole laying period. We collected odours on a piece of absorbent paper placed on the floor of the terrarium. We also created six other terrariums structurally similar to the previous ones and submitted to the same conditions as inhabited terrariums, but they were vacant. This method allows us to obtain pieces of paper differing only in the presence of olfactory cues. We changed the pieces of paper after utilization to avoid a second utilization. The odour was thus collected during 6 days which is sufficient to obtain olfactory cues (Aragon *et al.* in press). All neonates were tested the day after their birth. Behavioural measurements were performed in plastic terrariums of the same dimensions as maternal terrariums. A piece of egg box (shelter) was added in the centre of the terrarium allowing the lizards to hide and a bulb provided heat for thermoregulation. Each lizard was tested separately in a cleaned terrarium, beginning



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alternatively with the paper with the odour or with the paper without the odour. This allows us to completely separate the effect of olfactory cues from all other potential effects of experimental procedure. We placed the odorized paper under the shelter. The lizard could choose between staying under the shelter with a conspecific's odour or leaving the shelter and being exposed. We quantified the time spent under the shelter when faced with a conspecific's odour as a metric of social tolerance. The same observer performed all the tests. Each lizard was introduced in a terrarium with the piece of absorbent paper and left for 5 min to acclimate. Then, the time spent hidden under the shelter was measured during 10 min with the software 'The Observer'. After these measurements, the piece of paper was changed, but lizards were not moved. After 5 min, we again measured the time spent hidden under the shelter during 10 min. The lizard was then removed and placed in the terrarium of its mother. We reiterated the same procedure for all offspring. When it was impossible to test all neonates born within the same day, we randomly selected at least two juveniles per family (one male and one female) for testing. The tests done within the same day were temporally homogeneous for individual characteristics and subsequent density treatment ($p > 0.2$).

In April 2005, 32 one-year old lizards (i.e. two lizards per enclosure) were captured during a 4-day session. Lizards were individually maintained as described previously. Two days after capture, we measured the reaction to conspecific odour of all these lizards. The same protocol used with neonates was applied to measure the reaction as well as to obtain olfactory cues. For 17 of these 32 one-year old lizards, the reactions to conspecific odour were also tested at birth. This allowed us to test for the stability of the behaviours during the first year of life.

### (c) *Field study*

All males and females came from populations kept in semi-natural conditions in Foljuif (see §2*a*). In June 2004, 96 adult males and 176 adult females were captured. We then created 16 semi-natural populations with two density levels. Population densities were either high (adults: 8 males, 12 females; yearlings: 10 males, 10 females and 34 juveniles) or low (adults: 4 males, 6 females; yearlings: 5 males, 5 females and 17 juveniles) with each density level being applied to eight populations (Le Galliard *et al.* 2003). All 16 populations had age and sex structures similar to natural populations (Massot *et al.* 1992) and individual characteristics (i.e. body size, body mass and date of birth for juveniles) were not different between levels of density treatment for all age and sex classes ($p > 0.5$ for all). Males and all yearlings were released 7 days after their initial capture, whereas juveniles and their mothers were released 2 days after laying. The release of juveniles and females (just after females' laying) began three weeks after capture and spread over three weeks. However, 85% of the juveniles were released within two weeks after the laying started. We maintained the ratio between density treatments (1 : 2) during all the laying period by releasing juveniles accordingly, such that densities were different during all the releasing period. Moreover, no dispersal event was observed before all juveniles were released. Dispersal was monitored daily from release of the first family through hibernation. Dispersers were measured (body size and weight) and released in another population the same day. We released dispersers randomly in a high- or low-density population. High- and low-density populations received exactly the same number of juveniles, but juveniles were randomly assigned to a population. Therefore, on average, juveniles released in high- and low-density populations did not react differently to odour at birth (density in arrival population: $F_{1,11} = 0.23$, $p = 0.64$; density in arrival population × density in initial population: $F_{1,8} = 0.45$, $p = 0.52$). This procedure allowed us to measure a second dispersal attempt, and thus settlement decision depending on the densities in the destination and initial populations. After release in their destination population, dispersers had the possibility to disperse again in the same manner as the first dispersal. If a disperser again left its new population, we removed it from the experiment and we released it in a non-experimental enclosure. When a juvenile disperse from a population, an immigrant was released in the following days. It allows us to maintain the density constant, and thus to avoid changes in the intensity of density treatments.

### (d) *Statistical analyses*

Our analyses aimed to determine whether the dispersal status of lizards depended on the reaction to conspecific odours and to the density of their population. The dispersal status was analysed using the GLIMMIX procedure in SAS v. 8.02 (Littell *et al.* 1996) with a logit link function and a binomial error term. The fixed effects were the density of the population, the odour-dependent time spent hidden (time spent hidden when the piece of paper contained odours minus time spent hidden when the piece of paper contained no odour) and their interaction. We also added individual covariates (body length and body mass) and sex as additional factors. The random effects were populations nested within the density treatment and family nested within the population. The probability of a second dispersal event was analysed on all the juveniles released (juveniles tested for the reaction to odour and juveniles not tested) using the GENMOD procedure in SAS v. 8.02 with a logit link function and a binomial error term. The fixed effects were the density of the 'natal' population, the density of the arrival population, sex and all interaction terms. Dispersers were released equally in all populations and there were no family biases. Independent contrasts were performed for the first and second dispersal attempts using the CONTRAST option of each statistical procedure used to analyse dispersal probability. The correlation between reactions to conspecific odour at birth and after 1 year was tested using the MIXED procedure in SAS v. 8.02. This allowed us to add a population effect as a random factor and the density treatment as a fixed effect. We could thus test for environmental dependence of behavioural reaction. The assumptions of these models were verified on residuals. Likelihood ratios were used to test the significance of each factor or interaction term. Simplification of all these models was made using backward elimination of the non-significant terms. Significance level was set at $p = 0.05$.

## 3. RESULTS

### (a) *Reaction to conspecific odour throughout the life*

The reaction towards conspecific odour measured in April 2005 (1 year after the beginning of the experiment) was positively correlated with the reaction measured at birth ($n = 17$, $F_{1,7} = 13.17$, $p = 0.0084$, estimate $0.25 \pm 0.07$, $R^2 = 0.31$, figure 3). The density of the population did not affect the reaction after 1 year nor the correlation between



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Table 1. Natal dispersal probability depends on the reaction to conspecific odour at birth and the density in the population. (Dispersal probability was modelled with mixed effects logistic regressions using the GLIMMIX macro in SAS. The initial model included the density of the population, the odour-dependent time spent hidden (time spent hidden when the piece of paper contained odours minus time spent hidden when the piece of paper contained no odour), sex and body size at birth as fixed factors as well as the random effects of enclosure nested within the origin of immigrants and family nested within enclosure. The final model was obtained by backward elimination, dropping in a stepwise process all non-significant effects. Statistical tests were type III *F*-tests for fixed effects.)

| | natal dispersal probability |
|---|---|
| density | $F_{1,14}=2.10$, $p=0.17$ |
| reaction to conspecific odour at birth | $F_{1,145}=1.45$, $p=0.23$ |
| density×reaction to conspecific odour at birth | $F_{1,145}=5.79$, $p=0.0174$ |

the reactions throughout the life (density: $F_{1,6}=0.66$, $p=0.45$; reaction measured at birth×density: $F_{1,5}=0.01$, $p=0.92$). One year later, the reaction to odour did not also depend on the population of the juvenile (Wald *z*-tests–population: $z=0.77$, $p=0.22$; reaction measured at birth×population: $z=0.51$, $p=0.30$).

### (b) *Reaction to olfactory cues and dispersal decision*

The probability to disperse did not depend on the density of the population nor on the reaction to odour alone (table 1). However, the interaction between the density and the reaction to odour was significant (table 1). Independent contrasts revealed that the dispersal probability from low-density populations is positively related to the odour-dependent time spent hidden (i.e. difference of time spent hidden; $F_{1,145}=3.84$, $p=0.05$) or a high attraction for conspecific odour. In contrast, this relationship tended to be negative in high-density populations ($F_{1,145}=2.39$, $p=0.12$). A high dispersal probability from low-density populations was thus correlated to a high attraction for conspecific odour.

Non-dispersing juveniles of the two density treatments did not differ in the time spent with the male odour (residents: $F_{1,145}=0.95$, $p=0.33$; figure 1). Among dispersers, those from low population density spent more time with male odour than those from high population treatments (contrasts, dispersers: $F_{1,145}=8.58$, $p=0.004$; figure 1). Sex, body length and date of birth had no significant effect on the probability of dispersal (sex: $F_{1,143}=0.04$, $p=0.83$; body length: $F_{1,143}=0.36$, $p=0.55$; date of birth: $F_{1,143}=0.57$, $p=0.44$) but lizards in better condition at birth dispersed more (body condition: $F_{1,145}=4.95$, $p=0.03$).

### (c) *Settlement of dispersers*

Dispersers from low- and high-density populations (i.e. 52 juveniles) were introduced randomly in high- and low-density populations. All of the 16 populations received dispersers and we homogenized the number of dispersers across populations. Among all dispersers, 17% of dispersers left their arrival populations. The probability

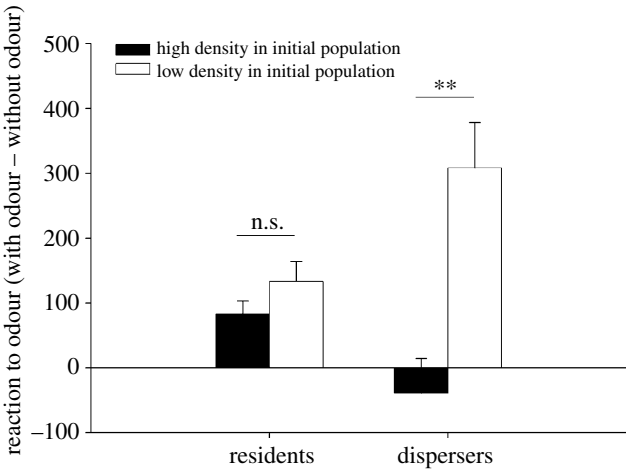


Figure 1. Reaction to olfactory cues at birth depending on densities in initial populations and dispersal status. Differences of time spent hidden with the olfactory cues minus the time spent hidden without the olfactory cues. Mean difference (seconds ± s.e.) in relation to density treatments and dispersal status is shown (n.s. $p>0.05$; $^{**}p<0.01$).

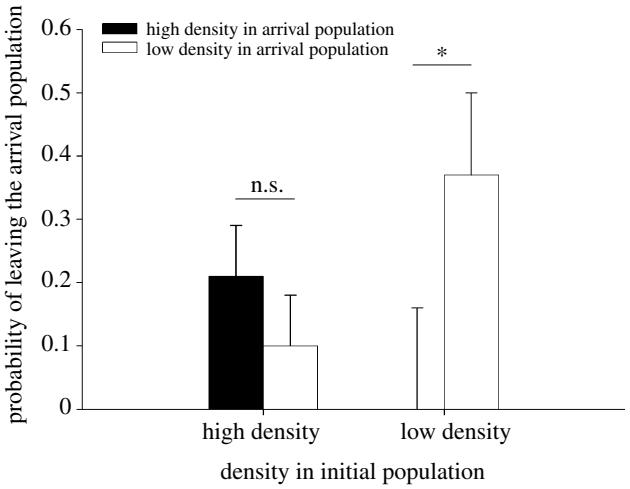


Figure 2. Settlement in arrival populations and interaction between densities in initial and in arrival populations. Differences between density treatments in the probability that a disperser leaves his arrival population. Mean probability (± s.e.) in relation to density treatments is shown (n.s. $p>0.05$, $^{*}p<0.05$).

of leaving their arrival population was dependant on the interaction between density of the arrival populations and density of the initial populations (initial density×arrival density: $\chi_1=6.33$, $p=0.0119$; figure 2). Independent contrasts showed that dispersers from low-density populations settled more in high-density populations than in low-density populations ($\chi_1=5.21$, $p=0.02$) and the opposite pattern was observed, but was not significant for dispersers from high-density populations ($\chi_1=1.25$, $p=0.2641$). Interestingly, no dispersers coming from low-density populations and introduced in high-density populations left their arrival populations. Female dispersers left their arrival populations more often than male dispersers ($\chi_1=4.31$, $p=0.0379$). All these effects remained significant when we added date of dispersal in the model and there was no relationship between date at dispersal and the probability of settlement ($\chi_1=1.32$, $p=0.25$).



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## 4. DISCUSSION

### (a) *Consistent social personalities*

The reaction towards the odour of a pair of males can be interpreted either as juvenile sensitivity to interactions among males and/or to their simple presence. During another experiment, we quantified some characteristics of the six pairs of males used to collect odour (e.g. males' body size, body condition, coloration, age, bites). Juveniles did not show any reaction towards the variation in males' characteristics within the pair ($p > 0.5$ for effects of males' body size, body condition, coloration, age and bites on reaction towards odour). If the juvenile sensitivity was linked to adult male interactions, pairs of males displaying strong interactions should not induce the same reaction as pairs of males displaying weak interactions (e.g. no bites). Therefore, only male presence is a more probable explanation for variation in sensitivity, which suggests that the juvenile reaction towards male odour measures social tolerance or phobia. In this study, we used the odour of adult males only, but juvenile reactions could be related to the sex of the signaller. As stated in §2, adult females seem to be perceived as important competitors by juveniles since they promote juvenile dispersal (Léna *et al.* 1998), and experimental manipulation of density has indeed shown that females are closer competitors of juveniles (yearlings) than adult males (Massot *et al.* 1992; Lecomte *et al.* 1994). Furthermore, the sensitivity of juveniles was not dependent on their gender, and we should not have observed such a result if the signal was indicating the gender of the adult. These points strongly suggest that males are an indicator of something else than their gender alone. One year later, the same individuals displayed a similar behaviour towards the presence of male odours as they did at birth and this reaction did not depend on the environmental conditions (i.e. density and population) undergone during juvenile growth. This demonstrates that the individual's response to a same social context is constant through time and context, a trait that is a characteristic of personalities. The above two results strongly suggest the existence of social personalities in this lizard species. Social personalities, here measured by the reaction to odour, might be part of a more general behavioural pattern. Indeed, personality traits, such as boldness, aggressiveness and exploration, are correlated types of behaviour (Verbeek *et al.* 1996; Marchetti & Drent 2000; Sih *et al.* 2004) which might correspond to a suit of behavioural traits defining some individual strategies. Some individuals therefore exhibit a set of personality traits likely to constitute behavioural syndromes (Sih *et al.* 2004), which can be genetically and/or developmentally controlled (Dufty *et al.* 2002; Sih *et al.* 2004). Our study develops the idea that behavioural syndromes may also exhibit a social component, which might be seen as complementary to other personality traits such as boldness, aggressiveness and exploration. For example, we might predict that, according to the pattern observed in other species, and particularly in humans, 'asocial' lizards will also be shyer and less aggressive individuals (figure 3).

### (b) *Social personalities, dispersal and habitat selection*

Individuals who dispersed from low- and high-density populations had different social phenotypes. Dispersers from low-density populations were attracted to the odour of males, while dispersers from high-density populations tended to be repulsed by male odour. Indeed, only dispersers from high-density populations reacted negatively to male odour. These results indicate that juveniles have different social personalities, which affect their reaction to social context (i.e. density). Some juveniles leave to search for more socially attractive or dense environments when faced with reduced social interactions. These individuals display social attraction to odour at birth. In contrast, other juveniles prefer to leave environments with too much social interaction. These individuals are repulsed by the presence of conspecifics at birth.

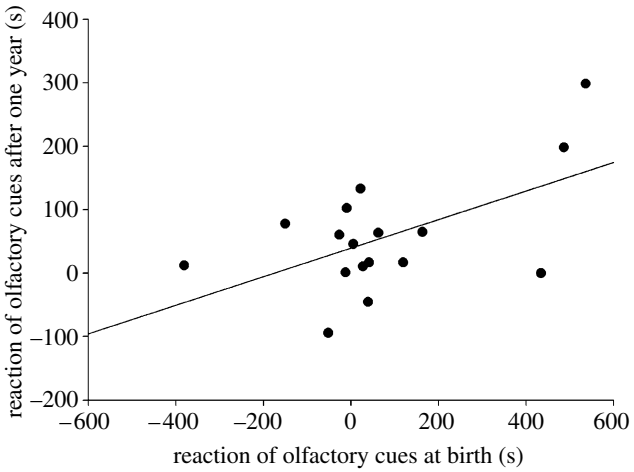


Figure 3. Reactions to olfactory cues through life. Relationship between reaction to olfactory cues at birth and after 1 year. Linear regression is shown.

If the above scenario is true, we should expect dispersers from low-density populations to settle more often when released in high-density destinations than when released in low-density destinations. This is indeed what we found. This result reinforces the idea that dispersers from low- and high-density populations exhibit different social personalities and search for different social habitats. All dispersers from low-density populations settled when they were released in a high-density population. Even if the number of dispersers was low (i.e. 52 dispersers), this dependence of settlement on the density in natal and arrival populations is completely concordant with the other results and strongly supports the hypothesis. The lack of secondary attempts for the dispersers originating from low-density populations and released in high ones is not the result from these individuals dying before being able to move again, because they were found to survive for at least a month after release. Furthermore, all secondary dispersal attempts were completed within 5 days of the release in their novel populations.

Population density is known to affect dispersal in numerous ways. Here, we showed that the perception of density varies among individuals, which results in strong variability of which individuals disperse with respect to natal density. Here, the age and context invariance of the behavioural response to adult male odour strongly suggests the existence of fixed social personalities (Aragon *et al.* in press; Meylan & Clobert submitted), which is subsequently associated with dispersal decisions. Low densities repulse some individuals while attract others. Our results contradict the assumption that every disperser prefers the same habitat. While several theoretical reviews



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have recently developed this idea (Stamps 2001; Clobert *et al.* 2004), experimental tests are still quite scarce. To explain such differences, both proximate and ultimate causes of dispersal should be considered as well as their associated costs and benefits (Massot *et al.* 2002). For example, costly kin interactions are selecting for the departure of pioneer individuals which are not sensitive to density (and might display their own particular behavioural syndrome; Cote *et al.* submitted; Léna *et al.* 1998; Le Galliard *et al.* 2003) while, even within the same species, beneficial kin-like interactions will promote philopatry with individuals displaying mutualistic or even altruistic behaviours. In the latter case, such behaviours have been proved to be adaptive (Sinervo & Clobert 2003; Sinervo *et al.* 2006*a*,*b*).

Intraspecific competition is likely to act in a different way. Indeed, high-density populations can indicate either a good quality habitat (conspecific attraction) or costs linked to conspecific competition. Both have been documented in our species (Massot *et al.* 1992; Léna *et al.* 1998; Le Galliard *et al.* 2003). First, conspecific attraction would be beneficial if the fitness of juveniles is increased in high-density populations (Shields *et al.* 1988; Stamps 2001). Proximate mechanisms of conspecific attraction have been shown to be reduced predation rate, reduced costs of settlement and increased future reproductive success (Shields *et al.* 1988; Stamps 2001). Conversely, conspecific repulsion might be explained by high levels of competition and aggressiveness (Shields *et al.* 1988; Stamps 2001). The latter causes should mostly affect lizards with low competitive abilities and low aggressive level, which might correspond to 'asocial' individuals. However, one might ask why/how such different personalities (syndromes) are maintained within a population. Recently, theoretical models have shown that the polymorphism of dispersal strategies can be generated and maintained whenever the direction of selection was different within the different patches within a metapopulation (Doebeli & Ruxton 1997). If variations in densities are sufficient to generate such differences in selective pressure within a metapopulation, one can then predict the existence of different dispersal strategies, i.e. different dispersal-based personalities or syndromes. The widespread existence of density-dependent dispersal strategies is however likely to depend on the possibility that a species has to acquire some knowledge about the density in its own and in surrounding populations. Some recent findings militate for such a possibility. First, common lizards have been recently demonstrated to acquire environmental information during social interactions (Aragon *et al.* in press; Boudjemadi *et al.* 1999) either through private or public (socially acquired) information. Second, there is evidence that they can recognize the dispersal status of conspecifics (Aragon *et al.* *a*,*b*). In this way, social personalities might reflect variable abilities in acquiring public information (Marchetti & Drent 2000) or variable balance between private and public information-based decision.

The existence of such social personality polymorphism might have a considerable impact on understanding the evolution of condition-dependent dispersal strategies. In our case, for example, the relationship between density and dispersal can then be either positive or negative depending on the frequency of each type of individual, and it offers an alternative explanation to the recently reported variations in the direction of the correlation between density and dispersal (Lambin *et al.* 2001; Le Galliard *et al.* 2003; Clobert *et al.* 2004). More generally, dispersers with different personalities (or behavioural syndromes) might be a good research avenue for understanding the multiple causes of dispersal evolution (Gandon & Michalakis 2001; Clobert *et al.* 2004) and the way they interact. Recent studies indeed propose that different selective pressures induce the evolution of dispersers with specific phenotypes in terms of morphology, physiology and also behaviour (Léna *et al.* 1998; Le Galliard *et al.* 2003; Meylan *et al.* 2004; Moore *et al.* 2006), leading to complex and variable associations among these phenotypic variables. Different selective pressures resulted in specific traits associations or 'phenotypic syndromes' conferred to philopatric or dispersing individuals such that it minimizes the cost associated with each strategy. For example, the common lizard seems to exhibit three dispersing phenotypic syndromes: (i) colonizers (i.e. dispersers with high success in empty habitat (Cote *et al.* submitted), mainly promoted by kin competition), (ii) dispersers attracted by low-density populations, and (iii) dispersers attracted by high-density populations. Such variations are also to be expected in philopatric strategies (i.e. sneaking, mutualistic or altruistic behaviour). These three types of dispersers should affect the composition of a metapopulation, both at a spatial and at a temporal scale. Indeed, an empty habitat should be colonized by the first type of dispersers, then dispersers attracted by low densities should reinforce the population, and finally dispersers of the third type should be attracted by high densities.

Our results should therefore have important implications in the understanding of metapopulation dynamics and dispersal evolution with respect to crowding. Particularly, it proposes an alternative explanation to opposite dispersal density-dependant responses. More generally, it might strongly change our views on metapopulation functioning and resilience. However, more research will be needed to better understand how and under which conditions these social personalities are produced, as well as their impact on metapopulation functioning and evolution.

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# MANUSCRIT 5

# Carotenoid-based colours reflect stress response in the common lizard

Soumis à *Proceedings of the Royal Society B: Biological Sciences*

# Carotenoid-based colours reflect stress response in the common lizard

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Key words: carotenoid-based coloration, carotenoid-availability, corticosterone, honest signalling, physiological stress response

Short title: carotenoid-based signals reflect stress response

## *Abstract*

Current studies suggest that carotenoid-based coloration might be a signal of stress resistance. Here, we test whether the common lizard's (*Lacerta vivipara*) ventral coloration signals the capacity to cope with stressors and/or carotenoid availability. We show that experimentally elevated blood corticosterone levels, which induce an animal's physiological stress response, led to increased redness. This shows that animals that produce more corticosterone have redder coloration, suggesting that the ventral coloration signals an animal's capacity to cope with stressors. Additionally, carotenoid ingestion did not affect the carotenoid-based colour expression. This suggests that carotenoid-based coloration is not always limited by carotenoid intake or uptake and that the corticosterone effect on coloration is most likely mediated by increased mobilisation of stored carotenoids. Our study thus suggests that the bright yellow-orange coloration may not necessarily signal foraging efficiency or immune competence, but also reflects an animal's ability to cope with stressors. Consequently, positive selection acting on redness selects for the ability of an individual to cope with stressors and thus for animals with efficient stress responses.

## Introduction

A growing body of studies shows that variation in carotenoid-based coloration depends on dietary access and may thus reveal an individual's foraging capacity (Kodric-Brown 1989; Hill 1992; Tschirren *et al.* 2003; Fitze *et al.* 2007), since carotenoids cannot be synthesised by animals (Goodwin 1984). Furthermore, other environmental factors such as general nutritional condition (Kodric-Brown 1989; Tschirren *et al.* 2003; Fitze *et al.* 2007) and health status (Milinski & Bakker 1990; Brawner *et al.* 2000; McGraw & Hill 2000) affect ornamental carotenoid pigmentation. Carotenoids are important for the immune system (Bendich 1989; Fitze *et al.* 2007) as they are used as antioxidants, which scavenge oxygen radicals (Blount *et al.* 2001; Alonso-Alvarez *et al.* 2004). The multiple functions may create trade-offs in carotenoid-limited animals. For example, during an immune challenge, animals may favour using carotenoids for immune function over using them for coloration (Blount *et al.* 2003; McGraw & Ardia 2003; Fitze *et al.* 2007). Similarly, it is suggested that animals preferentially use carotenoids for physiological stress responses instead of using them for coloration, potentially explaining why stressed animals usually exhibit reduced coloration (Milinski & Bakker 1990; Belthoff *et al.* 1994; Brawner *et al.* 2000; Blount *et al.* 2001). However, it is unclear whether the reduced coloration is indeed the result of a trade-off for carotenoids, or whether it is the result of reduced carotenoid-intake, e.g. due to reduced food availability or due to interactions with other animals, preventing them from foraging. In contrast, it has been shown that corticosterone, which initiates a physiological stress response (Axelrod & Reisine 1984) and thereby modifies an animal's behaviour and physiology (Wingfield & Ramenofsky 1999; Moore & Jessop 2003), positively affects survival (Comendant *et al.* 2003; Cote *et al.* 2006). This suggests that the physiological stress response *per se* may have a positive effect on the coloration and that the carotenoid-based coloration may indicate an animal's capacity to produce corticosterone and thus the capacity to cope with stressors.

Here, we investigate the effects of the physiological stress response on the common lizard's (*Lacerta vivipara*) ventral coloration. We activate an animal's physiological stress response by experimentally

67 increasing the blood corticosterone levels and compare the colour change with a control group. We
68 predict a negative colour change in the corticosterone-treated lizards if the physiological stress
69 response is responsible for the usually observed colour reduction. Further, to experimentally test
70 whether a trade-off for carotenoids between coloration and the physiological stress response is
71 responsible for a negative colour change, we provided half of the lizards of each treatment group with
72 additional carotenoids. We predict a negative colour change in the control-fed lizards with an activated
73 stress response, and no or a less negative colour change in the carotenoid-fed lizards with an activated
74 stress response.
75 However, if the physiological stress response is an adaptive tool to cope with stressors (Wingfield &
76 Ramenofsky 1999; Comendant *et al.* 2003; Cote *et al.* 2006), we predict a positive colour change in
77 lizards with increased stress responses. If carotenoid availability is an important determinant of
78 coloration, we also predict a positive colour change in the carotenoid-fed lizards.
79

## *Material and Methods*

### Species description

The common lizard is a small ovoviviparous *Lacertidae* inhabiting peat bogs and moist heath land. The ventral coloration of males ranges from yellow to red with dark spots. In females, the ventral coloration ranges from cream to "dark yellow-orange" with few dark spots (Bauwens *et al.* 1987). In stressful situations, the coloration of the common lizard fades and becomes more yellow (Le Galliard *et al.* 2007). The function of ventral coloration has rarely been investigated, but Bauwens *et al.* (1987) suggested that it might play an important role in inducing courtship patterns and Czeczuga (1980) speculated that the yellow-orange coloration stems from carotenoids, but clear evidence is lacking. We therefore first investigated which pigments are responsible for the bright yellow-red ventral coloration and thereafter investigated whether the ventral coloration might be correlated with individual characteristics as in many other species.

### Determination of colour pigments

### Sample collection

To analyse which pigments are responsible for the yellow–orange belly coloration of the common lizard, we analysed the skin contents of nine adult common lizard males originating from an experimental population located at the Ecological Research Station of Foljuif (Seine-et-Marne, 48°17'N, 2°41'E). After capture, the males were decapitated and the ventral skin was detached from the muscles. Thereafter, the skins were weighed and individually stored in 1ml acetone at -80°C until analyses.

### Carotenoid extraction and HPLC analysis

Carotenoids were extracted from both the skins and the acetone solution. The skins were washed in hexane, dried, weighed and homogenized in methanol in a Retsch MM 2000 micronizer (Hann, Germany) with ZrO containers, at 27 Hz for 15 minutes. The residue was filtered (GHP Acrodisc 13

mm) and the methanol was evaporated (ThermoSavant SPD111V, New York, USA). The carotenoid residue was finally dissolved in 10µl tetrahydrofuran (THF) and 90µl of the mobile phase (70:30 acetonitrile:methanol) and immediately analyzed by High Performance Liquid Chromatography (HPLC, see below).

The sample (60-80µl) was injected with isocratic mobile phase into a RP-18 column (YMC Europe GmbH, Schermbeck, Germany) fitted on a ThermoFinnigan (San Jose, USA) HPLC system with a PS4000 ternary pump, an AS3000 autosampler, and an UV6000 diode-array UV/VIS detector. Chromatograms were obtained and analysed with ChromQuest 4.0 software (ThermoFinnigan, San Jose, USA). The carotenoids were identified and quantified using lutein and zeaxanthin standards. All concentrations are calculated as µg/g dry skin.

## Pigments responsible for the yellow-orange belly coloration

After putting the skins into acetone, the yellow-orange skin coloration disappeared within one hour and became a bluish colour. This shows that the yellow-orange skin coloration of common lizards stems from carotenoids and not from other pigments (McGraw *et al.* 2004). In total, the skin contained 54.09µg±4.67s.e. carotenoids per gram of tissue, among them lutein, zeaxanthin, astaxanthin, and canthaxanthin. Based on the dry weight of the skins (0.031g ±0.002s.e.), we estimated that the yellow-orange belly coloration derives from an absolute amount of 1.641µg±0.149s.e. of carotenoids. The skin's carotenoid concentration was negatively correlated with the lizard's hue ($F_{1,7}$=6.265, $p$=0.041) and explained 47.2% of the variance.

## Effects of stress response and carotenoid availability on belly coloration

## Pre - experimental procedures

Early in July 2002, we captured 88 adult males and 88 adult, pregnant females in four different lizard populations on the Mont-Lozère in the Cévennes (1500m asl., Massif Central, Southeastern France, 44°00'N, 3°45'E). Lizards were moved to the laboratory at the Ecological Research Station of Foljuif (Seine-et-Marne, 48°17'N, 2°41'E) where they were individually housed in terrariums (for details see

Fitze *et al.* 2005). Terrariums were numbered for individual identification and they were randomly distributed with respect to lizard body size and population of origin (all $p>0.6$). Lizards were maintained in the laboratory until all females gave birth. Thereafter, we measured the snout-vent length (SVL) and the tail length of each lizard to the nearest 1mm, the body mass to the nearest 0.002g, the number of ticks attached, and the coloration (see below).

## Experimental procedures

On August 2nd (hereafter referred to as day one), the experiment started. We randomly attributed lizards to the different treatments. The body mass of each lizard was measured on the second and on the 25$^{th}$ day of the experiment.

### *Corticosterone application*

On day one, eleven lizards per population and sex were randomly assigned to a corticosterone group and the remaining eleven lizards to a control group. The corticosterone treatment consisted of a daily application of 4.5µl of sesame oil mixed with corticosterone (3µg of corticosterone/µl oil). Control treated lizards were treated with 4.5µl of sesame oil only (Cote *et al.* 2006). The treatment was applied each evening on the back of the lizards starting on the second day and ending on day 23. The transdermal corticosterone application led to a three- to four-fold increase in basal blood corticosterone levels in both males and females (Cote *et al.* 2006). Thus, the induced increase was within the natural range of acute stress that can raise blood corticosterone levels of reptiles more than ten times the basal levels (Tyrrell & Cree 1998).

### *Carotenoid supplementation*

On day one, eleven lizards per population and sex were randomly assigned to a carotenoid supplementation group and the remaining eleven to a control group using a two-factorial design with corticosterone and carotenoid treatment as factors. Lizards of the carotenoid supplementation group were provided with the carotenoids lutein, zeaxanthin, and *ß*–carotene which are the most common carotenoids in green plants and which are naturally ingested when eating lepidopteran larvae (Partali *et*

156 *al.* 1987). The carotenoid ratio (lutein: 77.4%, zeaxanthin: 6.1%, and *ß*–carotene: 16.5% of total
157 carotenoid content) with which lizards were fed was similar to the one found in lepidopteran larvae
158 (Partali *et al.* 1987). We diluted 818mg lutein/zeaxanthin beadlets, that contained 5.58% lutein and
159 0.44% zeaxanthin, and 130mg *ß*–carotene beadlets (containing 7.5 % *ß*–carotene) in 100ml $H_2O$;
160 0.03ml of this solution was then injected into a moth larva using a sterile syringe. Since lizards can eat
161 more than six moth larvae (average weight 200mg) within 24 days and since lepidopteran larvae
162 contain an average of 0.0033mg carotenoids/g larvae (Partali *et al.* 1987), our carotenoid
163 supplementation corresponds to a carotenoid dose between five and 25 times the dose eaten under
164 semi-natural conditions. Since carotenoids provoke no negative effects (Olson & Owens 1998; for a
165 review), supplementing lizards with a higher-than-naturally ingested dose is unlikely to cause health
166 problems. Previous to supplementation, we injected the control moth larvae with 0.03 ml of a solution
167 consisting of 948mg control beadlets dissolved in 100ml $H_2O$. Control beadlets consisted of the same
168 ingredients as the carotenoid beadlets, with the exception of the carotenoids. All lizards were fed a
169 single moth larva every five days starting on the third day of the experiment and ending on the 23$^{rd}$ day
170 of the experiment. Only larvae of similar body mass were used (254mg±12.64s.e.). Live larvae were
171 presented to the lizards between 11:30 a.m. and 12:30 p.m. Lizards either immediately accepted
172 (attacked and ate the larvae) or refused the food item. In the latter case, we left the larva in the
173 terrarium and checked in the evening if the larva had been eaten. If not, they were removed from the
174 terrarium. This procedure avoided confounding a lizard's appetite with a refusal due to human induced
175 stress and it made sure that the exact number of larvae eaten during the entire experiment was known.
176

177 **Colour measurement**

178 Before the start of the experimental procedures and after the end of the experimental procedures, the
179 lizard's belly coloration was measured using a miniature spectroradiometer (USB2000, Ocean Optics
180 Inc., Dunedin, FL, USA) and a Xenon light source (PX-2 and R400-7-UV/VIS, Ocean Optics Inc),

over the 300nm to 700nm visual spectrum. Reflectance was measured in relation to a diffuse white standard (WS-1, Ocean Optics Inc.) uniformly reflecting 98-100% over the spectral range. For each lizard, we took a colour measurement on the breast, in the middle of the belly, and on the anal plate. The colour measurements corresponded to the average coloration on an approximately $1mm^2$ surface, avoiding black spots.

Since saturated carotenoid (and melanin) pigmentation remove virtually all reflectance in ultraviolet wavelengths (Hill & McGraw 2006), we restricted the analyses to the human visible spectrum (400nm–700nm). Using Endler's (1990) segment classification method, we derived objective estimates of hue (0-360°: 0°=red; 60°=yellow), chroma (0-100%), and brightness (0-100%), and used the means of these for the three measured body parts. The colour measurements were repeatable, as evidenced by repeating three times the same measurement on 218 lizards (Hue: $F_{216,434}$=6.99, $p$<0.0001, $r$=0.66; Chroma: $F_{217,437}$=7.01, $p$<0.0001, $r$=0.67; Brightness: $F_{217,437}$=10.5, $p$<0.0001, $r$=0.76; Lessells & Boag 1987).

## Statistics

We applied mixed model ANCOVAS to analyse correlations between phenotypic traits and coloration. The population was modelled as a random factor and sex as a fixed factor. The covariates SVL, tail length, body mass, and tick number were introduced as covariates and also their interactions with sex. The effects of carotenoid and corticosterone treatment on the lizard's ventral colour change (coloration after minus coloration before the experiment) were analysed using mixed model ANCOVAS with sex, carotenoid, and corticosterone treatment as fixed effects, population as a random effect and food consumption and body mass change as covariates. For the analysis of the treatment effects on the body mass change, we applied an ANOVA and for the effects on appetite, we applied a GLIMMIX with a poisson error and a log link using SAS v8.2.0. (Littell *et al.* 1996). For all analyses, the full model included all parameters and their interactions and the final model was determined using backward elimination. The assumptions of the models were tested. All measurements were taken blindly with

206 respect to treatment and the significance level was set at $p_{\text{two-sided}} \leq 0.05$ for all tests. One control treated
207 female died during the experiment and was therefore excluded from the analyses.
208

## *Results*

### Effects of corticosterone and carotenoids on belly coloration

During the experiment, the hue of the lizard's ventral coloration decreased from 71.6°±0.8s.e. to 67.6°±0.7s.e., i.e. towards a longer wavelength (more red) in all treatment groups (Fig.1A, $p \leq 0.046$) and the corticosterone treated lizards became significantly redder than the control lizards (table 1, Fig. 1A), as expected from increased carotenoid absorbance (Hill & McGraw 2006). The corticosterone treatment did not affect chroma and brightness (table 1, Fig. 1B,C) and there were no significant interactions between corticosterone treatment and the other parameters (all $p>0.1$). Furthermore, sex, population, food consumption, and body mass change did not significantly affect the colour change. Carotenoid supplementation did not change the ventral coloration (table 1, Fig. 1A-C) and there were no significant interactions between carotenoid treatment and the other parameters (all $p>0.1$). The changes in both chroma and brightness of all treatment groups were not different from zero (Fig.1B, C, all $p \geq 0.16$). Over the course of the experiment, lizards ate an average of 3.989 larvae ±0.129s.e. and thus the carotenoid fed lizards ate an average of 0.071mg ±0.002s.e. carotenoids. The average amount of ingested carotenoids corresponded to 43 times the amount of carotenoids responsible for the ventral coloration. The relative carotenoid doses supplied were higher than in two previous studies on great tits (*Parus major*) (Fitze *et al.* 2003b; Tschirren *et al.* 2003) and the carotenoids used were exactly the same. The power to find an effect of similar effect size ($d$) as the one encountered in Tschirren *et al.* (2003) ($d$=1.073; $\delta$=7.1) or in Fitze *et al.* (2003b) ($d$=0.841; $\delta$=5.6) was 100%.

### Effects of corticosterone and carotenoids on body mass and appetite.

Corticosterone-treated lizards ($F_{1,172}$=5.95, $p$=0.016, estimate: 0.099±0.041s.e.) showed enhanced appetite. There were no differences in appetite between carotenoid-fed and control-fed lizards ($F_{1,157}$=0.06, $p$=0.805; estimate: -0.010±0.040s.e.s). The interaction between carotenoid and corticosterone treatment was not significant ($F_{1,137}$<0.01, $p$=0.958). Females, in contrast to males,

($F_{1,172}$=33.28, $p$<0.001, estimate: 0.235±0.041s.e.) showed enhanced appetite. Population and all interactions did not significantly affect appetite ($p$>0.2).

Females increased their body mass while the body mass of the males remained almost constant ($F_{1,173}$=27.66, $p$<0.001, estimate: 0.055±0.010s.e.). The body mass change did not differ between corticosterone ($F_{1,172}$=0.51, $p$=0.478, estimate: -0.007±0.010s.e.) and carotenoid treatments ($F_{1,171}$=0.39, $p$=0.533, estimate: 0.007±0.001s.e.) and the interaction between carotenoid and corticosterone treatment was not significant ($F_{1,160}$=0.51, $p$=0.476). There were no significant differences between populations. None of the interactions were significant ($p$>0.05).

## Belly coloration in relation to sex and individual quality

Males (N=88) showed higher chroma (male: 0.325±0.007s.e., female: 0.268±0.008s.e.) and lower brightness (male: 0.141±0.003s.e., female: 0.218±0.003s.e.) than females (N=87, table 2), and there were no sex differences in hue. A discriminant analysis showed that the three colour parameters allowed the correct determination of a lizard's sex in 92.6% of the cases. There was a negative correlation between body mass (estimate: -3.905±1.586s.e.) and hue, indicating that individuals of higher body mass were redder (table 2). Tail length, body size, tick number, and the population did not predict hue (table 2). When checking for collinearity by including and excluding the different covariates in differing order, the final models were the same as those presented in table 2. The quadratic terms of body size, tail length, body mass, and tick number were not significant ($p$>0.1).

## Discussion

Stressed animals usually show reduced coloration and several studies suggest that the physiological stress response might be the cause of the observed reduction. However, it has recently been demonstrated that corticosterone, which initiates the physiological stress response, positively affects survival (Comendant *et al.* 2003; Cote *et al.* 2006). Corticosterone is therefore believed to be an adaptive tool that reduces the negative effects of stressors (Wingfield & Ramenofsky 1999; Comendant *et al.* 2003; Cote *et al.* 2006). This indicates that an animal's capacity to produce corticosterone in response to stressors reveals its capacity to cope with stressors. The finding that corticosterone might be an adaptive tool that reduces the negative effects of stressors further suggests that stressors (e.g. through negative effects on foraging) rather than the physiological stress response might be responsible for the observed colour reduction.

Our experiment demonstrates that the physiological stress response *per se* positively affects the lizard's carotenoid-based ventral coloration. Consequently, animals that are able to produce more corticosterone will be able to cope with more or more intense stressors. Our results thus indicate that the common lizard's ventral coloration signals an individual's capacity to cope with stressors. Positive selection acting on redness will therefore select for individuals that are better at coping with stressors. This supports the growing evidence that corticosterone production is an adaptive tool that reduces the negative effects of stressors in contrast to previous hypotheses suggesting that stressors negatively affect coloration due to the physiological stress response and/or due to a trade-off between the physiological stress response and the coloration for rare carotenoids (von Schantz *et al.* 1999). We simulated a situation with a long-lasting activation of the physiological stress response, as observed during repeated or chronic exposure to stressors (Lin *et al.* 2004). The behavioural adaptations to long-lasting stressors differ from acute stressors and involve, for example, a shift of energy substrates from storage sites to the blood stream (Vellucci 1997). Because neither carotenoid-availability nor body condition change explained the observed colour change in corticosterone-treated individuals, our

279 results suggest that corticosterone may have led to a reallocation of the carotenoids. This hypothesis is
280 supported by the fact that pigmentation is often under the control of hormones (such as androgens or
281 oestrogen) (Hill & McGraw 2006), suggesting that corticosterone may have a direct or indirect effect
282 on other hormones, leading to increased assimilation and/or allocation of carotenoids. However, to
283 understand the ultimate mechanisms by which corticosterone affects carotenoid-based coloration,
284 further experiments are needed.
285 In contrast to studies on birds and fishes (Milinski & Bakker 1990; Hill 1992; Blount *et al.* 2003;
286 Tschirren *et al.* 2003), carotenoid supplementation did not induce a colour change. We fed lizards the
287 carotenoids present in their skin and in their natural diet and the power of detecting a similar effect as
288 found in three independent carotenoid supplementation studies was 100% (nestlings were provided
289 with exactly the same carotenoids (Fitze *et al.* 2003a; Tschirren *et al.* 2003; Fitze *et al.* 2007).
290 Therefore, our results imply that carotenoid feeding does not affect the carotenoid-based coloration in
291 this species. Two hypotheses may explain these results. First, we found metabolized carotenoids in the
292 lizard's skin, suggesting that the lizards might have been unable to metabolize the ingested
293 carotenoids. It is, however, unlikely that time or energy availability might have constrained the
294 metabolization because the treatment lasted for 20 days, the lizards were active every day, and they
295 had access to *ad libitum* food. Second, the amount of carotenoids deposited may be mainly genetically
296 determined, as found in another lizard species (Sinervo *et al.* 2001), where coloration has been shown
297 to reveal an individual's life-history strategy (Sinervo *et al.* 2001; Sinervo & Clobert 2003), as
298 suggested for the common lizard (Vercken *et al. in press*). However, the corticosterone treatment
299 importantly affected the coloration, showing that the common lizard's belly coloration is at least partly
300 environmentally determined.
301 Our results indicate that the hue of the common lizard's ventral coloration is a condition-dependent
302 signal, since corticosterone treatment significantly modified the coloration and since we found a
303 positive correlation between a lizard's body condition and its redness. This finding is consistent with

304 studies on birds and fishes, where carotenoid-based coloration has been shown to be a condition-
305 dependent trait that honestly reflects an individual's quality (Hill 1991; Blount *et al.* 2003; Fitze *et al.*
306 2003a; Tschirren *et al.* 2003). This suggests that carotenoid-based coloration may have similar
307 functions in reptiles and thus that carotenoid-based coloration might be a condition-dependent trait in
308 many more animal taxa than believed so far.
309 In conclusion, our study suggests that the common lizard's carotenoid-based yellow-orange belly
310 coloration signals an individual's capacity to cope with stressors. Consequently, positive selection
311 acting on redness selects for the ability of an individual to cope with stressors and thus for animals
312 with efficient stress responses, rather than for optimal carotenoid foraging or optimal carotenoid
313 allocation. This result is in clear contrast to many studies investigating carotenoid-based coloration and
314 it suggests that carotenoid availability is not always the most important source of variation for colour
315 traits where carotenoids are involved.
316

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323

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Tables

Table 1. Effects of carotenoid supplementation and corticosterone treatment on colour change in hue, chroma, and brightness.

| Variable | hue | | chroma | | brightness | |
|---|---|---|---|---|---|---|
| | teststatistic | *p* | teststatistic | *p* | teststatistic | *p* |
| Carotenoid | $F_{1,164}<0.01$ | 0.981 | $F_{1,162}=0.225$ | 0.636 | $F_{1,168}=1.588$ | 0.209 |
| Corticosterone | $\mathbf{F_{1,168}=8.549}$ | **0.004** | $F_{1,161}=0.030$ | 0.863 | $F_{1,161}<0.01$ | 0.989 |
| Sex | $F_{1,167}=1.210$ | 0.273 | $F_{1,166}=0.600$ | 0.440 | $F_{1,165}=0.200$ | 0.655 |
| Number larvae eaten | $F_{1,166}=2.430$ | 0.121 | $F_{1,167}=2.986$ | 0.086 | $F_{1,166}=0.183$ | 0.669 |
| Body mass change | $F_{1,165}=0.157$ | 0.693 | $F_{1,168}=0.779$ | 0.379 | $F_{1,167}=1.735$ | 0.190 |
| Population | $F_{3,161}<0.01$ | 0.981 | $F_{3,163}=0.901$ | 0.442 | $F_{3,162}=0.074$ | 0.974 |

Table 2. Sex differences in coloration and correlations with body size, body condition, and parasite infestation. Given are the results from an ANCOVA with sex as a fixed factor, population as a random factor, and SVL, tail length, body mass, and tick number as covariates. The final model was determined using backward elimination and is plotted in bold.

| Variable | hue | | chroma | | brightness | |
|---|---|---|---|---|---|---|
| | teststatistic | *p* | teststatistic | *p* | teststatistic | *p* |
| sex | $F_{1,169}$=0.458 | 0.499 | **$F_{1,173}$=29.422** | **<0.001** | **$F_{1,173}$=327.894** | **<0.001** |
| SVL | $F_{1,171}$=0.802 | 0.372 | $F_{1,169}$=0.746 | 0.389 | $F_{1,172}$=1.595 | 0.208 |
| tail length | $F_{1,172}$=2.872 | 0.092 | $F_{1,168}$=0.256 | 0.614 | $F_{1,171}$=0.869 | 0.353 |
| body mass | **$F_{1,173}$=6.066** | **0.015** | $F_{1,167}$=0.048 | 0.828 | $F_{1,170}$=0.024 | 0.878 |
| tick number | $F_{1,170}$=0.955 | 0.330 | $F_{1,166}$=0.008 | 0.931 | $F_{1,169}$=0.015 | 0.902 |
| population | $F_{3,166}$<0.001 | 1.000 | $F_{3,170}$=1.564 | 0.200 | $F_{3,166}$<0.001 | 1.000 |

## *Figure legends*

Fig.1. Colour change in A) hue, B) chroma, and C) brightness in relation to carotenoid and corticosterone treatment. Means ±s.e. of the colour change (colour after treatment – colour before treatment) are given. For statistics see table 1.

**Figure 1A**

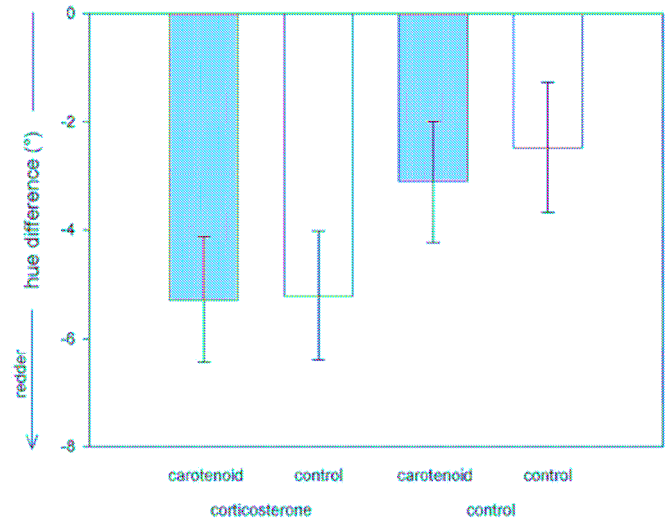



**Figure 1B**

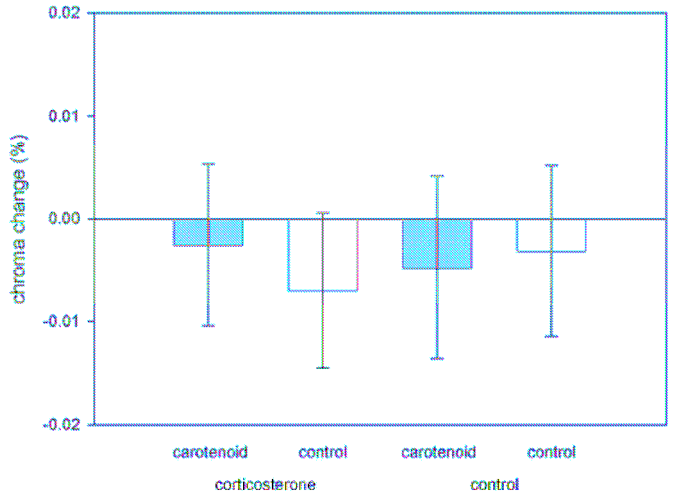
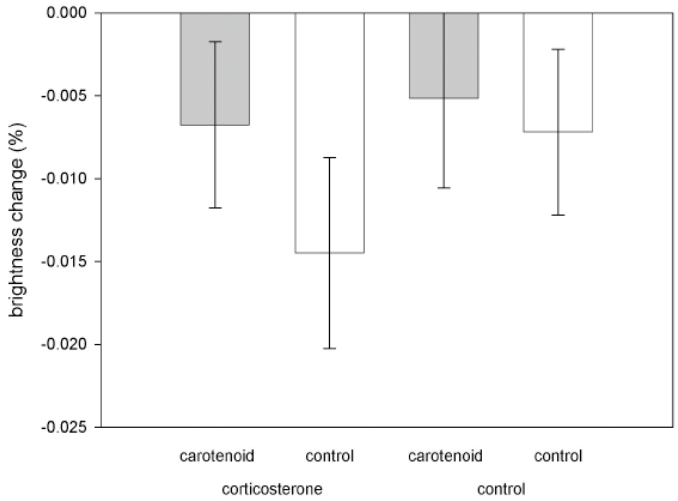



**Figure 1C**



# MANUSCRIT 6

# Experimental enhancement of corticosterone levels positively affects subsequent male survival

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# Experimental enhancement of corticosterone levels positively affects subsequent male survival

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**Abstract**

Corticosterone is an important hormone of the stress response that regulates physiological processes and modifies animal behavior. While it positively acts on locomotor activity, it may negatively affect reproduction and social activity. This suggests that corticosterone may promote behaviors that increase survival at the cost of reproduction. In this study, we experimentally investigate the link between corticosterone levels and survival in adult common lizards (*Lacerta vivipara*) by comparing corticosterone-treated with placebo-treated lizards. We experimentally show that corticosterone enhances energy expenditure, daily activity, food intake, and it modifies the behavioral time budget. Enhanced appetite of corticosterone-treated individuals compensated for increased energy expenditure and corticosterone-treated males showed increased survival. This suggests that corticosterone may promote behaviors that reduce stress and it shows that corticosterone per se does not reduce but directly or indirectly increases longer-term survival. This suggests that the production of corticosterone as a response to a stressor may be an adaptive mechanism that even controls survival.


*Keywords:* Corticosterone; Stress; Survival; Behavior; Common lizard; *Lacerta vivipara*; Activity; Food consumption

## Introduction

In response to stressful conditions, animals modify their behavior and physiology to avoid or balance negative effects of stress (Wingfield and Ramenofsky, 1999). A widespread physiological response is the production of glucocorticoids by the adrenal cortex (Harvey et al., 1984). This production leads to modifications in different physiological and behavioral processes (Greenberg and Wingfield, 1987; Lance, 1990; Silverin, 1998; Wingfield and Ramenofsky, 1999; Moore and Jessop, 2003) usually associated to enhanced energy consumption. Specifically, there is an increase of the energetic expenditure associated to greater catabolic processes (Holmes and Phillips, 1976). Beside many studies investigating the physiological and behavioral consequences of corticosterone in laboratory conditions (Sapolsky et al., 2000), some studies were conducted under field conditions in birds and reptiles (e.g., Astheimer et al., 1992; Breuner et al., 1998; Belliure et al., 2004; Moore and Mason, 2001, reviewed in Wingfield and Ramenofsky, 1999). Corticosterone, which is a widespread glucocorticoid in vertebrates, is shown to decrease reproductive and social activity and is suggested to increase locomotor activity in several vertebrates (Greenberg and Wingfield, 1987; DeNardo and Licht, 1993; Breuner et al., 1998, see also Astheimer et al., 1992; Moore and Jessop, 2003). Enhanced locomotor activity usually leads to better foraging capacity and to increased dispersal (Huey et al., 1984; Bennett and Huey, 1990; de Fraipont et al., 2000; Clobert et al., 2000), suggesting that corticosterone modifies behavior in order to directly or indirectly enhance survival (Wingfield and Ramenofsky, 1999; Breuner and Hahn, 2003). Increased dispersal may be an optimal strategy to escape stressful small-scale events that persist over a long time. To disperse

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would however be less adaptive if the stressful event only lasts for a short period or if conditions are not better, or even worse, in the potential dispersal area. It is therefore not surprising that long-lasting stressors (e.g., high animal density, or deviating climatic variables) have been suggested to provoke different physiological and behavioral responses than acute stressors (Silverin, 1998).

It is known that long-lasting stressors often lead to constantly enhanced corticosterone levels (Pravosudov et al., 2001; Romero and Wikelski, 2001), and that they may have negative consequences affecting immunocompetence, neural degeneration, or mortality (Morici et al., 1997; Berger et al., 2004, reviewed in McEwen et al., 1997 and in Sapolsky et al., 2000). Furthermore, long-lasting stress is frequently associated with increased energy expenditure (Pravosudov et al., 2001; Romero and Wikelski, 2001) and thus should be compensated for (Tataranni et al., 1996; Kitaysky et al., 2003). Some studies showed that enhanced stress might be compensated for by increased food consumption (reviewed in Sapolsky et al., 2000). For example, Lin et al. (2004) showed that corticosterone-treated broiler chickens increased their energy expenditure and consumed more food relative to their body weight. This suggests that corticosterone mediates the compensatory behavior and thus that releasing corticosterone into the blood may be an adaptive response to stressors.

In contrast to this hypothesis, several clinical studies and some observational field studies showed that stressors increase the blood corticosterone levels as well as mortality (McEwen et al., 1997; Morici et al., 1997; Romero and Wikelski, 2001; Eriksen et al., 2003). While many laboratory studies mainly investigate the physiological costs and thus exclude interactions with behavior, ecology, and the social environment, they usually do not disentangle the effects of the stressor and the effects of the corticosterone per se. For this reason, it is possible that the increased mortality in the stressed group would have been even higher without the presence of the increased blood corticosterone levels and thus that corticosterone may have positive effects on survival. Evidence that producing corticosterone might be an adaptive strategy to enhance survival and individual fitness comes from two field studies where corticosterone was exogenously administered on lizards (Sinervo and DeNardo, 1996; Comendant et al., 2003). These studies disentangled the effects of stressors and the effects induced by corticosterone in female lizards and found that the survival of the corticosterone administered females was enhanced in one, but not all years. Since the positive effect was found in one single year and since several other studies suggest that corticosterone may have negative but not positive effects, the effects of corticosterone are still far from understood (e.g., McEwen et al., 1997; Sapolsky et al., 2000). Consequently, evidence that corticosterone may be an adaptive mechanism that enhances survival is needed.

Here, we experimentally test the effect of long-lasting enhanced blood corticosterone levels on activity, body mass change, food consumption, and survival of adult male and female lizards, independent of the stressors. According to the current experimental evidence, we predict greater energy expenditure, enhanced food consumption, and enhanced activity for lizards treated with corticosterone.

## Methods

### *Species, study site, and breeding conditions*

The common lizard (*Lacerta vivipara* Jacquin, 1787) is a small lacertidae (adult snout-vent length: males 40–60 mm, females 45–75 mm) inhabiting humid habitats in Eurasia. It eats small insects, spiders, and earthworms (Avery, 1962) and its behavior is cryptic and difficult to observe under natural conditions (Clobert et al., 1994). Lizards become active in late March–beginning of April (Massot et al., 1992) and hibernation starts in late September. The winter survival of lizards in good body condition is usually higher than that of those in poorer body condition (Sorci and Clobert, 1999).

Prior to the experiment, in June 2002, we collected 176 adult (>1 years old) common lizards (88 males and 88 pregnant females) from 4 different populations in Southern France (all of them were located in the vicinity of the Mont Lozère, France, 44°27′ N, 3°44′ E). The collection of both sexes allowed for the determination of sex-differences in the stress response. For later identification, lizards were individually marked by toe-clipping. To provide each lizard with the same standardized environment (food, water, heat, social interactions), lizards were individually housed in plastic terrariums (25 × 15.5 × 15 cm, Le Galliard et al., 2003) containing a litter of 3 cm at the Ecological Research Station of Foljuif (Seine-et-Marne, 48°17′ N, 2°41′ E). In one corner of the terrarium a bulb provided heat for thermoregulation and light from 9:00 a.m. to 12:00 a.m. and from 1:00 p.m. to 5:00 p.m.. An egg carton and a plastic tube were added allowing the lizards to hide. Lizards were able to behave normally and escaping behavior (e.g., scratching on the walls) was rare (1,3% of the time during behavioral test). The authors attest the adherence to *the National Institutes of Health Guide for Care and Use of Laboratory Animals*. Female lizards gave birth in the terrarium and all offspring were thereafter released into semi-natural populations. After the last female gave birth (approximately 1 month after capture), all lizards were kept for another 2 weeks under the same standardized conditions. Thereafter the described experiment was started (July 2002).

### *Experimental corticosterone application*

44 females and 44 males (11 lizards of each population and of each sex) were randomly chosen and treated with corticosterone, while the remaining 44 females and 44 males were placebo treated. Because temperature is very important

for reptiles (Huey, 1974) and since it might be heterogeneous in the rearing room, we randomly distributed the same number of treatments and sexes per shelf and floor. There was no effect of the position (shelf and floor) on treatment, sex, body size, and body mass ($P > 0.45$ for shelf, floor, and all interactions). There were no morphological differences between the treatment groups (snout-vent length: $F_{1,173} = 0.04$, $P = 0.83$ and body mass: $F_{1,173} = 0.01$, $P = 0.91$).

The corticosterone treatment consisted of a daily application of 4.5 μl of sesame oil mixed with corticosterone (3μg of corticosterone per μl of oil), while the placebo treatment consisted of a daily application of 4.5 μl of sesame oil only. The application was realized in the evening on the back of the lizards daily for 22 days (for more details see Meylan et al., 2003) starting on the second day of the experiment. Hormonal treatments were applied in the evening for two reasons. First, the temperature in the terrariums decreased during the evening so the lizards were less active and more easily handled. Second, lower temperature reduced the risk of evaporation of the solution before it crossed the skin. This non-invasive method is similar to that described by Knapp and Moore (1997). It has been frequently used in the common lizard and has been shown to enhance basal corticosterone levels (Meylan et al., 2003; Belliure et al., 2004). Meylan et al. (2003) found that basal blood corticosterone levels of free-living females that were housed in the laboratory for 1 day averaged 21.64 ng/ml (max. 101.97 ng/ml). In June 2002, we additionally captured another 49 females and 21 males in two natural populations located in the vicinity of the Mont Lozère (France, 44°27′ N, 3°44′ E) to investigate sex differences in basal blood corticosterone levels. To allow the lizards to recover from capture-induced stress, they were as well housed in the laboratory for 1 day before blood sampling. The blood corticosterone levels were analyzed using the same method as described in Meylan et al. (2003). The basal corticosterone levels averaged: 77.03 ± 5.44 ng/ml (range: 1 to 181 ng/ml), and there were no significant differences between the sexes ($F_{1,66} = 1.58$, $P = 0.21$). In Meylan et al.'s study, the same transdermal corticosterone application that was used in this experiment was applied daily for 20 days. It led to an increase of the blood corticosterone levels within 1 h. Thereafter, the blood corticosterone levels remained at a similar level over the subsequent 2 days, and rose to an average of 281.9 ng/ml that remained almost constant over the remaining 15 study days (Meylan et al., 2003). Thus, transdermal corticosterone application led to a five- to ten-fold increase of the basal blood corticosterone levels and to an average level being 100 ng/ml above the blood concentration measured in natural populations. Our manipulation does probably not yet correspond to pharmacological doses but to high physiological doses because it was most likely still within the naturally occurring range of acute stress that can rise blood corticosterone levels of reptiles more than ten times the basal levels (e.g., Tyrrell and Cree, 1998). During the indoor experiments and after release into the semi-natural populations, we omitted measuring the blood corticosterone levels because taking blood would most likely have affected the survival of the lizards (Meylan et al., 2003) and because data on the effects of administering corticosterone during a similar time period (June–July) and for a similar number of days (20 days) already exists (Meylan et al., 2003).

### *Body mass measurement and food consumption*

Each lizard was offered 1 *Pyralis* sp. larva every 5 days starting on the second day of the experiment. Only larvae of similar body mass were used for feeding (254 mg ± 12.64 SE). No food was present in the terrariums and terrariums were closed with grids of narrow width of mesh. Consequently, lizards were able to eat food provided by us only. Alive larvae were presented to the lizards with pliers between 11:30 and 12:30. Lizards either immediately accepted (attacked and ate the larvae) or refused the food item. In the latter case, we left the larva in the terrarium and we checked in the evening if the larva had been eaten. This procedure avoided confounding the appetite with a refusal due to human induced stress. The body mass of each lizard was measured with a precision of 2 mg both on the first day of the experiment (the day before the first feeding) and on the 24th day of the experiment (two days after the last feeding). Water was available ad libitum.

### *Activity*

Activity was measured in the rearing terrarium on the 19th day of the experiment. As lizards spent the night below the egg carton, in the ground, or in the tube, they were hidden to the observer. Each 15 min starting on 9:00 a.m. until 12:00 a.m., a naive observer noted if lizards were active and thus visible (out of the egg carton, out of the ground, or out of the tube). If they were visible, the observer distinguished between four behaviors: basking below the light (upright head position and increased respiration, see Carpenter and Ferguson, 1977; Huey, 1982 for a precise description), moving (walking around in the terrarium), scratching (de Fraipont et al., 2000), or being immobile (see Lecomte (1993) for a completed review of behaviors). An inactive lizard (not moving, scratching or basking) was defined as being immobile. A lizard grating on the walls of the terrarium or in the soil was defined as scratching (de Fraipont et al., 2000). After emergence, we counted the number of times a lizard showed a given behavior (basking, scratching, moving, being immobile). The time of emergence is considered as the time when a lizard left his overnight shelter for the first time.

### *Survival*

At the end of August 2002 (two days after the last corticosterone application), lizards were released into 5

outdoor enclosures. Enclosures contain of 10 × 10m of natural habitat being enclosed by plastic walls and being protected from terrestrial and avian predators (Lecomte and Clobert, 1996). All lizards were recaptured by hand in April 2003 over 8 successive days. Body mass and snout-vent length was measured. Captured lizards were brought to the laboratory where they were housed until the capture was finished. All lizards were recaptured within the first two capture days. The escape-proof enclosure and the absence of alive lizards during the subsequent six capture days guaranteed that all survivors were collected. Because the common lizard is living in dense vegetation and because it intensively uses natural cavities and mouse holes, it was not possible to find dead lizards, which made an identification of the cause of mortality impossible. For these reasons and due to the cryptic behavior of this species it is as well difficult to observe the lizard's behavior in the outdoor enclosures and thus behavioral measurements following release were omitted.

For the survival measurement, lizards of different sexes were released in enclosures containing one sex only (3 enclosures for males and 2 enclosures for females). These enclosures also contained non-experimental lizards of the same sex as the released lizards. Non-experimental lizards were non-treated lizards, which were held in the laboratory for a similar length of time as the lizards used in this experiment. After releasing the experimental lizards, all enclosures contained the same total number of individuals. Per enclosure, we released the same number of individuals of each treatment (male enclosures: 12, 14, or 18 of each treatment; female enclosures: 22 of each treatment in one enclosure and in the other enclosure 22 and 21 females (one female died during the experiment)). Body mass and body size did not differ between enclosures ($P > 0.25$, for simple effects and all interactions).

### *Statistics*

The number of larvae eaten and the activity parameters (time of emergence, numbers of each behavior) were analyzed by using the GENMOD procedure in SAS v8.02 with a logistic regression, a cumulative logit link, and a multinomial distribution. We conducted a repeated measures logistic regression with the counts of each behavior (basking, scratching, moving, being immobile) as four repeated measures per individual (GEE model). This analysis allows for the estimation of treatment-induced differences in the partitioning of the time budget among the four behaviors. The body mass change during the experiment (body mass after the end of the treatment minus body mass before the beginning of the treatment) was analyzed using Proc GLM. Heteroscedasticity and normality assumptions of the residuals were in all presented models fulfilled. Survival was determined as 0 = not survived and 1 = survived and it was analyzed using the GLIMMIX procedure (Littell et al., 1996) using a logit link function and a binomial error term. The full model contained the simple factors (treatment, sex, enclosure) and all interactions. Enclosures were modeled as a random effect nested within sex. Simplification of all models was made using backward elimination of the non-significant interactions and factors. For the analysis of the body condition, body mass was the dependent variable and the body length was added to the model as covariate (Darlington and Smulders, 2001). The significance level was set at $P = 0.05$. As population of origin and its interactions with the treatment were not significant in any analyses ($P > 0.20$), we do not present these effects. One female treated with placebo died before release and was therefore excluded from the analyses.

## Results

### *Food consumption and body mass*

Lizards treated with corticosterone ate more larvae during the experiment than lizards treated with placebo ($\chi^2_1 = 15.35$, $P < 0.001$, Fig. 1A). Females ate more than males ($\chi^2_1 = 27.50$, $P < 0.001$) and there was no significant interaction between treatment and sex ($\chi^2_1 = 0.53$, $P = 0.467$), showing that the corticosterone application induced the same appetite enhancement in males and females. Separate analyses show that in the corticosterone-treated individuals the appetite was increased in both males ($\chi^2_1 = 9.40$, $P = 0.0022$) and females ($\chi^2_1 = 4.97$, $P = 0.0258$).

Corticosterone had no significant effect on the body mass change when using a model that did not include food consumption ($F_{1,172} = 0.002$, $P = 0.96$). Since the corticosterone effect on appetite could hide an effect of the hormone treatment on the body mass change, we included the food consumption into the model as a covariate. Food consumption was positively correlated with the body mass change (Table 1) and corticosterone-treated individuals increased their body mass less than placebo-treated individuals (Table 1, Fig. 1B). Females put on significantly more body mass than males (Table 1, Fig. 1B). And there was no significant interaction between the sex and the corticosterone treatment in body mass change (Table 1). Separate analyses show that body mass change was more positive in corticosterone-treated males ($F_{1,85} = 4.07$, $P = 0.047$) and females ($F_{1,84} = 7.58$, $P = 0.0072$) compared to placebo-treated animals.

### *Activity*

Lizards treated with corticosterone were active significantly earlier in the morning (Table 2A, Fig. 2) than placebo-treated lizards. There were no significant differences between males and females (Table 2A), and the interaction between treatment and sex was not significant ($\chi^2_1 = 0.11$, $P = 0.227$). We analyzed the partitioning of the time among the four quantified behaviors using a repeated

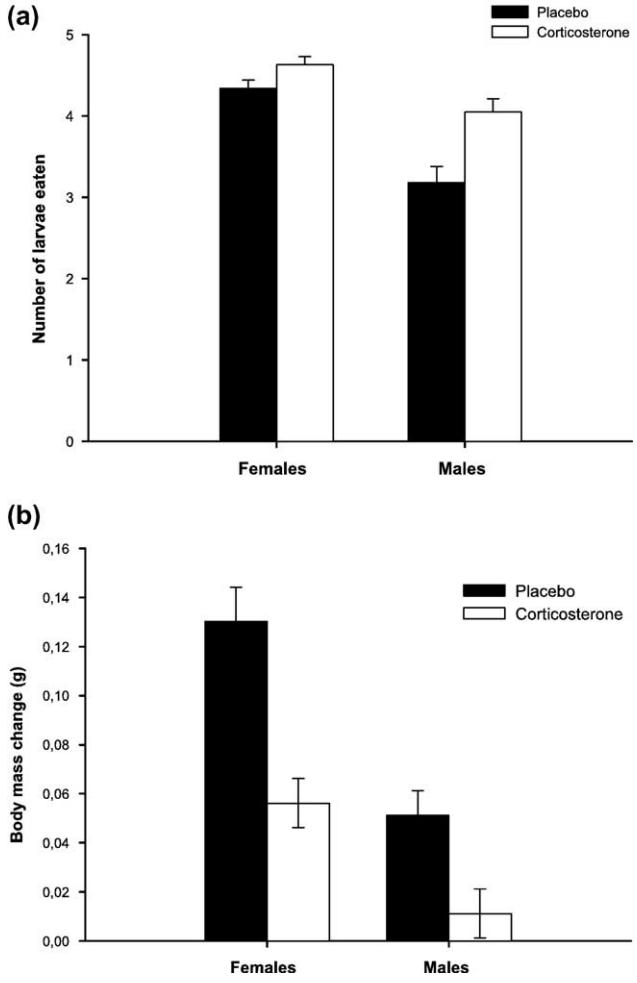


Fig. 1. (a) Food consumption in relation to the corticosterone treatment in female and male lizards. Shown are the mean numbers of larvae eaten (±S.E.) during the 22 days of treatment. (b) Treatment induced mean (±S.E.) body mass change (body mass at the end of the laboratory experiment-body mass at the start of the experiment) of male and female lizards adjusted for food consumption.

measurements model. As lizards treated with corticosterone were active earlier, we were able to quantify their behavior during a longer period. Emergence and activity patterns could thus be confounded. We therefore included the time a lizard was active (the number of times the lizard's behavior was quantified between emergence and 12 o'clock), hereafter referred to as 'activity length', as a covariate in the repeated measures analysis. Activity length and the type of behavior explained a significant part of the variance (Table 2B). The interaction between corticosterone treatment and the type of behavior was significant (Table 2B, Fig. 3), showing that lizards treated with corticosterone partitioned their time of activity differently among behaviors. The corticosterone treatment per se and the sex did not significantly affect the behavior (Table 2B). The interactions of the corticosterone treatment and the type of behavior with sex were not significant (sex × corticosterone: $\chi^2_1 = 2.09$, $P = 0.148$; sex × type: $\chi^2_1 = 2.78$, $P = 0.596$). To investigate the significance of the corticosterone treatment on the partitioning of the time among behaviors (interaction: corticosterone × type of behavior) we applied independent contrasts. Lizards treated with corticosterone were significantly less immobile and basked more than placebo-treated lizards (immobility: $\chi^2_1 = 4.28$, $P = 0.039$; basking: $\chi^2_1 = 5.42$, $P = 0.020$, Fig. 3). There was no significant effect of the treatment on scratching and moving (scratching: $\chi^2_1 = 1.63$, $P = 0.202$; moving: $\chi^2_1 = 2.02$, $P = 0.155$, Fig. 3).

Table 1
Body mass change in relation to corticosterone treatment, sex and food consumption

| Factors | *df* | F | P | % variance explained |
|---|---|---|---|---|
| Treatment | 1,171 | 7.108 | 0.008 | 2 |
| Sex | 1,171 | 11.291 | 0.001 | 3 |
| Interaction | 1,170 | 1.47 | 0.227 | 0.004 |
| Number of larvae eaten | 1,171 | 98.029 | <0.001 | 29 |

Table 2
Activity in relation to corticosterone treatment and sex

| | (A) Emergence | (B) Quantity of behavior |
|---|---|---|
| Corticosterone | $\chi^2_1 = 12.23$, $P = 0.001$ | $\chi^2_1 = 0.00$, $P = 0.987$ |
| Sex | $\chi^2_1 = 0.06$, $P = 0.805$ | $\chi^2_1 = 0.09$, $P = 0.759$ |
| Type of behavior | | $\chi^2_3 = 142.14$, $P < 0.001$ |
| Corticosterone × Type | | $\chi^2_3 = 8.50$, $P = 0.037$ |
| Activity length | | $\chi^2_1 = 36.25$, $P < 0.001$ |

(A) Effect of corticosterone treatment and sex on the time of emergence from the overnight stay. Logistic regression with a multinomial distribution and a cumulative logit link. (B) Effect of corticosterone treatment, sex, and activity length on the number of times a given behavior was observed. Repeated measures logistic regression (multinomial distribution and cumulative logit link) with the type of behavior (immobility, basking, moving, scratching) as repeats.

*Survival*

32 of 44 corticosterone and 19 of 44 placebo-treated males survived until spring 2003, while 9 of 44 cortico-

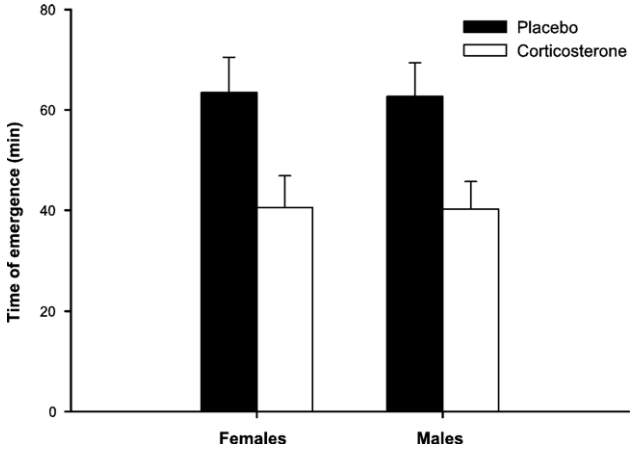


Fig. 2. Time of emergence from the overnight stay of female and male lizards in relation to the corticosterone treatment. Mean time of emergence (min after 9:00 a.m. ±S.E.) per sex and treatment group shown.

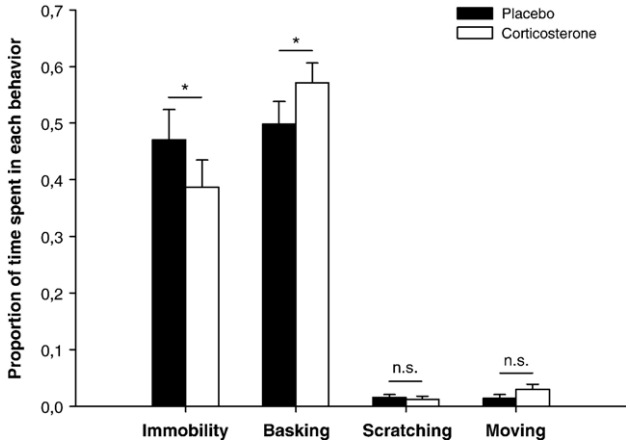


Fig. 3. Partitioning of the time between the different behaviors in relation to the corticosterone treatment. The graph shows the proportion of time a lizard spent immobile, basking, moving or scratching between emergence from the overnight stay until 12 a.m. An asterisk (*) represents a significant difference between treatments.

sterone and 13 of 43 placebo-treated females survived. Males had a higher survival probability than females ($F_{1,3}$ = 15.65, $P$ = 0.029, males = 0.58 ± 0.05 females = 0.25 ± 0.05) and there was a significant interaction between the sex and the corticosterone treatment on survival ($F_{1,168}$ = 6.78, $P$ = 0.010, Fig. 4). Corticosterone-treated males ($F_{1,84}$ = 7.60, $P$ = 0.007), but not females ($F_{1,84}$ = 1.06, $P$ = 0.305), showed significantly enhanced survival and there was no main effect of corticosterone treatment on survival ($F_{1,168}$ = 1.15, $P$ = 0.284). Placebo-treated lizards survived with the similar probability as the non-experimental lizards (Survival probability per enclosure averaged over all enclosures: placebo lizards: 36% ± 0.12 se, non-treated lizards: 30% ± 0.15 se, $F_{1,109}$ = 1.43 $P$ = 0.235). The corticosterone treatment did not have long-lasting effects on body condition ($F_{1,66}$ = 1.41, $P$ = 0.239), on body size ($F_{1,67}$ = 0.12, $P$ = 0.733), or on growth ($F_{1,67}$ = 0.22, $P$ = 0.642).

## Discussion

This experiment shows that corticosterone enhances food consumption, modifies behavior, and directly or indirectly affects male survival.

Lizards spent most of their time basking and immobile. Contrasting to another study in this species corticosterone did not significantly enhance the frequency of moving behavior (e.g., Belliure et al., 2004). However, corticosterone-treated lizards became active earlier in the morning and spent less time immobile after emergence, suggesting that their daily activity was increased. This supports the hypothesis that corticosterone enhances activity, potentially leading to the avoidance or compensation of the negative effects of the stressor (Wingfield and Ramenofsky, 1999; Breuner et al., 1998; de Fraipont et al., 2000; Breuner and Hahn, 2003). In some contexts enhanced activity could however be negative for the lizard due to greater foraging or dispersal movements and the resulting increased predation risk (Christian and Tracy, 1981; Clobert et al., 2000).

Lizards treated with corticosterone did not get heavier than placebo-treated lizards, but corticosterone significantly enhanced food consumption, showing that they put on less weight per food item. Consistent with other studies, this result suggests that corticosterone-treated lizards expended more energy due to corticosterone induced higher metabolic and behavioral activity (Gleeson et al., 1993; Tataranni et al., 1996; Breuner and Hahn, 2003). Despite the enhanced activity, lizards did not reduce body mass, showing that they compensated enhanced energy expenditure by increasing food consumption (e.g., Tataranni et al., 1996; Kitaysky et al., 2003).

In this study, survival, which can be a major component of fitness, was affected by the corticosterone treatment. Males treated with corticosterone survived significantly better than those treated with placebo and there was no effect in females. Several non-mutually exclusive hypotheses may explain how survival could have been affected by the corticosterone treatment. First, body condition, which is an important factor determining survival (Sorci and Clobert, 1999), may have been enhanced due to the increased food consumption. Because there were no condition differences between the treatment groups neither before nor after hibernation, this hypothesis is unlikely. Second, corticosterone might have reduced the social interactions (Tokarz, 1987; DeNardo and Licht, 1993) and thus the intrasexual competition in the outdoor enclosures, which may have led to increased survival. Because females are less aggressive than males (Heulin, 1988) and because lizards were maintained in enclosures consisting of one sex, female survival may not have been affected by the corticosterone treatment. However, in male-enclosures the male–male competition might have been high and certainly higher than in a mixed-sex enclosure of the same population density. Thus, corticosterone which reduces the social interactions

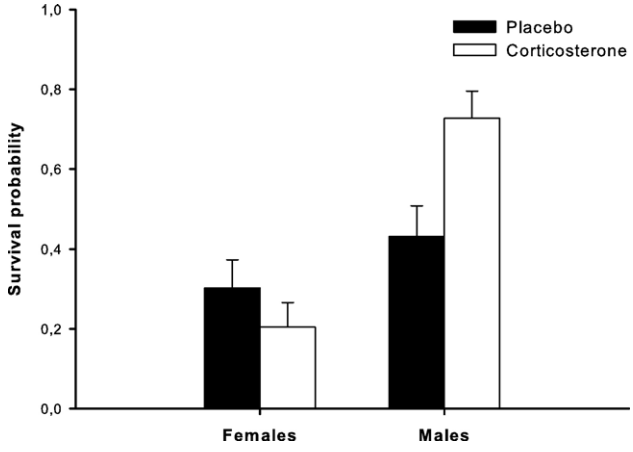


Fig. 4. Survival of placebo- and corticosterone-treated male and female lizards from September to April. Mean survival probability (±S.E.) between treatments and sexes is shown.

(Tokarz, 1987; DeNardo and Licht, 1993) may have led to a better survival of the corticosterone treated compared to the placebo-treated individuals. Besides these mechanisms, there are many other possible mechanisms that may have led to the increased survival of corticosterone-treated males. In this study, we, however, cannot distinguish between direct corticosterone effects or corticosterone-induced behavioral and physiological changes that led to increased survival, because reliable behavioral data after release are hard to obtain, because blood corticosterone levels before and after hibernation are unknown, and most importantly because the underlying mechanisms can only be explored using specifically designed experiments.

The absence of a corticosterone effect on females' survival could be due to several mechanisms including: sex-differences in hormonal levels (DeNardo and Sinervo, 1994a,b; Knobil and Neill, 1994; Jones et al., 1997), immunoglobulin levels (Tschirren et al., 2003), behavioral patterns (Heulin, 1988), life-history traits (Pilorge et al., 1987), and ecological requirements (Pilorge et al., 1987). Trying to understand the mechanisms is far beyond the scope of the present experiment. Consequently, further experiments are needed to explain the mechanisms leading to the observed sex-differences in survival.

Contrary to our study, Romero and Wikelski (2001) found a negative correlation between survival and the corticosterone level in wild iguanas. In Romero and Wikelski's study, El Niño led to both decreased food availability and increased corticosterone levels. Therefore, the negative correlation between corticosterone and survival in this particular study might be explained by reduced food availability. Our study, clearly shows, that corticosterone has direct or indirect (via its effects on behavior and physiology) positive effects on male survival and no negative effects on female survival. These findings are further supported by similar results showing that juvenile common lizards born from corticosterone-treated mothers as well survived better (Meylan and Clobert, 2005). It further suggests that animals suffering from external stressors may compensate the effects of the stressors on body condition by enhancing, e.g., food intake. As a result, corticosterone levels might be increased, but they may not necessarily lead to reduced survival, indicating that a negative correlation between corticosterone levels and survival may be context-dependent (see as well McEwen et al.'s review (1997) on the context-dependent effects of corticosterone on immune function).

Our study shows that corticosterone provokes behavioral modifications, probably in order to counterbalance the direct physiological costs of the metabolic stress. We further demonstrate that on the long-term corticosterone and/or its effects on behavior and/or physiology has a positive effect on male and no negative effect on female survival, which is an important determinant of fitness. Our results therefore suggest, that the production of corticosterone is, at least in common lizards, an adaptive response to environmental stressors.

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# MANUSCRIT 7

## Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio

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# Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio

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body size;
clutch sex ratio;
Fisher's sex allocation theory;
maternal investment;
population sex ratio;
sex allocation.

## Abstract

Sex allocation theory predicts that facultative maternal investment in the rare sex should be favoured by natural selection when breeders experience predictable variation in adult sex ratios (ASRs). We found significant spatial and predictable interannual changes in local ASRs within a natural population of the common lizard where the mean ASR is female-biased, thus validating the key assumptions of adaptive sex ratio models. We tested for facultative maternal investment in the rare sex during and after an experimental perturbation of the ASR by creating populations with female-biased or male-biased ASR. Mothers did not adjust their clutch sex ratio during or after the ASR perturbation, but produced sons with a higher body condition in male-biased populations. However, this differential sex allocation did not result in growth or survival differences in offspring. Our results thus contradict the predictions of adaptive models and challenge the idea that facultative investment in the rare sex might be a mechanism regulating the population sex ratio.

## Introduction

Fisher argued that the evolution of parental investment into sons and daughters should be influenced by fitness returns from differential investment into the sexes, such that higher fitness returns in one sex selects for stronger parental investment in that sex (Fisher, 1930; Charnov, 1982; Frank, 1990). Higher fitness returns in one sex can be the consequence of demographic disequilibria if the rare sex benefits from a lower intrasexual competition (Fisher, 1930). Werren & Charnov (1978) showed that a facultative investment in the rare sex could also be selected for in species being subjected to variations in adult population sex ratios (ASRs). In their article, Werren & Charnov (1978) modelled species whose generations are overlapping and in which females adjust their sex-biased investment in relation to the local ASR. In such species, conditions favouring a facultative investment in the rare sex are (i) variable ASRs experienced by the parents and (ii) predictability in ASRs experienced by offspring later in their life (Werren & Charnov, 1978; Bensch *et al.*, 1999).

Fisher's theory was originally phrased as a differential investment in males and females (Fisher, 1930; Frank, 1990), thus including both sex ratio (the proportion of one sex) and sex allocation (the proportion of resources invested in one sex). It is therefore indispensable to assess sex ratio and sex allocation tactics as well as the sex-specific offspring fitness when testing the predictions of Werren and Charnov's model. The ability of species with genotypic sex determination (GSD) to adjust their sex ratio has been questioned due to constraints imposed by the Mendelian segregation of sex chromosomes (Frank, 1990; Oddie, 1998). Case studies in birds and mammals provided strong support for adaptive adjustment of the sex ratio at birth (reviewed by Cockburn *et al.*, 2002), but evidence is lacking in many species (Krackow, 1995; Ewen *et al.*, 2004). Studies in lizards (Reptilia, Squamata) suggest several potential mechanisms by which females might adjust their sex-biased investment. In GSD species,

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mothers could control sex ratio via gamete selection and differential abortion of embryos (Blackburn, 1998; Calsbeek & Sinervo, 2004). These mechanisms might be under environmental control through the effects of gonadotropin and steroid hormones (Krackow, 1995; Sinervo, personal communication), and could therefore be influenced by variation in ASR. Furthermore, studies have demonstrated mechanisms of temperature-dependent sex determination in lizards (Robert & Thompson, 2001; Shine, 2002; Wapstra *et al.*, 2004), suggesting that mothers can control the sex ratio by selecting the temperature at which their offspring develop. Finally, mother lizards can allocate more resources to one sex by biasing the amount of yolk or steroid hormones deposited in the egg (e.g. Olsson & Shine, 2001; Painter *et al.*, 2002). This differential allocation might influence the number and/or the quality of the recruiting offspring, and thus the fitness returns of the sex-specific parental investment.

Here, we used the common lizard (*Lacerta vivipara* Jacquin, 1787) as a model system to experimentally test Werren and Charnov's predictions. Like the species envisioned by Werren & Charnov (1978), the common lizard is characterized by overlapping generations that share small and nonexclusive home ranges (Massot *et al.*, 1992). In natural populations variation in local ASRs can result from sexual differences in survival and movement (Massot *et al.*, 1992). Furthermore, female common lizards can perceive ASR variation of their environment by optical or chemical cues (Bauwens *et al.*, 1987). In this viviparous species, the sex at birth is determined (at least partly) genetically by a modified ZZ/ZW chromosomal system (Chevalier *et al.*, 1979). Transfer of maternal metabolites and steroids during egg formation (synchronized with mating) and during embryonic development (through a primitive chorioallantoic placenta) allow for maternal effects (Panigel, 1956; Gavaud, 1986). Females are the heterogametic sex (ZW) and have thus the potential to control sex-biased investment through pre-ovulation control of chromosome segregation, selective sex-specific abortion of the ovulated follicles, and sex-biased investment into the eggs. Maternal control of offspring life history traits has been demonstrated in this species (e.g. Meylan & Clobert, 2004) and sex-specific prenatal effects on offspring morphology are known (Uller *et al.*, 2004). In the common lizard, the clutch sex ratio at birth varies with environmental conditions (pp. 69–83 in Leturque, 2002). Higher habitat humidity in the study of Lorenzon *et al.* (2001) was associated with more male-biased sex ratios at birth and experimentally increased maternal corticosterone levels led to more female-biased clutches in the experiment by Meylan & Clobert (2004). These results indicate that sex ratios can be adjusted in response to external cues. Because experimental treatments were applied during the last month of gestation in both studies, sex-specific mortality of embryos might have been the adjustment mechanism (Leturque, 2002).

We first studied spatial and interannual variations in local ASR in a natural population of the common lizard monitored from 1989 to 2001 (Clobert *et al.*, 1994). In this population, the mean ASR is female-biased (Massot *et al.*, 1992). Using information on natural ASR variation, we then experimentally tested for facultative maternal investment in the rare sex. We simulated a temporary deviation of the ASR from its natural (female-biased) situation. This approach corresponds to the 'dynamic tests' of Fisherian sex ratio adjustment theory (Bull & Charnov, 1988) and matches the population dynamics envisioned in 'perturbation models' (Werren & Charnov, 1978; West & Godfray, 1997). We created populations with a female-biased ASR (control) and populations with a male-biased ASR (treatment) during a first breeding episode. We then translocated all individuals into populations with female-biased ASR (control) for a second breeding episode. According to the model developed by Werren & Charnov (1978), we predict that mothers should bias their sex ratio and/or sex allocation towards the rare sex.

## Materials and methods

### Study species

The common lizard *L. vivipara* is a small Lacertidae [adult snout-vent length (SVL): 50–70 mm]. In early spring, males emerge on average 1 month earlier than females from hibernation and mating occurs in April. Females can start reproducing at the age of 1 year and almost all females reproduce at the age of 2 years (Boudjemadi *et al.*, 1999). Parturitions last from the beginning of June until the end of July. Females lay on average five transparent, soft-shelled eggs (range: 1–12). The offspring hatch within the same day and thereafter are autonomous. Individuals were marked with a unique code using toe clipping.

### Adult sex ratio variations in a natural population

We define the ASR as the proportion of males among adult individuals. As part of a long-term population monitoring, a site located at the Mont Lozère (1420 m above sea level, 44°30′N, 3°45′E) has been studied from 1989 to 2001 (Clobert *et al.*, 1994). The study population was monitored each year during late spring and during late summer, and the code, position and sex of the reproducing (aged more than 1-year old) individuals were identified. The study site was divided in neighbourhoods of 20 by 20 m to monitor interannual and spatial variations in the local ASRs. The neighbourhood's area corresponds to the maximum home range area of female lizards breeding in this population and is a pertinent choice to study social environments in this species (Clobert *et al.*, 1994). The repeated monitoring was used to calculate the year-specific capture probabilities sepa-

rately for males and females in our study site. Sex-specific capture probabilities were estimated with Cormack–Jolly–Seber models [$\Phi(t)$, $P(t)$] fitted on the mark-recapture data including sex as a factor, using a likelihood-based approach (Lebreton *et al.*, 1992), and assuming similar capture probabilities among neighbourhoods. We checked with GOF tests that there was no significant heterogeneity in capture probabilities using the Test 2 + Test 3 of the Cormack–Jolly–Seber model in RELEASE (Lebreton *et al.*, 1992) (males: $\chi^2_{13} = 5.16$, $P =$ n.s.; females: $\chi^2_{33} = 30.43$, $P =$ n.s.). Subsequently we estimated the number of males and females present in each neighbourhood in late spring by dividing the number of adult males or females seen in each neighbourhood by our estimates of sex-specific capture probability. The estimated number of females per neighbourhood varied from 0 to 34 (mean = 6.35 ± 0.41 SE, $n = 197$). Because we were interested in ASR variations experienced by breeding females, neighbourhoods where no adult female were seen were excluded from the analyses.

## Experimental procedures

The experimental study was carried out in semi-natural populations at the Ecological Research Station of Foljuif (60 m above sea level, 48°17′N, 2°41′E) using lizards from natural populations of the Mont Lozère area. Experimental populations were housed in 12 outdoor enclosures (10 × 10 m). The enclosure size corresponds to the female's core home range size. Enclosures were located in a natural meadow and were surrounded by plastic walls to prevent lizards from escaping [see Boudjemadi *et al.* (1999) for more details]. Lizards were able to disperse by using a 20 m long dispersal corridor ending in a pitfall trap. Dispersing lizards were collected daily and introduced into a new population of the same ASR treatment. Less than 10% of the individuals dispersed during the study and dispersal probability were not affected by treatments, except in adult females during the first summer (Le Galliard & Fitze, unpublished results). The female dispersal behaviour did not affect their reproductive characteristics (differences between resident and dispersing females in fecundity: $P = 0.18$, clutch sex ratio: $P = 0.52$, offspring morphology: all $P > 0.67$), and resident and dispersing females were therefore analysed together.

In June–July 2002, six randomly chosen enclosures were populated with an ASR biased towards females. This treatment corresponds to the average ASR observed in natural populations and thus serves as a control. In another six enclosures, we initiated populations with a male-biased ASR (treatment, see Table 1). Yearling and juvenile sex ratios were held constant in all populations (1 : 1) as well as the proportion of yearling, juvenile and adult lizards. The initiated population structure corresponds to the equilibrium population structure observed in the wild (Massot *et al.*, 1992). The ASR of the control populations (ASR = 0.22) corresponds to the average ASR of the natural population studied, while the ASR of the treatment populations (ASR = 0.78) corresponds to the extreme ASRs observed in the same natural population. Before release, SVL was measured to the nearest mm and body mass was measured to the nearest mg.

**Table 1** Mean age and sex structure per treatment in six treatment (male-biased) and six control (female-biased) populations at the start of the study. Data are mean ± SD.

| | Treatment populations | | Control populations | |
|---|---|---|---|---|
| Age class | Males | Females | Males | Females |
| Juveniles | 21.3 ± 0.5 | 21.8 ± 0.7 | 21 ± 0.6 | 22.3 ± 1.1 |
| Yearlings | 6 ± 0 | 6 ± 0 | 6 ± 0 | 6 ± 0 |
| Adults | 14 ± 0 | 4 ± 0 | 4 ± 0 | 14 ± 0 |

In early June 2003, all surviving lizards were captured. The ASR was still different between treatment and control populations (treatment: 0.80 ± 0.03 SE; control: 0.37 ± 0.04 SE; $\chi^2_1 = 53.50$, $P < 0.001$). Females were housed in individual terraria (25 × 15 × 15 cm) under standardized conditions (Le Galliard *et al.*, 2003b). Terraria were checked daily for freshly laid clutches at 9:00 and 14:00 o'clock. Approximately 1 h after clutch detection, viable offspring ($n = 549$), dead offspring ($n = 62$) and late aborted embryos ($n = 50$) were measured for SVL, tail length and body mass, and they were sexed by counting the number of ventral scales (Lecomte *et al.*, 1992). This method correctly determines the offspring sex in 96% of the cases, as evidenced using three cohorts of juveniles that were again sexed at the age of 1 year, where sex-attribution is unambiguous ($n = 525$ recaptures; Le Galliard, unpublished data). Aborted embryos were distinguished from dead offspring (offspring that did not hatch) by the developmental stage: dead offspring were melanin-pigmented and fully developed with a similar body shape as viable offspring (Dufaure & Hubert, 1961). The same person took all measurements.

Animals were then released into new, unknown enclosures containing a female-biased ASR and thus corresponding to the control situation simulated during the first year of this experiment. This 'common garden' experiment allowed for the measurement of the benefits of sex-biased offspring investment, independent of any direct effects of the ASR (e.g. survival or growth effects) 1 year after the ASR perturbation. Two days after hatching, both the living offspring (532 of 549) and their mothers from the first year of the experiment were released into eight new enclosures. Offspring and mothers were released with a homogeneous sample of adult males and yearlings. In each enclosure, 18 adult females, 10 adult males and 12 yearlings (sex ratio 1 : 1) were introduced to create a female-biased ASR (36% of adult males). Within each enclosure, the offspring sex ratio was held constant (sex ratio: 0.48 ± 0.038 SE) and the

proportions of offspring originating from control and treatment populations were similar (proportion of offspring originating from control populations: 0.08 ± 0.02 SE; $\chi^2_7 = 10.92$, $P = 0.14$). At the end of May 2004, all surviving lizards were recaptured and females were housed in individual terraria. Clutch sex ratio and offspring morphology were measured at birth using the same procedures as described above.

### Statistical analysis

We analysed the results of the experiment using mixed-effects models in SAS (Littell *et al.*, 1996). Sex ratio (proportion of males in the clutch) and sex-specific survival probability of the offspring were modelled with the GLIMMIX procedure using a logit link and a binomial error term. The goodness of fit of the models was checked with a Pearson chi-square test (McCullagh & Nelder, 1989). Offspring morphology (SVL, tail length and body condition) and sex-specific body growth rates of offspring were analysed with general linear mixed models using the MIXED procedure. The latter models' assumptions (normality and homogeneous variance of residuals) were fulfilled in all cases. All models contained at least the following factors: ASR treatment, mother age class (juvenile, yearling or adult), SVL of the mother and their interactions as fixed effects, as well as the random effect of the enclosure nested within treatment and the random effect of the family nested within enclosure and treatment. For survival and growth rates of the first generation of offspring, we included potential differences between release enclosures by adding release enclosure as a random factor. The final models were selected after backward elimination of nonsignificant terms.

All offspring sexed at birth were included in the analysis of the sex ratio at birth ($n = 651$ observations from 117 families). We tested for potential differences among the offspring's developmental classes (late aborted embryos, dead offspring and viable offspring) by including a categorical variable with three levels into the model. The clutch sex ratio 1 year after birth was analysed as the proportion of surviving male offspring per number of surviving offspring ($n = 66$ families). For the analyses of offspring SVL, tail length and body condition (body mass adjusted for body length by including SVL as a covariate in the analysis), late aborted embryos were excluded and a categorical factor (dead or viable) was included into the model to distinguish between the two developmental classes.

## Results

### Adult sex ratio variations

The local ASRs varied from 0 to 0.77 in the natural population (average ASR = 18 ± 0.18 SD, 22 neighbourhoods surveyed during 12 years). In a total of 16 neighbourhoods, sufficient data was available for the analysis of local ASR variations over five subsequent years. ASRs varied significantly among years and neighbourhoods (logistic regression, neighbourhood: $\chi^2_{15} = 41.24$, $P < 0.001$; year: $\chi^2_4 = 68.97$, $P < 0.0001$). In 21 instances, ASRs could be measured during two consecutive years within the same neighbourhood. Local ASRs during two consecutive years were positively correlated [ANOVA, see Lessels & Boag (1987), $F_{20,21} = 3.16$, $P < 0.01$, intra-class correlation coefficient: $r = 0.52$]. Similar interannual variation was detected at larger spatial scales, but spatial variation in ASR was only significant at scales below 25 m. When analysing fluctuations in the ASR at the population level during 12 years, ASR in year $t$ was positively correlated with ASR in year $t + 1$ ($F_{10,11} = 3.35$, $P < 0.05$, $r = 0.54$).

### Sex ratio adjustment during the manipulation

We modelled sex ratio at birth and sex ratio 1 year after birth with mixed effects logistic regressions. The goodness of fit test of these models showed no evidence of extra-binomial variation (sex ratio at birth: $\chi^2_{639} = 622.4$, $P =$ n.s.; sex ratio 1 year after birth: $\chi^2_{149} = 151.0$, $P =$ n.s.). The sex ratio at birth in our semi-natural populations did not differ from the Mendelian expectation for a species with genotypic sex determination [average clutch sex ratio = 0.48 (0.43, 0.53) (95% CI) males per clutch]. The sex ratio at birth was 0.53 (0.38, 0.68) in male-biased populations and 0.48 (0.41, 0.55) in control populations. The differences between ASR treatments were not significant ($F_{1,10} = 0.92$, $P =$ n.s.). Mother SVL, mother age and the interactions between these factors and the ASR treatment did not affect the sex ratio at birth (all $P > 0.30$). The sex ratio at birth was however significantly different among developmental classes ($F_{2,532} = 4.29$, $P < 0.05$). The sex ratio was 0.71 (0.55, 0.83) in aborted embryos, 0.51 (0.38, 0.64) in dead offspring, and 0.46 (0.41, 0.52) in viable offspring. These differences in sex ratio among developmental stages were not affected by the ASR treatment (interaction ASR treatment × developmental class: $F_{2,530} = 0.04$, $P =$ n.s.). Furthermore, the clutch sex ratio 1 year after birth was not significantly affected by the ASR treatment ($F_{1,8} = 0.42$, $P =$ n.s.). The clutch sex ratio 1 year after birth was 0.50 (0.21, 0.79) in treatment populations and 0.40 (0.31, 0.50) in control populations.

The absence of a clutch sex ratio adjustment in response to the ASR manipulation may be the result of a lack of power due to the relatively low number of clutches in male-biased populations ($n = 20$). Therefore, the minimum detectable effect size (defined according to Quinn & Keough (2002) as the sex ratio contrast between ASR treatments associated with a power of 0.80) was calculated using Monte Carlo simulations (1000 data sets with a clutch size distribution within each population similar to our sample). The minimum

detectable effect size at birth was a clutch sex ratio contrast of approximately 0.17 between ASR treatments, suggesting that our statistical tests had reasonable power.

### Sex allocation adjustment during the manipulation

The ASR treatment had no effect on the sexual dimorphism in SVL (effect of sex × ASR treatment: $F_{1,497} = 1.38$, $P =$ n.s.) and in tail length at birth ($F_{1,496} = 0.001$, $P =$ n.s., Fig. 1), but influenced the sexual dimorphism for body condition at birth ($F_{1,495} = 9.24$, $P < 0.01$). Male offspring had higher body condition in male-biased populations than in control populations (contrast = 18.3 mg adjusted mass ± 6.84 SE, $P < 0.01$), while female offspring showed no difference between ASR treatments (contrast = 5.39 mg adjusted mass ± 6.48 SE, $P =$ n.s., Fig. 1). This difference was not due to intersexual differences in body mass between the ASR treatments (effect of sex × ASR treatment on body mass: $F_{1,498} = 0.12$, $P =$ n.s.).

Despite the differences in body condition at birth between male-biased and control populations, the ASR treatments had no long-lasting effects on the performances of the offspring as measured by their sex-specific annual survival probability (effect of sex × ASR treatment: $F_{1,506} = 0.13$, $P =$ n.s., $n = 532$) and growth rates (effect of sex × ASR treatment: $F_{1,120} = 12.47$, $P = 0.12$; size at birth: $F_{1,120} = 13.78$, $P < 0.001$; date of birth: $F_{1,120} = 7.72$, $P < 0.01$, $n = 141$; see Table 2).

### Sex-biased maternal investment after the manipulation

Of the 890 juvenile, yearling and adult females that were introduced in our experimental populations in 2002, 71 survived until the second reproductive episode in 2004 (1 year after the ASR manipulation), and 38 gave birth to offspring that could be sexed at birth ($n = 162$ offspring). The clutch sex ratio at birth of the surviving females was on average 0.48 (0.40, 0.56) (95% CI), and did not differ between ASR treatments ($F_{1,10} = 0.41$, $P = 0.53$). The clutch sex ratio was 0.50 (0.40, 0.60) for females originating from control populations and 0.46 (0.32, 0.59) for females originating from male-biased populations. The mother's SVL, age and the interactions between these factors and the ASR treatments did not affect the sex ratio of the clutch (all $P > 0.08$).

Sex allocation was studied by analysing the SVL, tail length and body condition of offspring born 1 year after the ASR perturbation (Table 3). After backward elimination of the nonsignificant terms, the ASR treatment had no effect on offspring SVL (effects of ASR treatment: $F_{1,10} = 0.52$, $P =$ n.s.; sex: $F_{1,121} = 17.60$, $P < 0.0001$; sex × ASR treatment: $F_{1,121} = 0.41$, $P =$ n.s.; mother age: $F_{2,121} = 4.74$, $P < 0.01$, $n = 161$), tail length (effects of ASR treatment: $F_{1,10} = 0.63$, $P =$ n.s.; sex: $F_{1,121} = 2.92$, $P = 0.09$; sex × ASR treatment: $F_{1,121} = 0.01$, $P =$ n.s.; mother age: $F_{2,121} = 5.31$, $P < 0.01$) and body condition (effects of ASR treatment: $F_{1,10} = 0.51$, $P =$ n.s.; sex: $F_{1,119} = 8.14$, $P < 0.01$; sex × ASR treatment:

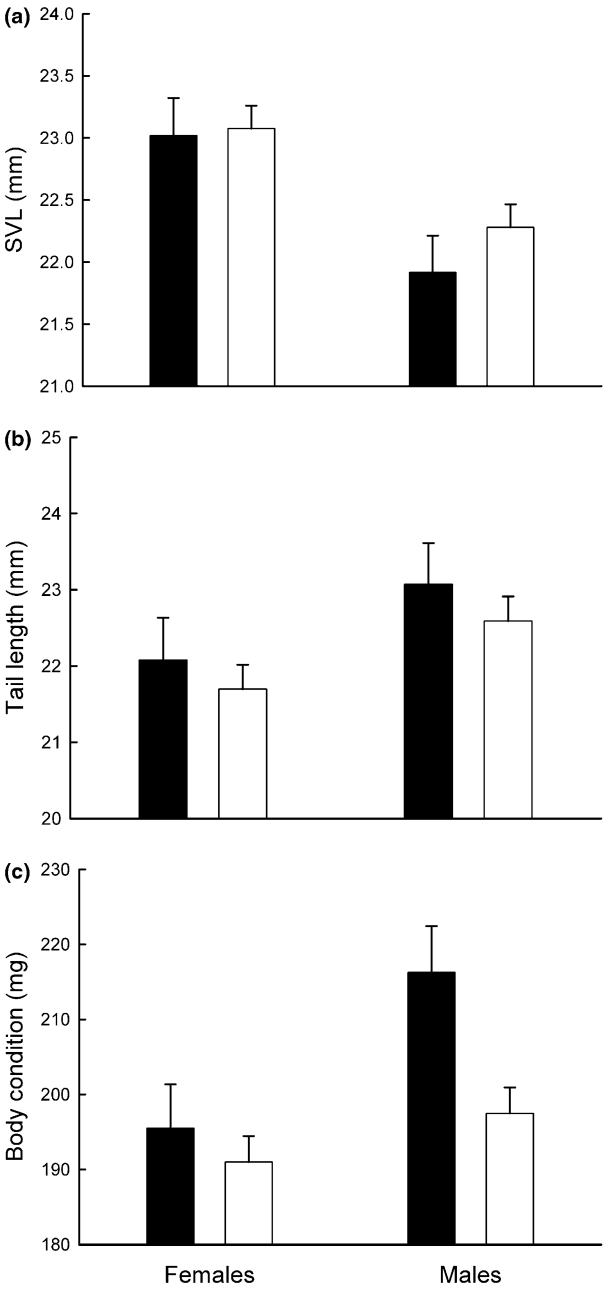


**Fig. 1** Direct effects of the ASR treatment on SVL (a), tail length (b) and body condition (c). Least-squares mean (±SE) of male and female offspring in treatment (filled bars, male-biased) and control (empty bars, female-biased) populations are presented (models described in the text). Males were smaller at birth ($F_{1,498} = 224.70$, $P < 0.0001$), had a longer tail length ($F_{1,497} = 64.48$, $P < 0.0001$), and a higher body condition ($F_{1,495} = 44.35$, $P < 0.0001$) than females, but body mass did not differ between the sexes ($F_{1,498} = 0.12$, $P = 0.73$).

**Table 2** Mean annual survival probability and growth rate of offspring per ASR treatment and sex. Data are the least-squares mean (±SE) of the models discussed in the text.

| | Treatment populations | | Control populations | |
|---|---|---|---|---|
| | Males | Females | Males | Females |
| Annual survival | 0.27 ± 0.09 | 0.27 ± 0.10 | 0.25 ± 0.03 | 0.31 ± 0.03 |
| Annual growth rate (mm) | 29.3 ± 1.64 | 27.2 ± 1.76 | 27.2 ± 0.62 | 28.8 ± 0.56 |

**Table 3** Mean SVL, tail length and body condition of offspring born during the second reproductive episode per ASR treatment (population of the mother during the first reproductive episode) and sex. Mothers were all translocated in control populations during 1 year after the end of the sex ratio manipulation. Data are least-squares mean (±SE) of the models discussed in the text.

| | Treatment populations | | Control populations | |
|---|---|---|---|---|
| | Males | Females | Males | Females |
| Offspring SVL (mm) | 20.85 ± 0.52 | 21.5 ± 0.52 | 21.18 ± 0.45 | 22.06 ± 0.45 |
| Offspring tail length (mm) | 20.05 ± 0.96 | 19.3 ± 0.96 | 20.44 ± 0.86 | 19.73 ± 0.86 |
| Offspring body condition (mg) | 156.6 ± 11.16 | 152.8 ± 11.08 | 168.7 ± 10.19 | 155.9 ± 10.2 |

$F_{1,119} = 2.60$, $P = 0.11$; mother age: $F_{2,119} = 6.60$, $P < 0.01$; offspring development class: $F_{1,119} = 7.86$, $P < 0.01$; SVL: $F_{1,119} = 116.7$, $P < 0.0001$).

## Discussion

We found significant variation in the ASR both at the scale of a mother's home range and between years in the studied natural population of the common lizard. Furthermore, the local ASR of year *t* predicted the ASR of year *t* + *1* within the same population. Thus, the two conditions for the evolution of facultative investment in the rare sex were met: (i) variable local ASRs experienced by mothers and (ii) predictability of the local variation in the ASR. Nevertheless, we experimentally demonstrated that mothers did not adjust their clutch sex ratio during and after the ASR manipulation, although the individuals used in our experiment stemmed from the same geographic area as the natural population does. Contrary to the predictions made by sex allocation theory, females produced sons with a higher body condition in male-biased compared to female-biased populations. However, this sex-biased maternal allocation had no detectable long-lasting effects on the sex-specific growth and survival of the offspring.

The significance of the obtained results could be weakened if the social organization would have been disrupted due to the semi-natural conditions during our experiment. However, our experimental setting is not likely to have confounded this study, because the population density and the ASRs were within the range of their natural variation (Massot *et al.*, 1992; Clobert *et al.*, 1994). Further, dispersal rates, the timing of the dispersal, the mating system, density dependence, as well as selection on life history traits were found to be unaltered in the enclosures compared to the natural situation (Le Galliard *et al.*, 2003a; Laloi *et al.*, 2004; Lecomte *et al.*, 2004; Le Galliard *et al.*, 2004). Finally, the mean sex ratio at birth observed in this study is similar to the one observed in natural populations and is not changed by transplantation of the lizards (Clobert *et al.*, 1994; Boudjemadi *et al.*, 1999).

### Patterns of sex ratio

Evidence for an adjustment of the sex ratio at birth in favour of the rare sex is scarce and ambiguous in vertebrates (Trivers, 1985; Cockburn *et al.*, 2002). Luummaa *et al.* (1998) found facultative sex ratio allocation into the rare sex in rural populations of humans in Finland (see also Ranta *et al.*, 2000), Olsson & Shine (2001) observed a similar trend in viviparous skinks from Tasmania, and Byholm *et al.* (2002) described a mechanism balancing local offspring sex ratio towards the rarer sex in goshawks. However, these empirical studies did not test the assumptions of the sex ratio models and could also be plagued by several confounding factors correlated with local sex ratios in the wild. Another investigation of facultative sex ratio adjustment in a natural reed warbler population strongly supported the assumptions of the sex ratio models, but did not detect a sex ratio adjustment in relation to the ASR (Bensch *et al.*, 1999). Further, two experimental studies in vertebrates failed to detect adjustments of the sex ratio at birth in response to a perturbation of the population sex ratio (Brown, 1982; Bond *et al.*, 2003). Our results are in line with the latter studies, suggesting that a sex ratio adjustment in relation to the population sex ratio might be rare in vertebrates.

Given the fact that the basic assumptions of Werren and Charnov's model (1978) are fulfilled and given the ability of the common lizard to control the clutch sex ratio (Leturque, 2002), our results indicate that the selective benefits of a facultative adjustment into the rare sex might be too weak. We suggest that benefits of facultative investment into the rare sex might be diminished by frequency dependence, intersexual interactions, and the costs of sex ratio adjustment. First, the advantages of a facultative investment in the rare sex are frequency-dependent and restricted in space (Frank, 1990). Benefits might therefore be lost if most females are employing this strategy (Bensch *et al.*, 1999) and if offspring settle outside their natal home range (Ranta *et al.*, 2000). Simulations have shown that sex allocation can be locally maladaptive when mothers lack information about the environment experienced by their

offspring (Ranta *et al.*, 2000). However, our population monitoring indicates that a significant proportion of the juveniles are recaptured within the scale (25 × 25 m) at which spatial variations in the ASR occur and can be experienced by their mothers (proportion of recruits aged 1 year = 65.9%, $n = 1040$; 2 years = 68.2%, $n = 918$). Therefore, our results are unlikely to be explained by the fact that mothers and offspring frequently experience different ASRs and thus by the spatial structure of the population.

Furthermore, Fisherian models assume that intrasexual competition is the critical determinant of the lifetime reproductive success of each sex (Frank, 1990). It is therefore beneficial to produce the rare sex that enjoys a lower intrasexual competition. This assumption neglects the role of intersexual interactions. We found that sexual aggression by males induced lower survival, lower fecundity and delayed parturitions in female common lizards inhabiting male-biased populations (Le Galliard & Fitze, unpublished results). Thus, daughters produced in areas where sex ratios have been distorted towards males suffer reduced reproductive success, which selects against a facultative investment towards daughters in areas where the ASR is male-biased.

Finally, there might be constraints associated with a flexible adjustment of the sex ratio (Krackow, 1995). The Mendelian inheritance of the sex chromosomes might be too rigid and biasing the sex ratio at birth might be costly (Oddie, 1998). For example, sex ratio skews can have negative effects on the rare sex within the clutch. In the viviparous common lizard, offspring are influenced by hormonal interactions with their siblings *in utero*, and it has recently been found that a prenatal exposure to steroids produced by the common sex within the clutch reduces the fitness of the rare sex (Uller *et al.*, 2004). Such negative effects of skewed sex ratios at birth generate selection for sex ratio homeostasis (Uller, 2003).

### Patterns of sex allocation

Sex allocation theory also predicts that mothers should invest more resources in the rare sex (Olsson & Shine, 2001). Contrasting to these expectations, mothers produced more corpulent sons in male-biased than in female-biased populations, which might be explained by several mutually exclusive hypotheses. First, there might exist a direct correlation of maternal condition with sex-biased investment, such that higher maternal condition is associated with higher investment in sons (Trivers & Willard, 1973). This hypothesis is however not supported since we found no difference in maternal condition between treatments (post-parturition body condition, $F_{1,10} = 0.03$, $P =$ n.s.), no differential survival of the females according to treatment and body condition at the start of our manipulation (effect of treatment × body condition on annual survival probability in juvenile females: $F_{1,168} = 0.39$, $P =$ n.s.; in yearling and adult females: $F_{1,164} = 0.07$, $P =$ n.s.), and no relationship between clutch sex ratio at birth and maternal condition ($F_{1,104} = 1.09$, $P =$ n.s.).

Alternatively, treatment effects could have been mediated by the quality of the females' mating partners (Sheldon, 2000) since competition among males for access to females should be stronger and the scope for female choice should be bigger in male-biased than in female-biased populations (Kvarnemo & Ahnesjö, 1996). As a result, females may have copulated with more attractive partners of higher quality in male-biased populations. To investigate this question, we used paternity data obtained during our study (Fitze *et al.*, unpublished results). Females of the two ASR treatments did not mate with males of significantly different SVL ($F_{1,10} = 0.79$, $P =$ n.s.), tail length ($F_{1,10} = 0.49$, $P =$ n.s.) or body condition ($F_{1,10} < 0.01$, $P =$ n.s.). However, females tended to mate with older males in male-biased populations ($F_{1,10} = 4.54$, $P = 0.06$), suggesting that male offspring condition might have changed due to sex-biased maternal investment depending on the mate's age [see Sheldon (2000) for a review].

A last explanation may be direct fitness advantages gained when producing more corpulent sons in male-biased populations. However, sex-specific differences in offspring condition between treatments had no detectable consequences on the performances of the offspring later in their life. Hence, it is difficult to conclude what the advantages of differential maternal investment are. To clarify this point, additional experiments (e.g. reciprocal transplants of offspring from male-biased and female-biased populations) should investigate in more details the fitness consequences of differential maternal investment.

## Conclusions

We experimentally showed that mothers neither adjusted their clutch sex ratio nor the sex-specific offspring survival towards the rare sex, but found that mothers produced sons with a higher body condition in male-biased populations. We suggest that benefits of facultative investment in the rare sex might be diminished by frequency-dependent selection, intersexual interactions, and the costs of sex ratio adjustment. For example, as male frequency increases, intrasexual competition between females decreases and females suffer from stronger intersexual competition, which may select against the production of daughters. Although such modifications of the social system could generate selective pressures on sex-biased maternal investment, current models fail to take them into account (Frank, 1990). Our results thus urge for the development of more detailed models to better predict facultative maternal investment in the rare sex.

Our results are in line with a recent review that suggests that facultative primary sex ratio variation is not a consistent biological phenomenon (Ewen *et al.*, 2004).

This implies that facultative maternal investment in the rare sex may not be a widespread strategy used to compensate perturbations of the population sex ratio. Instead, short-term changes in sex-specific migration and mortality rates, or frequency dependent selection on heritable variation in sex-biased investment, may be the principal mechanisms maintaining the usually stable population sex ratios.

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# MANUSCRIT 8

# Lifetime and intergenerational fitness consequences of multiple mating attempts for female lizards

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# Lifetime and intergenerational fitness consequences of multiple mating attempts for female lizards

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## ABSTRACT

Male mating behaviors harmful to females have been described in a wide range of species. However, the fitness consequences of potentially harmful male behaviors have been rarely quantified throughout the lifetime of females and their offspring, especially for long-lived organisms under natural conditions. Here, lifetime and intergenerational consequences of multiple mating attempts were investigated in female common lizards (*Lacerta vivipara*) using field experiments. We manipulated the number of multiple mating attempts for females by creating different population sex ratios during one year, and then monitored females and their first generation of offspring in a common garden during two additional years. We found significant lifetime fitness costs of multiple mating attempts for females. The direct costs were partly mitigated by compensatory responses of females late in life but not by indirect benefits through offspring growth, offspring survival and daughters' fecundity. These results support recent empirical findings showing that the direct costs of mating are not outweighed by indirect benefits.

## INTRODUCTION

In females, mating interactions with males may vary from mutualistic to antagonistic (Andersson 1994; Arnqvist & Rowe 2005). Males may provide females with direct benefits, such as parental care, or indirect benefits, for example good genes for parasite resistance (Andersson 1994). On the other hand, males can use coercive strategies to gain mating advantages, like sexual harassment or infanticide (Clutton-Brock & Parker 1995; Chapman *et al.* 2003). Indeed, behavioral studies spanning a broad range of species suggest that males often harm females during mating (reviewed by (Arnqvist & Rowe 2005). For example, females can suffer significant costs due to multiple mating attempts by males, such as higher energy expenditure (e.g., (Rowe *et al.* 1994), reduced fecundity from exposure to toxic male seminal fluids (e.g., (Chapman *et al.* 1995), or lower survival caused by traumatic inseminations (e.g., (Crudington & Siva-Jothy 2000). These harmful male behaviors should promote a sexual conflict where males and females evolve sexually antagonistic adaptations and counter-adaptations (Parker 1979; Holland & Rice 1998; Gavrilets *et al.* 2001).

Empirical data supporting the hypothesis of a sexual conflict have accumulated but our current knowledge suffers from two main drawbacks (reviewed in (Orteiza *et al.* 2005). First, the net costs of male behavior have been rarely quantified throughout the lifetime of females. Lifetime costs of multiple mating are well documented only in a few laboratory systems, such as fruit flies or dung flies (e.g., (Chapman *et al.* 1995; Martin & Hosken 2003), but similar studies are exceedingly rare for longer-lived organism and/or in natural conditions (see (Maklakov *et al.* 2005) and references therein). For example, the costs and benefits of multiple mating may be affected by laboratory conditions, where e.g. population density and food availability are different than in the wild (Hosken & Tregenza 2006). Second, whether females can counterbalance the direct costs of mating by indirect benefits through offspring quality is still debated (e.g., (Cordero & Eberhard 2003; Pizarri & Snook 2003; Arnqvist &

Rowe 2005). For example, (Cameron *et al.* 2003) showed that indirect benefits could play a role in the maintenance of apparently harmful male mating behaviors provided females obtain "good genes" that increase the average survival or sexual competitiveness of their offspring (e.g., (Kokko 2001). The relative magnitude of the direct costs and indirect benefits for females has been recently quantified in laboratory populations of fruit flies and house crickets, as well as for a subset of bird species (Arnqvist & Kirkpatrick 2005; Head *et al.* 2005; Orteiza *et al.* 2005; Stewart *et al.* 2005; Rice *et al.* 2006). These studies yielded contradictory results, suggesting that assessments of intergenerational effects in a larger number of systems and in more natural conditions are needed (Hosken & Tregenza 2006).

Here, we quantify lifetime and intergenerational fitness consequences of a sexual conflict for female common lizards (*Lacerta vivipara* Jacquin 1787) under near field conditions. We manipulated the sexual conflict due to multiple mating attempts by changing exposure to males for females during one year using an adult sex ratio manipulation (Fitze et al. 2005). Earlier, an adult male-biased sex ratio was found to increase the number of multiple mating attempts for females and the number of multiple genetic partners in a clutch (see Methods and (Fitze et al. 2005)).We also reported that the current survival and fecundity of female lizards plummet as a consequence of multiple male mating attempts (Fitze et al. 2005; Le Galliard et al. 2005b). The behavioral mechanism underlying the negative effects of males on females was sexual aggression by males (Le Galliard et al. 2005b). However, it still remains unknown whether these current costs of multiple mating for females may be compensated, or even outweighed, by putative positive responses later in the life and/or by indirect benefits through offspring quality. For example, female common lizards may gain indirect benefits from more multiple mating in male-biased populations, through a higher genetic diversity of their clutch, bet-hedging against genetic defects and/or "good genes" for the viability of their offspring (Laloi *et al.* 2004; Fitze *et al.* 2005; Richard *et al.* 2005). By

monitoring females and their first generation of offspring during two additional years in a common garden with a female-biased sex ratio, we were able to test for possible trade-offs between successive reproductive events and for indirect benefits through offspring quality. Our study thus allows investigating the short- and long-term fitness consequences of potentially harmful male mating behaviors for females and their offspring, which are especially important for the understanding of the sexual conflict in long-lived organisms.

## MATERIAL AND METHODS

### *Study species*

*Lacerta vivipara* is a small ground-dwelling ovoviparous lizard species in which sexes share overlapping home ranges and adults breed once a year (Lecomte et al. 1994). In this species, the sexual dimorphism involves differences in body shape and coloration patterns (Bauwens et al. 1987). Females reach larger adult snout-vent length (SVL) and have duller ventral coloration than males (Massot et al. 1992). In females, the carotenoid-based ventral coloration extends from the throat to the basis of the tail, ranges from light yellow to orange, and is not fully developed before adulthood (age $\geq$ 2 years, (Cote 2002). A previous experiment found a strong plasticity of the ventral coloration of female lizards, which was indicative of the stress, hence potential condition, of the individual (Cote and Fitze, unpub. res.).

### *Experimental design*

We maintained 12 experimental populations in enclosures located in a natural meadow at the Ecological Research Station of Foljuif (France, 60 m a.s.l., 48°17'N, 2°41'E). The enclosure's habitat matched the natural habitat of the species and each enclosure (10 × 10 m) was surrounded by plastic walls to prevent lizards from escaping (see (Boudjemadi *et al.* 1999) for more details). Lizards introduced in these populations at the start of the study (June 2002)

were obtained from natural populations of the Cévennes area (44°30' N, 3°45' E, 1400–1600 m above sea level) and marked by toe clipping.

A detailed description of the experimental procedures has been given elsewhere (Fitze *et al.* 2005; Le Galliard *et al.* 2005a; Le Galliard *et al.* 2005b) and we briefly summarize our study design here (see also Figure 1). To enhance exposure to males, we created 6 populations with a male-biased adult sex ratio and compared the fate of females from these populations with that of females from 6 populations with a female-biased adult sex ratio (Figure 1). Yearling ($n$ = 12 per population) and juvenile ($n$ = 42-45 per population) sex ratios were hold constant and balanced (50:50) in all populations. The adult sex ratio ($n$ = 18 adults per population) of the female-biased populations (22 % of males) corresponds to the mean adult sex ratio in a natural habitat from which the source lizards originated (average adult sex ratio = 18 % ± 0.18 s.d.). The adult sex ratio of male-biased populations (78 % of males) corresponds to the extremes in the same natural habitat (Le Galliard et al. 2005a).

We have previously reported on the number of mating attempts for all females that survived the first year of this experiment (Fitze et al. 2005). To this aim, we counted the number of matins scars on the belly of the females and assessed multiple-partner mating by determining paternity of all fertilized eggs using microsatellite genotyping. Our analyses demonstrated (1) that female lizards were subjected to an overall three-fold increase in the number of mating attempts by males in male-biased populations (3.62 versus 1.49 per female, (Le Galliard et al. 2005b)), (2) that this effect was stronger in females that had multiply sired clutches than in monandrous females (Fitze et al. 2005), and (3) that male-biased sex ratios increased the number of multiply sired clutches for polyandrous females (Fitze et al. 2005). Altogether, these results indicate that mating rate was higher in the male-biased populations than in the female-biased populations.

Adult sex ratios vary significantly though time and space in natural common lizard populations (Le Galliard et al. 2005a), with extreme deviations towards male-biased sex ratios (> 60 % adult males) occurring in ca. 10 % of the social neighborhoods inhabited by female lizards. After one year of sex ratio manipulation, we therefore released all alive females ($n$ = 148) from male-biased and female-biased populations and their alive offspring ($n$ = 551) into new populations with a female-biased sex ratio to mimic the long-term mean sex ratio experienced by female lizards (Figure 1). Within each enclosure, the offspring sex ratio was held constant (1:1) and the proportion of offspring originating from male-biased and female-biased populations was similar. We monitored females and their first generation offspring during two additional years following the sex ratio manipulation by recapturing lizards in each enclosure during late May of each year (Figure 1).

*Monitoring procedures*

Before release and for each capture, snout-vent length (SVL) was measured to the nearest mm and body mass was measured to the nearest mg using an electronic scale. Captured female lizards were housed in individual terrariums in the laboratory (Figure 1). Females were classified as gravid or non-gravid by palpation of the abdominal cavity and their terrariums were checked daily for newborns at 9:00 and 14:00 o'clock. Approximately 1 hour after detection of newborns, mothers were removed from their terrariums and the number of dead and viable offspring was counted. All offspring were measured for SVL, tail length, and body mass at the day of oviposition.

Of all adult females, we measured the carotenoid-based ventral coloration on the middle of the thorax before release (June 2002) and one day after capture (June 2003 and June 2004), using a spectrophotometer (USB2000, Ocean Optics Inc., Dunedin, FL, USA), a xenon light source (PX-2, Ocean Optics Inc.) and a reflection probe (R400-7-UV/VIS, Ocean Optics Inc.) following standard procedures (Endler 1990; Hill & Graw 2006). We obtained a measure of

the spectral reflectance in the interval 200–800 nm, but restricted our analyses to the human visible spectrum (400–700 nm) since carotenoid pigments reflect light only in this range (Hill 1998). We used the reflectance spectra to measure the hue, which is an angular measurement indicating the redness of the ventral coloration and where pure red refers to 0°, followed by orange (40-45°) and yellow (90°). The computation of the hue was done according to Endler's segment classification (1990) with the program COLOR 1.4 (available on request from jmrossi@snv.jussieu.fr). We found a high and significant repeatability of hue measurements ($n$ = 218 individuals, 3 measurements per individual, $F_{217,437} = 6.97$, $P < 0.0001$, $r = 0.67$).

*Statistical analysis*

We first analyzed the consequences of the sex ratio manipulation on the current reproductive characteristics and the carotenoid-based ventral coloration in females. We investigated carotenoid-based ventral coloration, since carotenoid-based coloration is believed to honestly reflect individual quality (Olson & Owens 1998) and thus may respond plastically to sexual conflicts. We next analyzed lifetime effects for females, including delayed responses to the sexual conflict, later in life. Finally, we studied the body growth, survival and reproduction of the first generation of offspring in order to quantify the intergenerational effects of the sex ratio manipulation.

For the analysis of the female traits, all models contained the following factors: adult sex ratio treatment and female age class as fixed effects (juvenile, yearlings and adults), SVL of the female as a covariate, and enclosure nested within treatment as a random factor. For the analysis of the offspring traits, the model also included a random effect of family nested within enclosure. When studying effects of the treatments during the second and third year of the experiment, the models further included release enclosure as a random effect. Initial models contained all factors and their interactions, and selection was done backward. Normally distributed variables were analyzed with linear models using the MIXED procedure

in SAS (Littell et al. 1996) and the assumptions of these models (normality and homogeneous variance of residuals) were fulfilled. Binomial data were modeled with logistic regression using the GLIMMIX procedure with a logit link (Littell et al. 1996). The goodness of fit of logistic regressions was checked with a Pearson chi-square test (McCullagh & Nelder 1989).

## RESULTS

### *Current effects of the sex ratio manipulation*

In the first study year, the mortality of yearling and adult females was increased dramatically by male excess (logit survival contrast = –2.470 ± 0.05 s.e., $P < 0.0001$), while the survival of juvenile females was not significantly affected (contrast = –0.686 ± 0.42 s.e., $P = 0.10$; see (Le Galliard *et al.* 2005b). Gravid females produced on average 1.95 viable offspring (± 0.62 s.e.) less in male-biased populations (Poisson regression, treatment: $F_{1,10} = 8.44$, $P = 0.02$; SVL: $F_{1,111} = 56.5$, $P < 0.0001$). Furthermore, oviposition date was affected by a significant interaction between treatment and age class ($F_{2,107} = 4.08$, $P = 0.02$). In male-biased populations, adult females oviposited on average 10.38 days (± 2.96 s.e.) later than in female-biased populations ($P = 0.0007$), while the treatment had no effect on oviposition date in juveniles (0.69 days ± 2.06 s.e., $P = 0.74$) and yearlings (0.88 days ± 2.59 s.e., $P = 0.73$). Finally, the sex ratio manipulation also affected the hue change in adult females (treatment: $F_{1,7} = 10.85$, $P = 0.01$, $n = 62$). The ventral coloration of females in female-biased populations got more orange (change = -9.25 ± 3.25 s.e., $P = 0.02$), while in females of male-biased populations it got slightly (but not significantly) yellower (change = 6.83 ± 4.63 s.e., $P = 0.18$).

### *Lifetime effects of the sex ratio manipulation*

We quantified the total reproductive success (*TRS*) of each female released in the experiment as

$$TRS = S(2002 \rightarrow 2003)\left[F_{2003} + S(2003 \rightarrow 2004) \times \left[F_{2004} + S(2004 \rightarrow 2005) \times F_{2005}\right]\right], \quad (1)$$

where $S$ stands for annual survival probability and $F$ stands for annual fecundity (number of viable offspring produced each year). The *TRS* was affected by the sex ratio treatment, the age, and the interaction between sex ratio treatment and age (treatment: $F_{1,10} = 25.37$, $P = 0.0005$; age class: $F_{2,425} = 19.84$, $P < 0.0001$; treatment × age class: $F_{2,425} = 13.26$, $P < 0.0001$, $n = 441$). Yearling and adult females had lower *TRS* in male-biased populations (Tukey contrasts, all $P < 0.0001$), but not juvenile females (Tukey contrast, $P = 0.66$; Figure 2A). When analyzing reproductive success conditional on survival during the first year of the experiment [i.e., $S(2002 \rightarrow 2003) = 1$ in equation (1)], we found no difference between treatments (treatment: $F_{1,10} = 0.10$, $P = 0.76$; age class: $F_{2,144} = 12.17$, $P < 0.0001$; treatment × age class: $F_{2,142} = 0.55$, $P = 0.57$, $n = 158$, Figure 2B). Therefore, fecundity costs of male mating attempts during the first year of the experiment were compensated by life history responses later in life.

To further understand these compensatory life history responses, we analyzed the body growth, survival, reproductive characteristics and ventral coloration of females after the sex ratio manipulation (see Figure 1). The sex ratio treatment had no detectable effects on body growth during the first, on fecundity during the first and on all life history traits studied during the second year following the treatment (all $P > 0.32$). However, three positive delayed responses were observed in females from male-biased populations during the first year following the sex ratio manipulation. Firstly, the annual survival probability of females from male-biased populations was 0.70 [0.49,0.85] (95% CI), but only 0.42 [0.32,0.53] for females from female-biased populations, a significant difference ($F_{1,10} = 6.87$, $P = 0.03$, $n = 148$). Secondly, clutch success (the proportion of viable eggs per clutch) was higher for females

from male-biased populations (0.89 [0.59,0.98] (95% CI)) than from female-biased populations (0.49 [0.29,0.69], $F_{1,10} = 7.15$, $P = 0.02$). Thirdly, ventral coloration shifted more strongly towards orange in adult females from male-biased populations (change = -24.16 ± 3.88 s.e., $P < 0.0001$) than in adult females from female-biased population (change = -4.27 ± 1.50 s.e., $P = 0.01$; treatment: $F_{1,6} = 8.61$, $P = 0.03$; hue(2003): $F_{1,7} = 16.72$, $P = 0.005$, $n$ = 23).

### *Intergeneration effects of the sex ratio manipulation*

Offspring body condition at hatching was higher in male-biased than in female-biased populations, but the sex ratio manipulation had no effect on SVL and tail length of the first generation of offspring at hatching (Table 1). Offspring survival, body growth and the annual fecundity of female offspring were not affected by the maternal sex ratio treatment at the juvenile ($n$ = 551 released individuals) and at the yearling stage ($n$ = 130 released individuals, all $P > 0.51$). Offspring survival until the age of two years was 0.12 [0.09,0.16] (95% CI) in offspring whose mothers originated from male-biased populations and 0.14 [0.06,0.31] in offspring whose mothers originated from female-biased populations.

## DISCUSSION

Earlier, we reported that male-biased sex ratios increased the mating rate and the number of multiply sired clutches for polyandrous female *Lacerta vivipara* (Fitze et al. 2005). Furthermore, during the first year of the study, male-biased sex ratios caused females to survive and reproduce poorly relative to females from female-biased populations (Le Galliard et al. 2005b). Here, we quantified the lifetime and intergenerational fitness consequences of multiple mating attempts by monitoring females and their first generation of offspring during two additional years in a common garden with a female-biased sex ratio. Only 24 individuals out of 441 released females (ca. 5 %) and 68 out of 551 offspring of the first generation (ca.

12%) survived until the end of the study period, showing that our measurements of female and offspring fitness are close to lifetime reproductive success. The field experiment yielded three main results. First, we found unambiguous evidence for lower lifetime reproductive success in females of male-biased populations, and thus direct lifetime costs of multiple mating attempts. Second, females compensated later in life for the immediate fecundity costs due to multiple mating, implying that the main lifetime costs were the direct negative effects on female survival. Third, the direct lifetime costs of multiple mating were not mitigated by indirect benefits through offspring viability, offspring growth and/or daughters' fecundity.

*Lifetime effects*

In a previous study, we reported that the excess of adult males had immediate survival and fecundity costs for female lizards (Le Galliard et al. 2005b). Here, we further found that adult females of male-biased populations oviposited later in the season, which may reduce the time for growth and maturation of their offspring (Olsson & Shine 1997; Sinervo 1999). Male excess also caused a reduction in the redness of the ventral coloration in adult females. The mating behavior in this species can involve a ferocious battle where the male bites the female on the flanks during up to several hours, and male-biased sex ratios exacerbated the number of male mating attempts that females experienced (Fitze et al. 2005). The most likely behavioral mechanism of male harm on female current survival, reproduction and coloration was found to be sexual aggression by males (Le Galliard et al. 2005b). The proximate physiological and ecological processes could include direct injuries causing death or pathogen infection (Shine et al. 2001), harassment constraining critical foraging and basking activities (Magurran & Seghers 1994), and/or chronic stress that suppressed reproduction or immune defenses (Svensson et al. 2001).

Fitness costs in females were age-dependent: first, survival and total reproductive success were negatively affected by male excess in yearlings and in adults, but not

291 significantly in juvenile females; second, oviposition dates of females were affected by male
292 excess only in adult females. These results are somewhat surprising given that older females
293 have a larger body size and should potentially be more resistant to sexual aggression than
294 younger females (Clutton-Brock & Parker 1995). Age-dependent costs in female lizards could
295 be explained by the fact that older females emerge earlier from wintering than younger
296 females (Bauwens & Verheyen 1985), by age-assortative mating between male and female
297 lizards (Richard et al. 2005) and/or by male mating preferences for older females. As a
298 consequence, the adult sex ratio manipulation would have resulted in longer and/or more
299 intense male aggression during mating for older females.

300 The lifetime fitness effect of male excess on females was dominated by the immediate
301 survival costs, since it appeared that immediate fecundity costs of multiple mating attempts
302 were compensated by positive fitness responses of females later in their life. Females from
303 male-biased populations had higher survival and clutch success one year after the sex ratio
304 manipulation, and they also became more orange later in their life. Since we previously found
305 no differential selection on female's body size and condition during the first year of the
306 experiment (Le Galliard et al. 2005a), these compensatory responses can hardly be explained
307 by an inherent better quality of females from male-biased populations. Another, more likely,
308 explanation is that females from male-biased populations reinvested the energy saved during
309 their first breeding episode into future reproduction and therefore traded-off current with
310 future reproduction. Such life history responses may be a very general feature of sexual
311 conflicts in iteroparous species, which may enable females to mitigate some of the direct costs
312 of mating and therefore "do the best of a bad job" (Reyer *et al.* 1999; Lessels 2005).
313 However, the evolutionary impact of these counter-responses by females may be limited if
314 females lack the ability to avoid social environments where the risks of harmful mating are
315 high (Rowe et al. 1994), e.g. when population sex ratios are stable through time and space.

316 *Intergenerational effects*

317 Nonetheless multiple mating attempts by males cause direct costs for females, female lizards
318 may profit from multiple mating, given that large indirect benefits may counterbalance the
319 direct lifetime costs (e.g., (Kokko 2001; Cameron *et al.* 2003; Cordero & Eberhard 2003). We
320 have shown elsewhere that higher exposure to males increased the number of male mating
321 attempts and the number of multiply sired clutches for polyandrous females (Fitze et al.
322 2005). In turn, more multiple mating might bring indirect benefits for female common lizards,
323 through a higher genetic diversity of their clutch, bet-hedging against genetic defects and/or
324 "good genes" for their offspring (see (Laloi *et al.* 2004; Fitze *et al.* 2005; Richard *et al.* 2005)
325 for discussion of potential benefits for females of multiple mating in this species). However,
326 we found very limited evidence for such indirect benefits. Even though offspring condition at
327 hatching was higher in male-biased populations, putative gains of an enhanced body condition
328 at hatching did not significantly affect the components of offspring fitness investigated, which
329 included body growth, survival, and daughters' fecundity during the two first years following
330 birth.

331 One weakness of our study is that we failed to assess potential benefits of multiple
332 mating via sexual selection on sons (the "sexy son" hypothesis, (Weatherhead & Robertson
333 1979)). Several authors have claimed that large indirect benefits via sons' attractiveness may
334 often outweigh potential direct costs of multiple mating (e.g., (Kokko 2001; Cordero &
335 Eberhard 2003; Pizarri & Snook 2004), while others found poor empirical evidences of large
336 indirect benefits through sons' attractiveness (Arnqvist & Rowe 2005). In a recent study,
337 however, (Head *et al.* 2005) reported a two-fold increase in the sexual attractiveness of sons
338 derived from mating with preferred males, which compensated for a direct cost of mating in
339 female crickets. Here, in the absence of indirect benefits via offspring common lizards'
340 viability and fecundity, only a more than twelve-fold increase in the sexual attractiveness of

the sons could compensate for the direct lifetime costs of mating for females in this study (see Figure 2A). This seems an seems unrealistically large effect of a "sexy son" effect (Arnqvist & Rowe 2005) . Therefore, indirect benefits via sons' attractiveness are unlikely to counter-balance the direct lifetime costs detected here.

Relatively few studies have been able to assess most of the fitness consequences of multiple mating attempts for females, especially for long-lived organism under field conditions (Andersson 1994; Maklakov *et al.* 2005; Hosken & Tregenza 2006). Overall, our field experiment suggests no indirect benefits of multiple male mating attempts for females via viability selection on their offspring and fecundity selection on their daughters, but strong direct lifetime costs via current female survival. This result strengthens the conclusions of two other recent studies that quantified some of the direct and indirect fitness effects of multiple mating for females. In the fruit fly laboratory model system, (Orteiza *et al.* 2005) assessed that the direct lifetime fitness costs of multiple male mating attempts were 7-fold larger than the indirect fitness benefits for females (see also (Stewart *et al.* 2005; Rice *et al.* 2006)). Moreover, a review of few studies quantifying the relative forces of direct and indirect selection on female extra-pair copulation behavior in birds suggested that direct selection was about one order of magnitude stronger than indirect selection (Arnqvist & Kirkpatrick 2005). Thus, several studies at hand suggest that male mating behavior may impose serious costs on females that cannot be entirely compensated for.

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## TABLES

Table 1. Effects of sex ratio manipulation on offspring traits at hatching. Both dead and viable offspring were included in the analysis, and a categorical factor (dead or viable) was included into the model. Estimates are given for female-biased populations (F) and dead (D) offspring. Bold terms indicate significant effects after correction for multiple testing using a sequential Bonferroni procedure. Larger females produced longer and heavier offspring; offspring SVL, tail length, and body condition decreased with increasing clutch size; and hatching date was negatively correlated with offspring size and condition.

| | SVL | | Tail length | | Body condition | |
|---|---|---|---|---|---|---|
| Factors | Estimates ± s.e | Test statistics | Estimates ± s.e | Test statistics | Estimates ± s.e | Test statistics |
| Treatment (F) | 0.22 ± 0.35 | $F_{1,10} = 0.40$ | -0.32 ± 0.57 | $F_{1,10} = 0.33$ | **135.37 ± 35.7** | **$F_{1,10} = 14.86$ **** |
| Mother SVL | **0.11 ± 0.03** | **$F_{1,498} = 16.36$ ***** | **0.17 ± 0.04** | **$F_{1,497} = 14.42$ **** | **1.78 ± 0.50** | **$F_{1,495} = 12.60$ **** |
| Clutch size | **-0.18 ± 0.07** | **$F_{1,498} = 6.68$ *** | **-0.28 ± 0.11** | **$F_{1,497} = 6.56$ *** | **-3.87 ± 1.28** | **$F_{1,495} = 9.12$ **** |
| Hatching date | **-0.07 ± 0.01** | **$F_{1,498} = 19.46$ ***** | **-0.08 ± 0.02** | **$F_{1,497} = 12.31$ **** | **-0.81 ± 0.27** | **$F_{1,495} = 8.98$ **** |
| Offspring category (D) | 0.03 ± 0.14 | $F_{1,496} = 1.40$ | **-1.21 ± 0.25** | **$F_{1,494} = 23.70$ ***** | -4.03 ± 2.11 | $F_{1,494} = 3.63$ † |
| SVL at hatching | - | - | - | - | **15.55 ± 1.53** | **$F_{1,495} = 206.86$ ***** |
| Treatment × SVL at hatching | - | - | - | - | **-6.62 ± 1.65** | **$F_{1,495} = 16.07$ ***** |
| Enclosure(Treatment) | 0.13 ± 0.10 | $Z = 1.33$ | 0.33 ± 0.23 | $Z = 1.39$ † | 38.99 ± 32.82 | $Z = 1.19$ |
| Clutch(Enclosure, Treatment) | **0.70 ± 0.12** | **$Z = 5.89$ ***** | **1.71 ± 0.30** | **$Z = 5.60$ ***** | **233.19 ± 38.92** | **$Z = 5.99$ ***** |

† P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001

## FIGURES LEGENDS

Figure 1. Experimental design. The sexual conflict over multiple mating was first manipulated by changing the adult population sex ratio (ASR) from female-biased to male-biased (male excess). After one year, females and their offspring from both treatments were released in female-biased populations where they were maintained during two additional years. In the first year, 18 adult females, 10 adult males, 6 yearling males and 6 yearling females were introduced in each of 8 enclosures. In the second year, 9 adult females, 6 adult males, 8 yearling males and 8 yearling females were introduced in each of 16 enclosures. Lifetime and intergenerational fitness consequences were scored by measuring fitness components in females and their first generation of offspring during each year of the study (see text for more details).

Figure 2. Lifetime consequences of the sex ratio manipulation. A. Mean total reproductive success of female common lizards (± s.e.) per sex ratio treatment and age class. The total reproductive success was measured by counting the number of viable offspring produced by each female during the three years of the study. B. Mean reproductive success of female common lizards conditional on first year survival (± s.e.) per sex ratio treatment and age class. The reproductive success was measured as the total reproductive success conditional on survival during the first year of the experiment, which measures the balance between fecundity costs of multiple male mating attempts and compensatory responses of females later in their life (see equation (1) in the main text). Filled bars, male-biased populations; open bars, female-biased populations.

FIGURE 1

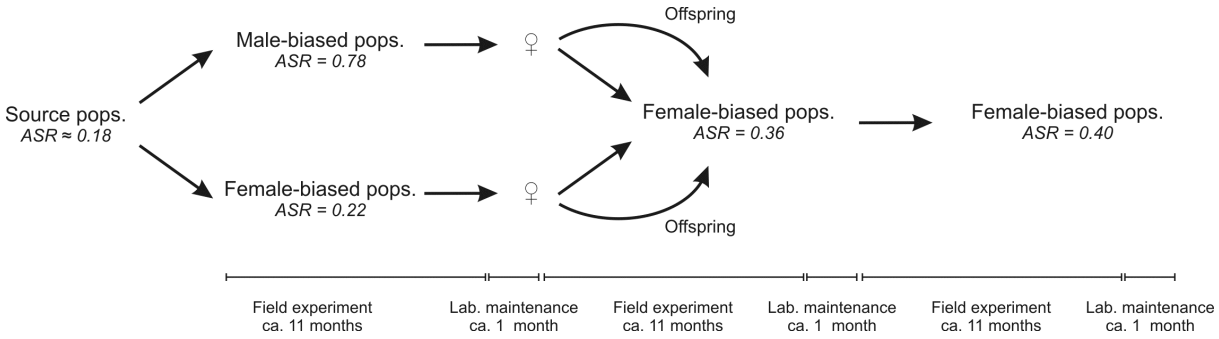
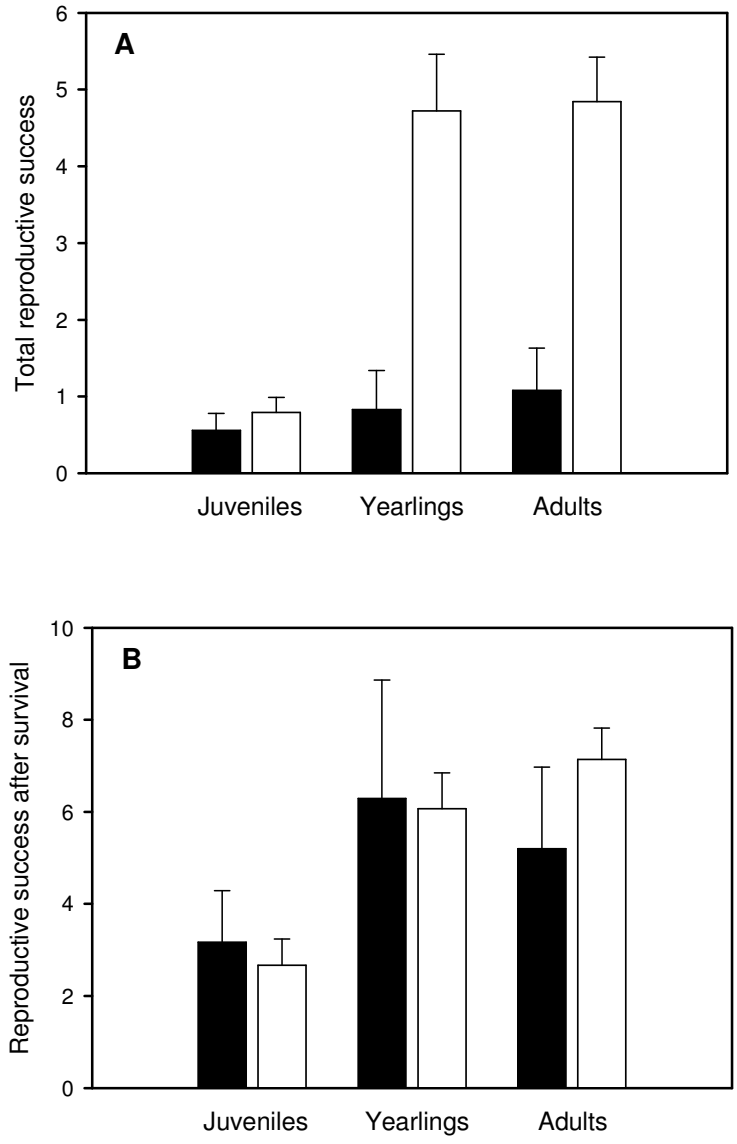

Source pops.
ASR ≈ 0.18
Male-biased pops.
ASR = 0.78
Female-biased pops.
ASR = 0.22
♀
♀
Offspring
Offspring
Female-biased pops.
ASR = 0.36
Female-biased pops.
ASR = 0.40
Field experiment
ca. 11 months
Lab. maintenance
ca. 1 month
Field experiment
ca. 11 months
Lab. maintenance
ca. 1 month
Field experiment
ca. 11 months
Lab. maintenance
ca. 1 month

FIGURE 2


A
Total reproductive success
0
1
2
3
4
5
6
Juveniles
Yearlings
Adults
B
Reproductive success after survival
0
2
4
6
8
10
Juveniles
Yearlings
Adults

# ANNEXES

# MANUSCRIT 9

# Context-dependent mate choice in female common lizards *Lacerta vivipara*

Soumis à *Behavioral Ecology and Sociobiology*

# Context-dependent mate choice in female common lizards *Lacerta vivipara*

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Running head: Context-dependent mate choice

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## *Abstract*

A recent theory proposes that optimal female mate choice should be context-dependent. However, few empirical evidence exists and the importance of male coercion for female mate choice is unknown. To address these questions, we investigated mate choice in females of the polygynandrous common lizard (*Lacerta vivipara*). We presented a single female to a single male in a staged mating experiment, which excludes non-random mating patterns potentially arising due to intra-sexual selection. We found that females rejected and fended off males and that females lasting longer to mate were choosier. This clearly shows that female mate choice exists in common lizards, suggesting that female mate choice might be much more frequent in reptiles than believed so far. To investigate context-dependent female mate choice we let females mate with several sequentially presented males. Compared to the first copulation, females mated with males of opposite body size during the second copulation. This indicates that female mate choice is dependent on the previous mating history. Our results further indicate that male coercion may compromise female mate choice suggesting that male coercion may importantly contribute to the observed huge variation in sexually selected male traits.



Keywords: context-dependent mate choice, coercion, body size, body condition, *Lacerta vivipara*, staged mating experiment, reptile

## *Introduction*

Mate choice is an important determinant of sexual selection (Darwin 1871; Andersson 1994), that may have profound implications for population viability (Bessa-Gomes et al. 2003). A huge amount of studies found that females show preferences for certain male characteristics (e.g. Bateson 1983; Andersson 1994; Eberhard 1996; Birkhead and Møller 1998). Female mate choice is believed to be more common than male mate choice because females classically produce a limited number of offspring while a male can produce an almost infinite number of offspring (Andersson 1994). In species where females may gain direct benefits from choosing a given male (e.g. through parental care, territory defence, access to good territories, nuptial gifts, protection from predators, etc.), males of better quality are typically preferred. However, in species where females do not gain direct benefits, it is less obvious why they should be choosy. Several hypotheses explain why female choice is beneficial. First, female choice might be exerted to enhance the offspring's genetic quality and thus good quality males should be preferred (Thornhill and Alcock 1983b; Birkhead and Møller 1998). Second, females may maximize the offspring's genetic diversity by favouring genetic dissimilar males (Zeh and Zeh 1996; Tregenza and Wedell 2000; Reusch et al. 2001; Mays and Hill 2004; Neff and Pitcher 2005). Third, females may simply hedge against sterility or genetic defects of the potential partners (Thornhill and Alcock 1983a; Birkhead and Møller 1998; Wolff and Macdonald 2004). Fourth, female choice may be favourable in variable social environments (Alonzo and Sinervo 2001) and thus, although rarely being documented (David et al. 2000; Jia et al. 2000; Qvarnstrom 2001), it might be context-dependent.

Disentangling between the different hypotheses is constrained by the difficulty to assess female choice under natural conditions, since non-random mating can usually be explained by mechanisms other than female mate choice (Bateson 1983; Birkhead and Møller 1998). First, it is known that intra-sexual competition in males, over access to females, may generate non-

78 random mating (e.g. Bateson 1983; Olsson 1993; Cooper and Vitt 1997). Better quality males
79 are typically dominant over lower quality males and exclude them from mating with good
80 quality females. As a consequence, assortative mating with respect to e.g. body size may arise
81 (Cooper and Vitt 1997). Second, trait-dependent emergence patterns from hibernation, or
82 trait-dependent differences in behaviour or conspicuousness (Bateson 1983; Olsson et al.
83 1996) may lead to non-random mating. Third, female choice might be constrained by sexual
84 harassment (Fitze et al. 2005) or by a female's condition (Richard et al. 2005). Since sexual
85 harassment and body condition are variable in time, a female's choice might also be context-
86 dependent. Consequently, only controlled experiments will allow disentangling between
87 female choice and these alternative sources of non-random mating.
88 Contrasting to mammals, birds and fish, there is very few evidence for the existence of female
89 choice in reptiles (Tokarz 1995; LeBas and Marshall 2001; LeBas 2002; Olsson et al. 2003).
90 The paucity of female choice is especially surprising because lizards are often sexually
91 dimorphic, frequently have extravagant traits, and numerous species have polygynandrous
92 mating systems (Stamps 1983). Several studies found under natural conditions that, in
93 reptiles, mating is not random with respect to body size (Olsson 1993; Cooper and Vitt 1997;
94 Shine et al. 2001; Lemaster and Mason 2002; Weatherhead et al. 2002; but see LeBas and
95 Marshall 2001) and studies suggesting that females prefer other male traits than body size are
96 rare (Olsson et al. 2003). Evidence for the existence of female mate choice is mainly derived
97 from observations under natural conditions. Because experimental evidence for the existence
98 of the above-mentioned alternative explanations has been provided (male-male competition,
99 size-dependent emergence patterns; e.g. Olsson 1993; Olsson et al. 1996; Cooper and Vitt
100 1997), these studies are not conclusively demonstrating the existence of female choice.
101 Indeed, female choice was experimentally demonstrated in only three species of lizards and
102 one species of snakes (Cooper and Vitt 1993; Censky 1997; Shine and Mason 2001). It is
103 therefore unknown whether in reptiles female mate choice is explaining the observed non-

104 random mating patterns or whether mainly the alternative scenarios are dominating. Similarly,
105 context-dependent female choice has been rarely demonstrated in lizards (Olsson et al. 2003),
106 and in snakes only Weatherhead et al.'s study (2002) provides weak evidence of its existence,
107 although a theoretical model predicts that context-dependent female choice would be the
108 optimal mating strategy, for at least one lizard species (Alonzo and Sinervo 2001).
109 We therefore designed a staged mating experiment in the common lizard (*Lacerta vivipara*),
110 which excludes intra-sexual selection, trait-dependent emergence patterns, and trait-dependent
111 differences in conspicuousness, to investigate both, whether female choice exists and whether
112 female choice is context-dependent. A previous study showed that the common lizard's
113 number of mate partners and fitness changed with age in a quadratic manner, with younger
114 and older females being more polyandrous than the intermediate-aged females, and with
115 intermediate-aged females having highest fitness (Richard et al. 2005). This suggests that
116 females may choose their mate partners, that only intermediate-aged females may exert their
117 choice (Richard et al. 2005) and thus that context-dependent female choice may exist. Further,
118 it is suggested that in the common lizard two types of females may exist: choosy females and
119 females that are less or not choosy (Fitze et al. 2005; Richard et al. 2005) and a recent study
120 indicates that male sexual aggression may be an important determinant of female fitness (Le
121 Galliard et al. 2005) and thus that it may importantly constrain a female's choice.
122 We conducted a staged mating experiment where we presented a single randomly chosen
123 male to a single female. If no copulation was observed, the male was removed and the female
124 was provided with a new male until the female copulated. This design thus excludes non-
125 random mating due to intra-sexual competition, non-random emergence patterns from
126 hibernation, non-random male encounter probabilities and non-random mating due to
127 differences in conspicuousness. To investigate whether females were choosy, we analysed
128 whether all females copulated and whether females copulated with all presented males. In
129 females that mated with the first presented male it is not possible to know whether or not they

might have been choosy. Consequently, we selected the females that did not mate with the first presented males and analysed whether the males with which a female copulated were different from the males with which they did not copulate and whether females that took longer to mate may have stronger preferences. To investigate whether females show repeatable preferences and to test for context-dependent female choice, dependent on the previous mating history, we continued presenting males to a female after the first copulation. In several species it is suggested that females might first mate with a non-optimal male, to ensure the fertilization of the eggs, and thereafter with an optimal male (Petrie et al. 1992). Therefore, we investigated whether there existed a correlation between the traits of the first and second copulating mate partners and we measured the repeatability of the female mate partner's characteristics. In this species the males grip the females on the posterior abdomen with their mouth, to initiate copulation, and then twist their body around the female, in order to introduce the hemi-penis into the female's cloacae (Bauwens and Verheyen 1985). These mating attempts may result immediately in copulation or in mating struggles that may or may not result in copulations (personal observations). This shows that male sexual coercion, which is defined as the use of force that functions to increase the chances that a female will mate (Smuts and Smuts 1993), exists. To investigate whether copulation was initiated due to sexual coercion or due to a female's will, we observed whether females allowed males to copulate or whether females tried to resist a copulation attempt. By analysing the first and the second copulating male's traits we further investigated whether context-dependent female choice based on the previous mating history may exist.

## *METHOD*

### Species description

The common lizard (*Lacerta vivipara*) is a small *Lacertidae* inhabiting non-exclusive home ranges in peat bogs and moist heath lands (Massot et al. 1992; Clobert et al. 1994). Males emerge from hibernation in February – March, approximately one month earlier than females. Directly after the females' emergence, copulations can be observed. In this species, adult males are dominant over one-year old males (Lecomte et al. 2004), and, although fights among males can be observed (Heulin 1988; personal observations M. De Fraipont), males seem to assess their competitive ability mainly without fighting (Clobert et al. 1994)). Mating lasts from a couple of minutes up to several hours (Heulin 1988). During mating attempts, a male grips the female on the posterior abdomen with its mouth, and then tries to twist its body around the female, in order to introduce its hemi-penis into the female's cloacae. As a result of the male's grip, the female's belly shows a U-shaped scar (Bauwens and Verheyen 1985). Female common lizards show a short receptive window during which they mate with several different partners (Heulin 1988). As a consequence females give birth to offspring, which are fathered by up to five different males (Laloi et al. 2004; Fitze et al. 2005; Richard et al. 2005). Two current studies indicate that female choice may exist and that it might be constrained by males trough male aggression (Fitze et al. 2005) and/or by female-age (Richard et al. 2005).

### Pre-experimental conditions

All experiments were conducted at the ecological field station of Foljuif (Saint-Pierre-lès-Nemours, Seine et Marne, France). In July of the years 2001 and 2002, female and male lizards (*Lacerta vivipara*) were captured by hand in enclosures at the ecological field station. The lizards originated from natural populations located on the Mont-Lozère in the Cévennes (1500 m asl., Massif Central, South-eastern France, 44°00'N, 3°45'E) and were introduced into the populations located at Foljuif in 1992, for the purpose of other studies (for example

178 Lecomte et al. 2004). For the present study, the captured lizards were introduced into empty
179 100 $m^2$ big outdoor enclosures, which contained natural vegetation, hides, rocks and two
180 ponds (for more details see Lecomte and Clobert 1996; Le Galliard 2003; Lecomte et al.
181 2004). Females and males were released in separate enclosures containing no individuals of
182 the opposite sex to prevent them from uncontrolled mating. In 2001 we established three
183 female and three male enclosures and in 2002 four female and four male enclosures. A similar
184 number of lizards was introduced into each of the enclosures. To protect the lizards from
185 avian predators the enclosures were covered with nets and to reduce the risk of shrew
186 predation, traps (Ugglan, Grahnab, Sweden) were placed inside and outside the enclosures.
187

188 **Laboratory conditions**

189 In early spring 2002 and 2003 the outdoor enclosures were regularly inspected to register
190 female emergence. Beside the sex-segregated enclosures, other enclosures containing female
191 and male lizards were regularly inspected, to determine the onset of mating. Mated females
192 were determined by the presence of mating scars, typically being present on the belly of
193 females after copulation (Bauwens and Verheyen 1985). The day when the first mating scars
194 were detected, female and male lizards were captured in the experimental enclosures.
195 Subsequent to the capture, lizards were weighed to the nearest 0,002 g and the snout-vent
196 length (SVL) was measured with 1mm precision. Thereafter all captured lizards were
197 introduced into individual terraria (25 x 15 x 15 cm), which were layered with soil and
198 equipped with a small water pond and two types of hides. Terrariums were numbered for
199 individual identification of the lizards and the same lizard stayed in the same terrarium during
200 the entire experiment. Terrariums were enlightened with an incandescent bulb (25 W) from
201 0900 to 1200 hours and from 1400 to 1700 hours. Lizards were fed with moth larvae (*Pyralis*
202 *sp.*) every four days and water was provided *ad libitum* (Le Galliard et al. 2003).
203

## Experimental method

In 2002 the mating experiments lasted from 31 March to 8 April and in 2003 from 7 April to 15 April. At the start of the experiment a randomly chosen female was introduced into an escape proof wooden box (2500 $cm^2$). Each wooden box contained two hides, to allow both, females and males to hide. Because only a limited number of boxes were available, not all females could be presented to a male directly after capture. The mating experiments started on average 3.36 days ± 0.23SE after capture. There was no correlation between the number of days a female stayed in the laboratory before the mating experiments started and her SVL ($F_{1,94}$ = 0.947, $P$ = 0.333) and her body mass ($F_{1,94}$ = 0.808, $P$ = 0.371). This shows that the time females stayed in the laboratory before the experiment started, was randomly attributed with respect to the female traits. Each wooden box contained a two shelters and a 40 W bulb, which provided light and heat. An additional UV-B neon light source provided UV-light to mimic the naturally occurring light. 2-4 minutes after releasing the females, a randomly selected male was introduced into the female box. The first daily mating experiment started at 0900 hours and the last experiment started not later than 1700 hours. Lizards were observed during one hour except if the lizards were still copulating one hour after the initiation of the encounter. In these cases copulations were observed until they ended and lizards were exchanged 5 minutes after the copulation ended. After one hour or after the end of the copulation, the males were removed from the female's box. Thereafter a new, randomly chosen male was introduced. This male presentation frequency was chosen because in a previous study, receptive females were gripped on the abdomen by 1.1 ± 0.9SE males per hour (range: 0.7 – 1.8 copulation attempts per hours; Heulin 1988). This procedure was followed until all females copulated with two or three males. In 2002, we quantified whether a female allowed a male to grip her abdomen and to subsequently copulate, or whether a female tried to resist. A female that tried to resist was defined as being a female that fended off a male's grip, by trying to escape or by biting the male, both usually resulting in mating-

struggles. This data allowed distinguishing between female choice and forced copulation, since resisting females indicate that they prefer not to mate with this male.

Statistical analyses revealed that males were presented in random order to females during the first (ANCOVA with SVL as dependent variable, female as random effect and male order as covariate: $F_{1,233} = 3.33$, $P = 0.07$) and during the second copulation attempt ($F_{1,165} = 1.77$, $P = 0.19$). A female-male encounter was defined as copulation when the male griped the female with the mouth on the posterior abdomen, when he successfully twisted the body around the female, and when his hemipenis penetrated the cloacae. If no successful copulation was observed during fifteen subsequent trials we stopped presenting males. If the last daily trial was finished and if a female did not yet copulate with two or three different males, we removed her from the wooden box and placed her back to the terrarium. The female then stayed over night in the shelves like all other lizards. The following morning she was again introduced into the same wooden box. On average males were presented to females on 2.82 days ± 0.17SE. Because in natural populations only 4-7% of the females give birth to offspring fathered by more than three different males (Laloi et al. 2004), females were allowed to copulate with three different males only. After the copulations took place, lizards were inspected for injuries caused by the inter-sexual interactions. No serious injuries (e.g. bleeding or loss of scales) could be found on females or males. However, mating scars, which typically arise due to the biting (Bauwens and Verheyen 1985), were visible on all mating females. Thereafter, the lizards were released in the new outdoor enclosures.

## Statistics

A total of 105 different females were used for this experiment. For the modelling of the different mating probabilities we used Proc GLIMMIX in SAS using a binomial error distribution and a logit link (Littell et al. 1996). To check for differences between years, we included year as random factor in all analyses and we explored the interaction effect of the

256 year with the covariates throughout. Non-significant interactions ($P > 0.05$) were backward
257 eliminated. In regression analyses, ANCOVAs and general linear models body condition was
258 modelled by adding body mass and SVL to the model as independent variables. In these
259 models, the effect of body mass was defined as body condition (Darlington and Smulders
260 2001; Garcia-Berthou 2001). For the analyses of body condition in non-parametric tests (e.g.
261 Spearman rank correlations) we used the residuals of the regression with SVL as independent
262 variable and body mass as the dependent variable. In several analyses dealing with the male's
263 body mass the degrees of freedom are reduced because measurements of four males were
264 missing.
265 The assumptions of the statistical models were verified in all cases (e.g. for ANCOVAs:
266 homoscedasticity and normality of the error; Quinn and Keough 2002). For the correlation
267 between the number of males presented to a female until the first copulation and the similarity
268 of the snout-vent length of the two partners, both the dependent and the independent variable
269 were log transformed to meet the assumptions. For some models, the assumptions were not
270 met after transformation. Consequently, we applied Spearman rank order correlations (SRC),
271 instead of parametric regression analyses, or Wilcoxon-signed ranks test (WSR) for the
272 analysis of paired samples (Siegel and Castellan 1988). The repeatability (r) of the mate
273 partner's traits was calculated according to Lessels and Boag (1987).
274

## RESULTS

### Female behaviour prior to copulation

Of the 223 encounters in 2002, 90 resulted in successful copulations. In 48 of the 223 encounters males gripped females on the posterior abdomen a couple of minutes before copulation. On average, males gripped females 16 minutes ± 3SE (range: 0 – 60 minutes) after the introduction into the female box. In 77.1% of the cases (37 of the 48 cases) a copulation was observed 9 minutes ± 2SE (range: 2 – 50 minutes) after the initiation of the grip. Males that gripped females during a couple of minutes before copulation, were not significantly different from those whose grip immediately resulted into copulation (SVL: $F_{1,88}$ = 0.228, $P$ = 0.634; body condition: $F_{1,88}$ = 0.351, $P$ = 0.555). In seven cases we observed that females were biting the gripping mate partner and in all seven cases the male previously gripped the females. This indicates that females tried to fend off the copulation attempt in 3.1%. In three of the seven occasions females were copulating with the mate partner after heavy battles, while in four occasions no copulation followed, indicating that forced mating may have happened in 3.33% of the copulations. Body size differences between partners that subsequently copulated (female body size – male body size = 2.33 mm ± 2.68SE; range: -1 until 5) were not significantly different from partners that were not copulating (3.50 mm ± 2.32SE; range: -3 until 10; $F_{1,5}$ = 0.108, $P$ = 0.755).

### First copulation

Nine females (8.6%) did not copulate with any male although we presented them at least fifteen different males (two of 47 females in 2002 and seven of 58 females in 2003). Females in good body condition were more likely to copulate (Proc GLIMMIX: $F_{1,102}$ = 4.60, $P$ = 0.034, logit slope: 3.110 ± 1.450SE) but the probability of copulating was not affected by the SVL ($F_{1,102}$ = 2.79, $P$ = 0.098, logit slope: -0.525 ± 0.314SE) and the year ($z$ < 0.01; $P$ = 1; all

300 interactions with year $P > 0.2$). On average the 96 females copulated with the $3.5^{th}$ ± 0.3SE
301 presented male (Fig. 1). 35 females (36.5%) mated with the first presented male.
302
303 **Copulation of the females not mating with the first presented male**
304 To investigate whether females might have been choosy and what kind of choice they exert,
305 we analysed the females that were not mating with the first presented male. In these females
306 the SVL difference and the body condition difference between partners that copulated was
307 smaller than the average difference of the partners that did not copulate (Table 1a).
308 There was a negative correlation between the number of males presented to a female until the
309 first copulation and the snout-vent length difference (female SVL - male SVL) of the
310 copulating partners (Table 2, 14.0% of total variance explained, Fig. 2). The SVL difference
311 of the mate partners was smaller in females engaging in a copulation after the presentation of
312 many males, while in females that copulated after the presentation of a few males the SVL
313 difference was bigger, suggesting that females that lasted longer to copulate were more
314 choosy. There was no significant correlation between the number of males presented to a
315 female until she copulated for the first time and the similarity of the copulating partners for
316 body condition (Table 2).
317
318 ***Second copulation***
319 Of the 73 females that copulated with a second male. 25 females copulated with the first male
320 presented after the first copulation. On average they copulated with the $2.3^{th}$ ± 0.3SE male
321 presented after the first copulation (maximum: $11^{th}$, 90%-quantile: $7^{th}$ male).
322 When considering the 48 females, which did not accept the male first presented after the first
323 copulation, we found that the SVL difference between partners that copulated tended to be
324 smaller than between partners that did not mate (Table 1b). The body condition difference of
325 copulating partners was smaller compared to partners that did not copulate (Table 1b).

## *Repeatability of a female's mate partner characteristics*

**First versus second copulation**

To investigate whether a female's mate partner characteristics may depend on a female's previous mating history we analysed the characteristics of the copulating males at the first and at the second copulation. The SVL of the first copulating male was negatively correlated with the SVL of the second copulating male ($F_{1,70}$ = 6.300, $P$ = 0.014, Fig. 3a; year: $F_{1,70}$ = 4.263, $P$ = 0.043; interaction $F_{1,69}$ < 0.001, $P$ = 0.990). No significant correlation was found between the body condition of the first and the second copulating male ($F_{1,68}$ = 1.325, $P$ = 0.254; year: $F_{1,69}$ < 0.001 $P$ = 0.999*;* interaction $F_{1,67}$ = 0.422, $P$ = 0.518).

During the second copulation, the difference in SVL between the accepted and not accepted males negatively correlated with the first copulating male's traits ($F_{1,45}$ = 4.759, $P$ = 0.034, estimate: -0.411 ± 0.188SE; Fig. 3b) and there was no such correlation for the body condition ($F_{1,44}$ = 0.069, $P$ = 0.795, estimate: -0.089 ± 0.257SE).

**All copulations**

Females did not copulate with males of similar SVL (ANOVA: $F_{72,121}$ = 0.739, $P$ = 0.919, repeatability ($r$) = -0.109) and body condition ($F_{71,118}$ = 1.092, $P$ = 0.332, $r$ = 0.034). The number of males that had to be presented to a female before the first, between the first and second and between the second and third copulation was repeatable ($F_{72,121}$ = 1.548, $P$ = 0.017, $r$ = 0.171).

## Discussion

*Female mate choice*

Femate mate choice has been demonstrated in a wide range of animal taxa (Bateson 1983; Andersson 1994; Eberhard 1996; Birkhead and Møller 1998). However, in reptiles conclusive evidence is rare (Tokarz 1995; LeBas and Marshall 2001; LeBas 2002) and is restricted to less than a hand full of studies (Cooper and Vitt 1993; Censky 1997; Shine and Mason 2001; Olsson et al. 2003). Our study shows that females were not mating with every possible male, neither during the first, nor during the second copulation. Further, the mate partners were of more similar body size, compared to the female's body size, than the partners that did not copulate. This shows that mating is not random with respect to body size. Since intra-sexual selection, non-random emergence patterns and differences in conspicuousness can be ruled out due to the experimental design, these results indicate that female or male mate choice must have let to the observed patterns. Our study provides unequivocal evidence for the existence of female choice. First, not all males that attempted to copulate were able to copulate. Second, females resisted the copulation attempts by fending off males. Third, the success of fending off was not dependent on the male's body size, indicating that females can fend off males of all body sizes and finally, the number of males that had to be presented to a female before copulation was repeatable. These results clearly indicate that females are exerting mate preferences, since neither male mate choice nor other mechanisms may explain these findings. Our results even suggest that females that took longer to mate were choosier, because the match of the mating partner's body size was better if more males had to be presented to a female. Consequently, our results are in line with the three reptile studies conclusively showing that females preferred big adult males and actively rejected courtship by small adult males (Cooper and Vitt 1993; Censky 1997; Shine and Mason 2001; but see LeBas and Marshall 2001), suggesting that female preferences for big males might be more

375 common in reptiles than believed so far. Our results also indicate that in reptiles similar mate
376 choice patterns may exist as in a wide range of taxa including amphibians, birds, insects and
377 fishes (Bateson 1983; Andersson 1994; Birkhead and Møller 1998).
378
379 *Multiple mating*
380 The negative correlation between the first and second copulating male's body size shows that
381 during the second copulation females mated with males of opposite body size. The fact that
382 the difference in body size between the accepted and not accepted males negatively correlated
383 with the first copulating male's body size, rules out that the negative correlation between the
384 first and second copulating male's body size simply arose by chance (if a female first mates
385 with a big male, she will automatically be more likely to mate with a smaller male during the
386 second copulation) and it implies that a female's mate choice depends on the previous mating
387 history. These results are also consistent with context-dependent female choice (Alonzo and
388 Sinervo 2001) and explain why the female's mate partners' traits were not repeatable among
389 copulations.
390
391 *Male coercion*
392 Two recent articles indicate that male sexual coercion may importantly affect population
393 dynamics and female choice in lizards (Fitze et al. 2005; Le Galliard et al. 2005). Our results
394 indeed show that males can force females to copulate. However, only in 1.4% of the
395 encounters males were copulating with the females after intense battles, indicating that forced
396 mating might be rare or depending on special circumstances (e.g. high male densities; Fitze et
397 al. 2005). However, sexual coercion may also be defined as the use by a male of threat of
398 force, that functions to increase the chances that a female will mate with him (Smuts and
399 Smuts 1993). Under this definition it would not be possible to estimate the importance of
400 sexual coercion by simple observation, since females may have traded-off the costs of fending

401 off with the costs of accepting to copulate with a given male (Smuts and Smuts 1993) and
402 thus they may not have intended to resist a male's copulation attempt. The observed outcome
403 may therefore be the result of female choice, which may however have been strongly
404 constrained by the potential costs of resisting a male's mating attempt and thus by the strength
405 of the given male. The finding that females mated with males of opposite body size during the
406 second copulation, compared to the first copulation, might be explained by sexual coercion.
407 Previous studies indicate that the copulation act per se might be costly for females, e.g.
408 through male-sexual harassment (Fitze et al. 2005; Le Galliard et al. 2005), which may
409 potentially lead to a female's exhaustion and thus may modify a female's choosiness. The
410 costs of mating may be male body size-dependent (Choe and Crespi 1997; Arnqvist and Rowe
411 2005) with bigger males imposing higher costs (e.g. due to stronger gripping). Consequently,
412 a female that first copulates with a big male would suffer under increased costs and thus
413 would be less able to be choosy during the second copulation and as a consequence may
414 accept to mate with a male of smaller body size. This might then lead to the observed negative
415 correlation between the first copulating male's body size and the second copulating male's
416 body size. Alternatively, the negative correlation may arise due to active female choice with
417 females preferring to mate with males of opposite body size. This alternative scenario is
418 however less likely, since the common lizard's body size is highly correlated with age
419 (Massot 1992) and since no theoretical studies show why females should prefer to mate with
420 males of different ages, instead of mating with the best performing males (Kokko 1997;
421 Kokko 1998). Our results thus indicate that male coercion through threat of fear, or through
422 physical costs of mating (Le Galliard et al. 2005), may importantly influence a female's mate
423 choice. Since the second mate partner was chosen according to the characteristics of the first
424 mate partner they are also consistent with context-dependent female-choice based on the
425 previous mating history.
426

*Clutch fertilization*

Interestingly, some did not produce a single fertilized egg. This finding may be surprising, since leaving out a reproductive event may importantly decrease the fitness of an animal that lives only for a few years (Clutton-Brock 1988). Because the probability of mating was positively correlated with body condition our results suggest that females in low condition may not copulate either to reduce the direct costs of mating or to reduce the costs of reproduction (e.g. Stearns 1992). Alternatively, females in low body condition may have been non-receptive (Andersson 1994; Shuster and Wade 2003) and thus they may have avoided to mate (Heulin 1988). This second hypothesis is more likely since female common lizards have a very small time window (4-10 days) during which they are receptive (Heulin 1988). However, measuring female receptivity is not a simple task and this study does not provide experimental evidence. Consequently, we are not able to disentangle between the different hypotheses.

## Conclusion

Our study shows that female common lizards exert mate preferences and that they may refuse not preferred males. Female choice was quite consistent across years, but females mated with different male phenotypes during their first and during their second copulation. Because, females mated with a male of opposite body size during the second copulation and because males are able to coerce females, our results further indicate that females may trade-off the costs of resisting male coercion with the costs of mating with a less-preferred male. The results are thus consistent with female-choice depended on the previous mating history. In contrast to recent findings in blue throats (*Luscinia svecica)* and sticklebacks (*Gasterosteus aculeatus)* where it has been shown that female mate preferences are imposing non-directional and non-static selection on males (Johnsen et al. 2000; Milinski et al. 2005), our results indicate that female-choice may be influenced by males through male coercion,

resulting in non-directional and non-static selection on males. Therefore, context-dependent female choice may not only arise due to genotype by environment interactions (David et al. 2000; Jia et al. 2000; Danielson-François et al. 2006), but due to constrained female choice e.g. due to sexual coercion or due to other female mating strategies (e.g. offspring diversification; Jennions and Petrie 2000; Mays and Hill 2004). Our results thus highlight that context-dependent female choice might be much more widespread than believed so far and that it may importantly contribute to the currently observed huge variation in sexually selected male traits. Finally, it stresses that the selective pressures leading to context-dependent female choice are far from being understood.

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# Tables

Table 1. Average trait differences (female trait – male trait) between copulating and not copulating partners: (a) at the first and (b) at the second copulation. Wilcoxon-signed rank tests for paired samples (WSR) are presented. Means and standard errors are given for copulating and not copulating partners.

| | (a) first copulation | | | | (b) second copulation | | | |
|---|---|---|---|---|---|---|---|---|
| trait | mean ±SE | | | | mean ±SE | | | |
| | copulating | not copulating | *N* | Teststatistik | copulating | not copulating | *N* | Teststatistik |
| SVL (mm) | 4.79 ± 0.57 | 6.26 ± 0.56 | 54 | $z = 3.603$*** | 5.21 ± 0.64 | 6.30 ± 0.49 | 47 | $z = 1.932$* |
| body condition (g/mm) | -0.14 ± 0.07 | -0.06 ± 0.06 | 55 | $z = 4.748$*** | -0.23 ± 0.09 | 0.05 ± 0.08 | 47 | $z = 3.175$** |

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.1$ after Bonferroni correction

Table 2. Correlation between the number of males presented to a female before copulation (n males) and the trait differences (Δ trait = female trait – male trait) of the two copulating partners at the first copulation. Results of an ANCOVA with year as random effect are presented.

| trait | parameter | test statistic | estimate ±SE |
|---|---|---|---|
| Δ SVL: | n males | $F_{1,58} = 9.594$** | -0.580 ± 0.187 |
| | year | $F_{1,58} = 0.694$ | |
| | interaction | $F_{1,57} = 0.347$ | |
| Δ body condition: | n males | $F_{1,56} = 1.581$ | -0.032 ± 0.026 |
| | year | $F_{1,56} < 0.001$ | |
| | interaction | $F_{1,55} = 0.247$ | |

** $P < 0.01$ after Bonferroni correction

## Figure legends:

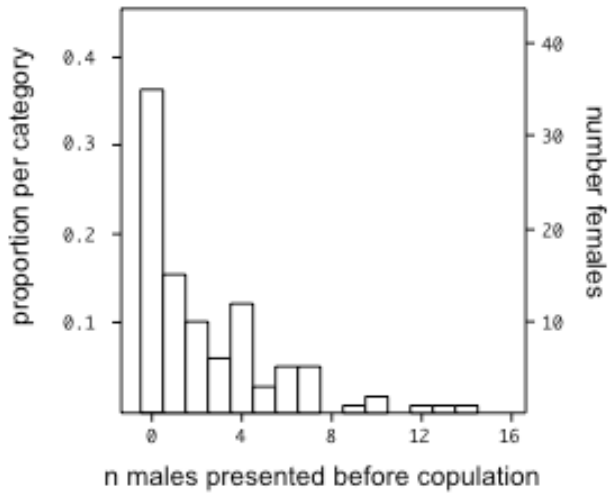
Figure 1. Distribution of the number of partners a female encountered before copulating with the first partner.

Figure 2. Female choosiness. Regression of the snout-vent length difference (female SVL - male SVL) of the mate partners during the first successful copulation in relation to the number of males a female faced before she copulated. The size of the dots refers to the number of observations (smallest dots: $N = 1$, biggest dots: $N = 4$). Plotted is the least square regression line.

Figure 3. (a) Correlation between the accepted partner's SVL at the first and second copulation. Dot size corresponds to the sample size (smallest dot: $N = 1$; largest dot: $N = 3$). (b) Correlation between the accepted partners SVL at the first copulation and the SVL difference of the accepted and not accepted males at the second copulation. Dot size corresponds to the sample size (smallest dot: $N = 1$; largest dot: $N = 2$). In both graphs the least square regression lines are plotted.

## Figures:

Figure 1.



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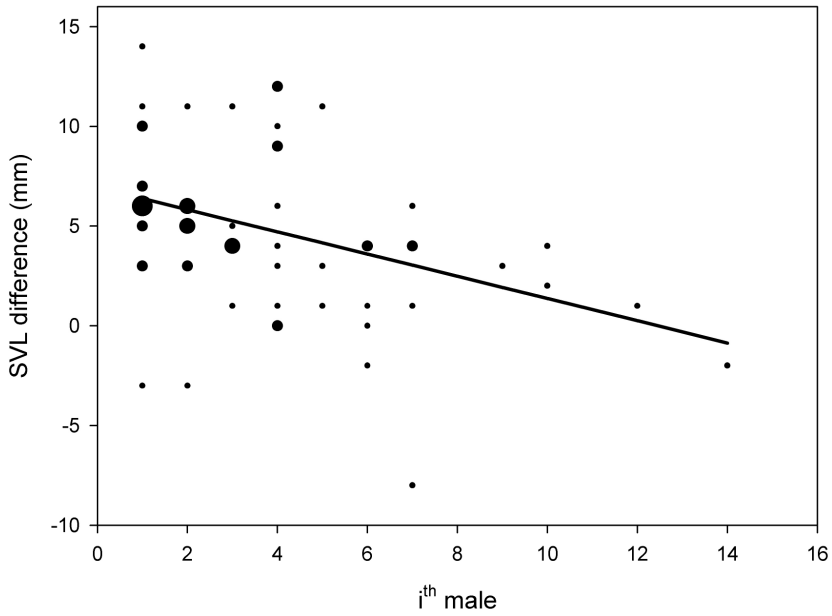
676 Figure 2.

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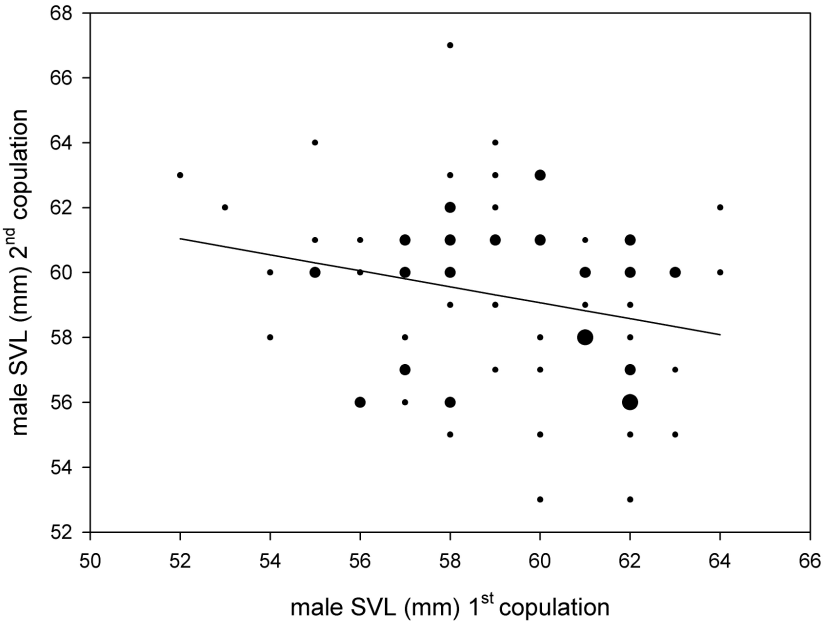
678 Fig. 3a

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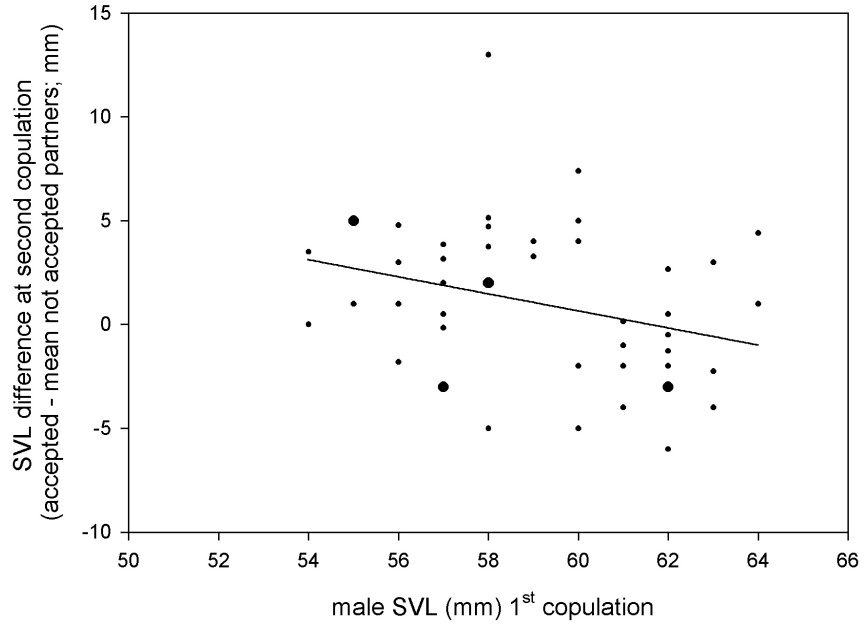
681 Fig. 3b.

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# MANUSCRIT 10

# Determinants of male fitness: disentangling between intra- and inter-sexual selection

Soumis à *Journal of Evolutionary Biology*

# Determinants of male fitness: disentangling between intra- and inter-sexual selection.

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Short title: Determinants of male fitness

## *Abstract*

Both intra- and inter-sexual selection may crucially determine a male's fitness. Their interplay, which has rarely been experimentally investigated, determines a male's optimal reproductive strategy and thus is of fundamental importance for the understanding of a male's behaviour. Here we investigated in the common lizard whether intra- or inter-sexual selection is mainly responsible for non-random mating patterns. We investigated which male traits predict a male's access to reproduction allowing for both selective pressures and comparing it with a staged mating experiment excluding all types of intra-sexual selection. We found that qualitatively better males were more likely to reproduce and that the sexual selection was two times stronger when allowing for both selective pressures, suggesting that inter- and intra-sexual selection determine male fitness and confirming the existence of multi-factorial sexual selection. Consequently, males should trade their investment between the traits being important for inter- and intra-sexual selection as to increase their fitness.



Keywords: intra-sexual selection, inter-sexual selection, male fitness, common lizard, *Lacerta vivipara*.

## Introduction

The optimal male strategy crucially depends on the mating system (Andersson, 1994; Shuster & Wade, 2003). In mating systems where intra-sexual selection through male-male competition is important, males should preferentially invest in fighting abilities, for example in well-developed weapons. In contrast, in mating systems where inter-sexual selection through female choice prevails, males should invest into the preferred traits, for example long tails, bright coloration or exaggerated displays. Consequently the mating system may lead to the evolution of specific male life-history strategies (Andersson, 1994).

In polygynous mating systems where males provide females with little more than sperm, it is widely accepted that male fitness importantly depends on the number of mating partners (Bateman, 1948). It is however much less clear what determines the number of mating partners and thus how the optimal male strategy is determined. In several taxa investigated so far, inter-sexual selection, e.g. through female choice, seems to be rare and intra-sexual selection through male-male competition is suggested to be predominant (for example in fish: (Gross, 1985), lizards: (Tokarz, 1995), anurans: (Halliday, 1998), insects: (Emlen, 1996)). In the species where intra- sexual selection has been documented, it is usually unknown whether inter-sexual selection is as well important and vice versa. Consequently, unless experimental studies investigate, within the same species, the presence or absence of the different types of sexual selection and their interplay, it will be unknown which will be the optimal male reproductive strategy.

In this article we investigated whether intra- and inter-sexual selection coexist and we investigated also their relative importance for a male's fitness. We used the common lizard (*Lacerta vivipara*) as a model system. The common lizard is a small ovoviviparous lizard that has a polygynandrous mating system (Laloi *et al.*, 2004; Fitze *et al.*, 2005; Richard *et al.*, 2005). Earlier studies indicate that intra-sexual selection may importantly determine male

reproductive success (Heulin, *et al.*, 1994) and that inter-sexual selection may be also important (Richard *et al.*, 2005). To assess the role of intra- and inter-sexual selection, we performed two different studies. First, we assessed in six independent lizard populations the paternity of each offspring, using microsatellite genotyping. This situation corresponds to a natural situation where intra- and inter-sexual selection may contribute to male reproductive success. The use of enclosed natural habitat guaranteed unaltered social interactions (Laloi *et al.*, 2004) and it allowed ascribing paternity and maternity with certainty, because the genetic profile of all present animals was known. In a second study we excluded intra-sexual selection using a staged mating experiment. By presenting a single male to a single female, we tested whether inter-sexual selection alone might cause non-random mating patterns. We predict random mating patterns in the second study if non-random mating in the first study is a consequence of intra-sexual selection only. However, the mating patterns should be similar in both studies if non-random mating is the consequence of inter-sexual selection. To further distinguish between the different types of inter-sexual selection, we investigated whether male- mate choice, female- mate choice or male sexual harassment may exist.

## *METHOD*

### Species description

The common lizard (*Lacerta vivipara* Jaquin, 1787) is a small ovoviviparous *Lacertidae* that inhabits peat bogs and moist heath land (Massot *et al.*, 1992). Both, males and females have nonexclusive territories (Richard *et al.*, 2005). Males emerge from hibernation between February and March, approximately one month earlier than females. After the female emergence the mating period starts. In this species, adult males are dominant over one-year old males (Lecomte *et al.*, 2004; Richard *et al.*, 2005), and fights among males can be observed (Heulin, 1988; personal observations J. Clobert). This indicates that intra-sexual

100 selection through male-male competition for access to females exists (see also Richard *et al.*,
101 2005), which is believed to be the norm in reptiles (Tokarz, 1995; LeBas & Marshall, 2001;
102 LeBas, 2002). Common lizards do not provide parental care or nuptial gifts (Heulin, 1988;
103 Clobert *et al.*, 1994; Léna & de Fraipont, 1998) and males provide females only with sperm of
104 low energy content (Depeiges *et al.*, 1987). Hence, the female's benefits of copulating with
105 several males might be only indirect (but see Fitze *et al.*, 2005), reducing the scope for female
106 mate choice. Some observations indicate that female choice may exist, since in a recent
107 experiment the proportion of polyandrous females was unaffected by the population sex-ratio
108 (Fitze *et al.*, 2005). This is in line with the three studies showing that also in reptiles inter-
109 sexual selection through female preferences for bigger sized males and thus through
110 directional female mate choice is existing (Cooper & Vitt, 1993; Censky, 1997; Shine &
111 Mason, 2001). Current work further suggests that male agression may importantly determine
112 male and female fitness (Fitze *et al.*, 2005; Le Galliard *et al.*, 2005c). Similar to almost all
113 except two reptile species (Orrell & Jenssen, 2002), it is not known whether common lizard
114 males prefer specific female traits and thus whether inter-sexual selection via male mate
115 choice exists.
116 Common lizard males may father offspring of up to 14 different females while females give
117 birth to offspring of up to five different males (Laloi *et al.*, 2004; Fitze *et al.*, 2005). The
118 copulation lasts up to several hours (Richard *et al.*, 2005) and may be quite violent, since a
119 male first grips the female on the posterior abdomen with its mouth, thereby producing
120 mating scars that can still be seen after several weeks (Bauwens & Verheyen, 1985; Fitze *et*
121 *al.*, 2005).
122

123 ## FIELD STUDY
124

125 ### Experimental setup
126

To measure male reproductive success under semi-natural conditions we created six independent lizard populations in July 2002 at the Ecological Research Station of Foljuif (Seine-et-Marne, France, 48°17'N, 2°41'E). Lizard populations were set-up in 100 $m^2$ big enclosures, whose size corresponds to the average female's home range size. Enclosures, surrounded by plastic walls to prevent lizards from escaping (for more details see Boudjemadi *et al.*, 1999a), contained natural vegetation, hides, rocks and two ponds (for more details see Lecomte *et al.*, 2004). Predation was excluded by using mist nets to ban avian predators and by trapping shrews outside and inside the populations as to make the two experiments comparable. This set-up allowed assessing paternity and maternity in all cases, since all potential fathers and all pregnant mothers are known. Further, it makes sure that the natural settings are provided and thus that the social interactions are unaltered compared to a completely natural population without spatial limitation (Laloi *et al.*, 2004).

In July 2002, we released in each enclosure 4 adult males and 14 adult females, 6 yearling males and 6 yearling females and 20-24 juveniles of each sex. The initial densities, the age-structure and the adult sex ratio correspond to the ones observed under natural conditions (Massot *et al.*, 1992; Le Galliard *et al.*, 2005b). In late May 2003 we recaptured all surviving lizards and assured that all alive lizards were captured by regularly controlling each population during the two weeks following initial capture. Subsequent to the capture we measured the body mass of all lizards to the nearest 0,002g and the snout-vent length (SVL). Unlike in the staged mating experiment described below, we did not recapture the lizards at the start of the mating season for two reasons. First, capturing lizards during the mating season may importantly affect the reproductive success of both males and females, since under the male-male competition scenario catching first the most competitive male, may lead to a reproductive advantage of the less competitive ones. Spring captures could then potentially alter the mating patterns. Second, in a previous study (Le Galliard *et al.*, 2005a), lizards captured in spring (early April) had the same characteristics when captured in May

(repeatability ($r$) of individual measurements taken in April and May: SVL: $F_{223,224}$=0.35, $P$<0.0001, $r$=0.68; body weight: $F_{223,224}$=2.46, $P$<0.0001, $r$=0.42) and the survival within this time period was very high 96,2% and was not trait-depend (SVL: $F_{1,131}$<0.001, $P$=0.963; body weight: $F_{1,131}$<0.001, $P$=0.957). Consequently, interpreting effects on SVL and body condition will not depend on whether the measurements were taken in April or May.

Captured females were individually maintained in numbered terraria (terraria size: 25 x 15 x 15 cm) under standardized conditions (heat, light, water, food) until parturition. Terraria were layered with soil and equipped with a small water pond and two types of hides. Every four days lizards were fed with moth larvae (*Pyralis sp.*) and we provided them with water *ad libitum* (for further details see Le Galliard *et al.*, 2003). After a female gave birth we carefully searched the terrarium for alive juveniles and for eggs. Thereafter females and juveniles were released into the outdoor populations.

## Paternity assignment

We collected a small part of the tip (1mm) of the re-growing tail of each offspring and of each lizard (before release). Of each egg without visible embryo, the entire egg was collected and all genetic samples were immediately stored in 70% ethanol, where they remained until DNA extraction. We extracted DNA of all collected samples using Perfect gDNA Blood Mini Isolation kit (Eppendorf). Thereafter we identified the putative fathers using five highly polymorphic microsatellite DNA loci (Lv-3-19, Lv-4-72, Lv-4-alpha, Lv-4-X, and Lv-4-115; (Boudjemadi *et al.*, 1999b). The exact method used for the extraction, the polymerase chain reaction (PCR), and the determination of the allelic size is described elsewhere (Laloi *et al.*, 2004). For each population, separate paternity assignments were done using Cervus 2.0 (Marshall *et al.*, 1998). Because the genetic profile of the mothers and of all potential fathers was known, the program was simply used to facilitate the attribution of the genetic father.

One female (clutch size = 4) laid an unfertilized clutch and one female laid one unfertilized egg. All other offspring could be successfully attributed to a single father.

## STAGED MATING EXPERIMENT

### Pre-experimental conditions

We conducted the experiments at the Ecological Research station of Foljuif. Both in July 2001 and July 2002 we introduced male and female lizards (*Lacerta vivipara*) into empty 100m$^2$ big outdoor enclosures, similar to those described above. Males and females were released in separate enclosures containing no individuals of the opposite sex, to prevent lizards from uncontrolled mating. In 2001 females were released into three and males into four different enclosures, and in 2002 five enclosures were used for females and six for males. We released approximately 40 adult lizards per population.

### Laboratory conditions

In early spring the enclosures were regularly inspected to register male and female emergence. We also monitored other enclosures, containing both male and female lizards, to determine the natural onset of the mating period. Mating activity was determined by the presence of mating scars present on the female's belly (Bauwens & Verheyen, 1985). When the first females with mating scars were detected, we started capturing the lizards of the experimental enclosures. Subsequent to the capture, we measured body mass and SVL. All captured lizards were then individually introduced into numbered terrariums and maintained under the same standardized conditions as described above. The same lizard stayed in the same terrarium during the entire experiment. To make sure that no interactions happened between sexes before the staged mating experiment males and females were kept on separate shelves.

## Experimental method

In 2002, the mating experiments lasted from March 31 to April 8 and in 2003 from April 7 to 15. At the start of the experiment, we introduced randomly chosen females into escape proof wooden boxes (2500 $cm^2$). Because only a limited number of boxes and females was available not all males could be presented to a female directly after capture. In males, the mating experiments therefore started on average 4.15 days ±0.19SE and in females, 3.36 days ±0.23SE after capture. There was no correlation between the number of days a male stayed in the laboratory before the mating experiments started and his SVL ($F_{1,198}$=0.877, $P$=0.350). This correlation was as well non-significant in females ($F_{1,94}$=0.947, $P$=0.333), showing that both males and females were well randomised. Each wooden box contained a shelter and a 40W bulb, which provided light and heat. To mimic natural daylight that consists also of UV light, we illuminated the wooden boxes with a UV light source (Iguana Light 5.0 UV-B, 40 W, ZooMed Laboratories, Inc., Sacramento, CA, USA).

We first released a female in the wooden boxes and 2-4 minutes later a randomly selected male was introduced in each box. Mating experiments started at 0900h and the last experiment started no later than 1700h. After introduction, we observed the lizards during one hour to determine the start, the end, and the number of copulations. These data allowed measuring the copulation duration with a precision of less than 3 minutes. A male-female encounter was defined as copulation when the male griped the female with the mouth on the posterior abdomen, when he successfully twisted the body around her, and when his hemipenis penetrated the cloacae. If copulations were not yet finished after one hour, we waited until they ended. After one hour, or 5 minutes after the end of the copulation, males were removed from the female's box. Males were placed back to their terrarium and they were presented to a new unknown female on average 1.3 days ±0.05SE later (range: 26 minutes – 6 days). If males were not copulating with any female after presenting at least five different females (on average 5.2 ± 0.2SE females), we stopped presenting them to new

females. A male was never presented twice to the same female and he was allowed to copulate with maximally three different females, because males sire offspring of up to 3 different females (Fitze *et al.*, 2005), see female-biased populations). The first successful copulation of a male is hereafter referred to as 'first copulation'. If a male thereafter copulated with a second female, this copulation is referred to as 'second copulation'. After the experiments all lizards were released into the outdoor enclosures.

In the field study we measured male fitness by determining a male's fertilization success and in the staged mating experiment we measured a male's copulation success. These two measures might be different, because males may transfer non-fertile or non-mature sperm and because females may select sperm (Birkhead, 1998). However, in an earlier study, we found a highly significant positive correlation between the number of females with which a male copulated and the number of females for which he fertilized eggs ($F_{1,134} = 89.06$, $P << 0.001$, $r = 0.64$; Fitze *et al.*, 2005). This indicates that copulation success predicts fertilization success and thus that the two measurements estimate a male's fitness similarly well.

## Statistics

### Field study

85 males were recaptured at the end of May 2003. The paternity analysis revealed that ten not recaptured males were fathering offspring. These ten males must have died between the copulation and the end of May, because we searched for alive lizards during two weeks, and because all alive lizards were captured within the first two days. Consequently, no spring measurements could be obtained and thus only the 85 recaptured males whose traits could be measured, were included into the below presented analyses.

### Staged mating experiment

For the second experiment we used a total of 200 different males and 96 different females. As in the first experiment the probability of copulating was modelled using the Proc GLIMMIX procedure. The different covariates were simultaneously introduced and the enclosure of origin, the year and their interactions with the covariates were included as random effects.

For the analyses of body condition in nonparametric tests (for example Spearman rank correlations) we used the residuals of the regression with SVL as independent and body weight as the dependent variable. In several analyses dealing with the male's body weight the degrees of freedom are reduced because the measurements of four males were missing. For some models the assumptions were not met even after transformation. Consequently, we applied Spearman rank order correlations (SRC) instead of parametric regression analyses, or Wilcoxon-signed ranks test (WSR) for the analysis of paired samples. In WSR samples sizes may considerably vary among tests due to pair-wise differences equalling zero (Siegel & Castellan, 1988). The repeatability ($r$) of the mate partner's traits was calculated according to Lessells & Boag (1987).

**Statistics used in both studies**

In the field study the probability of reproducing and in the staged mating experiment the probability of copulating was modelled using the Proc GLIMMIX procedure in SAS with a binomial error distribution and a logit link (Littell *et al.*, 1996). The starting model included all covariates, population and year as random factors as well as the interactions between the population and the covariates and the interactions between year and the covariates. Not significant interactions and covariates were backward eliminated. To check for stabilizing or disruptive selection we modelled the different covariates as well as quadratic terms (Lande & Arnold, 1983). Standardized logistic selection gradients were calculated according to Janzen & Stern (1998). Body size and body weight were usually positively correlated (e.g. in the field study: SVL and body weight were positively correlated with each other ($P$<0.05).

Consequently, the final model obtained by backward elimination could simply have arisen due to collinearity (Quinn & Keough, 2002). However, if the final model derived using forward selection coincides with that one given by backward selection, there will be no risk that the results arose due to collinearity (Quinn & Keough, 2002). We therefore used as well forward selection and we state for each of the models whether forward selection let to the same results. The assumptions of the statistical models were verified in all cases (Quinn & Keough, 2002).

# *RESULTS*

## FIELD EXPERIMENT

Of the 85 males that were recaptured in 2003 37 (43.5%) were not fathering a single offspring. The probability of fertilizing eggs increased with increasing body weight (Table 1, Fig.1.). Body size was not significantly predicting the probability of fertilizing eggs (Table 1). The population was not significant and there were no significant interactions between the population and the male traits (all $P > 0.1$). A model using forward selection let to the same final model, showing that there existed no collinearity problem (for more details see methods). Quadratic terms were not significant ($SVL^2$: $F_{1,72}=0.25$, $P=0.618$; body $weight^2$: $F_{1,73}=0.48$, $P=0.491$) and also their interactions with population were not significant (all $P>0.1$).

## STAGED MATING EXPERIMENT

### *Probability of copulating*

Of the 200 males used during this experiment 79 (39.5%) did not copulate with a single female. The probability that a male copulated with a female increased with increasing body weight (Table 2; Fig. 2). Body size, year and population were not significantly affecting the

probability of copulating (Table 2). Similarly, the interactions between year or population and the covariates were all not significant ($P$>0.1). A model using forward selection let to the same final model, showing that there existed no collinearity problem. Quadratic terms were not significant (SVL$^2$: $F_{1,188}$=0.12, $P$=0.727; body weight$^2$: $F_{1,186}$=0.02, $P$=0.882) and also their interactions with population or year were not significant (all $P$>0.1). The percentage of males that were not copulating with a single female was similar to the percentage of males that did not father a single egg in the field study ($X^2$=0.252, $P$=0.616).

## *First copulation*

On average the 121 males copulated with the 1.86$^{th}$±0.12SE presented female (Fig.3) and 67 males (55.4%) mated with the first presented female. To investigate whether inter-sexual selection through male mate choice may exist, we analysed the 54 males, which did not copulate with the first presented female and which thus might have been choosy. We found that the SVL of the female with which a male copulated was bigger and showed a higher body condition than the average SVL or body condition of the females with which he was not copulating (Table 3a). The interactions between year and the repeated measures were not significant (all $P$>0.1).

## *Second copulation*

52 of the 121 copulating males copulated with a second female. Males that copulated a second time showed significantly better body condition ($F_{1,114}$=6.907, $P$=0.010, estimate [males copulating a second time]: 0.102±0.038se) compared to males that copulated only once. There were no differences in SVL ($F_{1,118}$=1.963, $P$=0.164). Year was not significant in all cases ($P$≥0.1) and there were no significant interactions between the year and the number of times a male copulated (once vs more than once copulated: all $P$>0.2).

During the second copulation males copulated on average with the 1.4$^{th}$±0.1SE presented female (maximum: 4$^{th}$, 90%-quantile: 2.7$^{th}$ female) and 39 of the 52 males copulated with the

first presented female. Like in the first copulation, the SVL of the female with which a male copulated was bigger than the average SVL of the females with which he was not copulating (Table 3b). There were no significant difference in body condition between copulating and non-copulating females (Table 3b) and the interactions between year and the repeated measures were not significant (all $P>0.1$). Additionally, the copulation duration of the first copulation did not predict how many females had to be presented to a male until he copulated a second time (SRC: $Rho=0.217$, $P=0.477$).

### *Repeatability of a male's mate partner characteristics*

Male's that mated with two or three different females did not copulate with females of similar SVL (ANOVA: $F_{51,56}=0.805$, $P=0.782$, repeatability ($r$) =-0.103) and body condition ($F_{51,56}=1.162$, $P= 0.291$, $r=0.072$). Similarly, the number of females that had to be presented to a male before he copulated was not repeatable ($F_{51,56}=0.875$, $P=0.684$, $r=-0.064$).

## *Discussion*

Our results reveal that the mating patterns observed in the two studies are similar. First, both the probability of fathering offspring in the first study and the probability of copulating in the second study, increased with male body condition. Second, body size and the population of origin did not predict the probability of reproducing. Third, no stabilizing or disruptive sexual selection could be observed in either of the two studies and fourth in both experiments many males were not mating with a single female and the percentage of non-mating males was not different. The results thus indicate that in both studies positive directional sexual selection was acting on male quality, which is consistent with the mating patterns found in other taxa (e.g. in insects, amphibians, fish, birds and mammals (Andersson, 1994; Shuster & Wade, 2003)), and in reptiles (see Olsson & Madsen, (1998), for a review). However, in most of these taxa it is not known whether the observed patterns are imposed by intra- and / or inter-sexual selection. Thus behavioural, morphological and life-history adaptations of both males

365 and females can hardly be understood (Andersson, 1994; Shuster & Wade, 2003). In contrast,
366 our study allows distinguishing between intra- and inter-sexual selection. The fact that in the
367 staged mating experiment, which excludes all types of intra-sexual selection, the observed
368 patterns were similar to the patterns observed in the field study, which includes all types of
369 intra- and inter-sexual selection, clearly demonstrates that in this species inter-sexual selection
370 imposes an important selective pressure on male reproduction. The strength of the sexual
371 selection acting on males was twice as high in the field study compared to the staged mating
372 experiment. This suggests, that beside inter-sexual selection as well intra-sexual selection,
373 whose existence has been demonstrated in earlier studies (Lecomte *et al.*, 2004; Richard *et al.*,
374 2005), may contribute to a male's fitness.
375 The inter-sexual selection acting on male quality observed in the staged mating experiment
376 might be imposed by at least four different selective pressures, for which our study does or
377 does not provide evidence. First, male mate choice might be present (Olsson, 1993) because a
378 male's mate partners were bigger and in better body condition, compared to those with which
379 a male was not mating. However, the male's mate partner characteristics were not repeatable
380 and male mate choice can not explain why small males in the staged mating experiment were
381 less likely to copulate, since not to copulate with a female is a bad strategy in species where
382 males provide females with little more than sperm (Bateman, 1948). Second, inter-sexual
383 selection imposed by female mate choice may explain why better quality males were more
384 likely to reproduce. However, female mate choice cannot explain why the females with which
385 males copulated were of bigger size than those with which they did not copulate. Third, the
386 sperm production or the sperm maturity may limit the male's copulation probability and thus
387 intrinsic factors may affect male behaviour (Olsson, 1993; Olsson & Madsen, 1996).
388 However, neither the copulation duration of the first copulation ($F_{1,110}$=0.91, $P$=0.342)
389 predicted whether a male copulated a second time, nor did the inter-copulation interval (time
390 between the first and the second copulation) affect the probability of copulating with the first

391 presented female during the second copulation ($F_{1,49}$=0.87, $P$=0.356) and the interactions
392 between inter-copulation interval and the male quality were not significant (all interactions:
393 $F_{1,44}\leq$2.12, $P\geq$0.153). It is therefore, unlikely that sperm maturation and / or sperm limitation
394 may have caused the observed patterns. Forth, male sexual harassment (Fitze *et al.*, 2005; Le
395 Galliard *et al.*, 2005c) may lead to the observed positive relationship between male quality
396 and access to reproduction, since better quality males might be better in harassing.
397 All together our results partially support the existence of inter-sexual selection by male mate
398 choice, female mate choice and sexual harassment, while intrinsic factors are unlike the cause
399 of the observed patterns. Most importantly, neither inter-sexual selection imposed by males
400 nor inter-sexual selection imposed by females can explain all results, suggesting that multi-
401 factorial inter-sexual selection may act on male reproductive success. However, the evidence
402 for the different mechanisms of inter-sexual selection is of purely observational nature and
403 only experimental studies may explain which mechanisms of inter-sexual selection let to the
404 observed patterns. Consequently, the presented evidence for the different mechanisms of
405 inter-sexual selection should be interpreted with caution.
406 In summary, our study contrasts the general believe that either inter- or intra-sexual selection
407 determine male reproductive success, since it experimentally demonstrates that inter-sexual
408 selection is importantly determining male reproductive success and since intra-sexual
409 selection is likely to be responsible for the stronger sexual selection in the field study. Our
410 findings on inter-sexual selection are consistent with female mate choice, male mate choice
411 and sexual harassment but not with intrinsic factors determining a male's reproductive
412 success. The study thus indicates that both intra-sexual selection imposed by male-male
413 competition (Lecomte *et al.*, 2004; Richard *et al.*, 2005) and inter-sexual selection may exist
414 concurrently and thus that male reproductive success is the result of multi-factorial sexual
415 selection, suggesting that males should find the optimal balance between investing in the traits
416 favourable for inter-sexual selection and intra-sexual selection.

417

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519

## *Tables:*

Table 1. Probability of reproducing in relation to male body size and body condition. Data from the field study are shown. The results of a GLIMMIX model are provided. The logistic estimates and the standardized selection gradients are given.

| Trait | test statistic | *P* | estimates (± se) | selection gradient |
|---|---|---|---|---|
| body weight | $F_{1,83}$=25.58 | <0.001 | 2.427±0.480 | 0.467 |
| body size (SVL) | $F_{1,82}$=0.93 | 0.338 | 0.164±0.170 | 0.143 |
| population | $z = 0$ | 1 | | |

Table 2. Probability of copulating in relation to male body size and body weight. Data from the staged mating experiment are shown. The results of GLIMMIX model including year and the enclosure as random effects are provided. The logistic estimates and the standardized selection gradients are given.

| Trait | test statistic | *P* | estimates (± se) | selection gradient |
|---|---|---|---|---|
| body weight | $F_{1,194} = 15.02$ | 0.0001 | 1.076 ± 0.278 | 0.231 |
| body size (SVL) | $F_{1,192} = 0.58$ | 0.448 | 0.059 ± 0.078 | 0.031 |
| year | $z = 0.60$ | 0.376 | | |
| population | $z = 0$ | 1 | | |

Table 3. Differences between females with which a male did or did not copulate during a) the first and b) the second copulation. Repeated measures analysis with the female traits of copulating and the mean traits of the non-copulating females as repeated measures.

| Trait | copulating mean ± se | noncopulating mean ± se | test statistic | P |
|---|---|---|---|---|
| a) first copulation | | | | |
| SVL (mm) | 64.5 ± 0.5 | 62.7 ± 0.4 | $F_{1,53} = 7.881$ | 0.004 |
| body condition | 0.103 ± 0.061 | -0.143 ± 0.059 | $F_{1,53} = 8.571$ | 0.005 |
| b) second copulation | | | | |
| SVL (mm) | 63.5 ± 1.2 | 66.5 ± 1.2 | $F_{1,12} = 5.970$ | 0.031 |
| body condition | 0.174 ± 0.291 | 0.023 ± 0.204 | $F_{1,12} = 0.284$ | 0.604 |

Figure 1. Probability of fertilizing at least one egg in relation to body weight. The dot size corresponds to the sample size (small dots N = 1; large dots N = 2). The line corresponds to the predicted relationship between body weight and the probability of copulating.

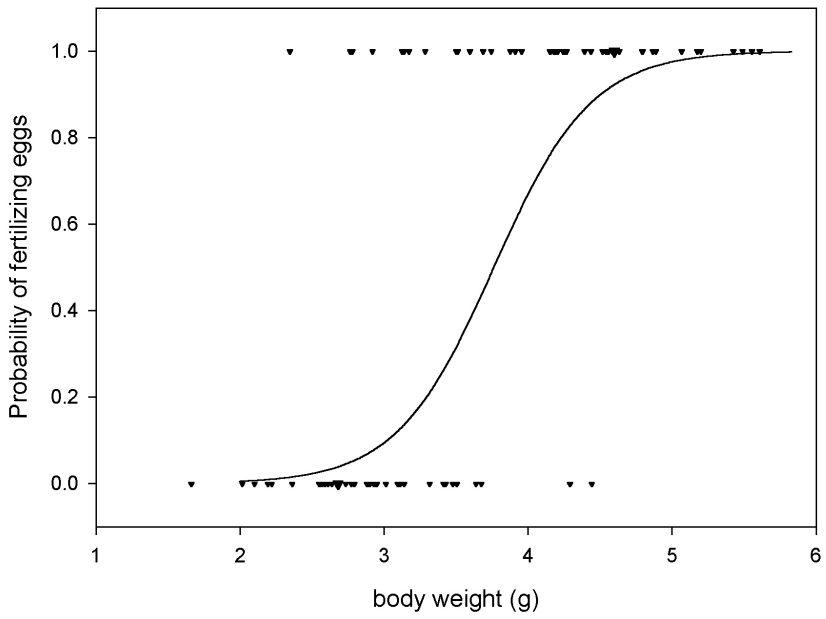
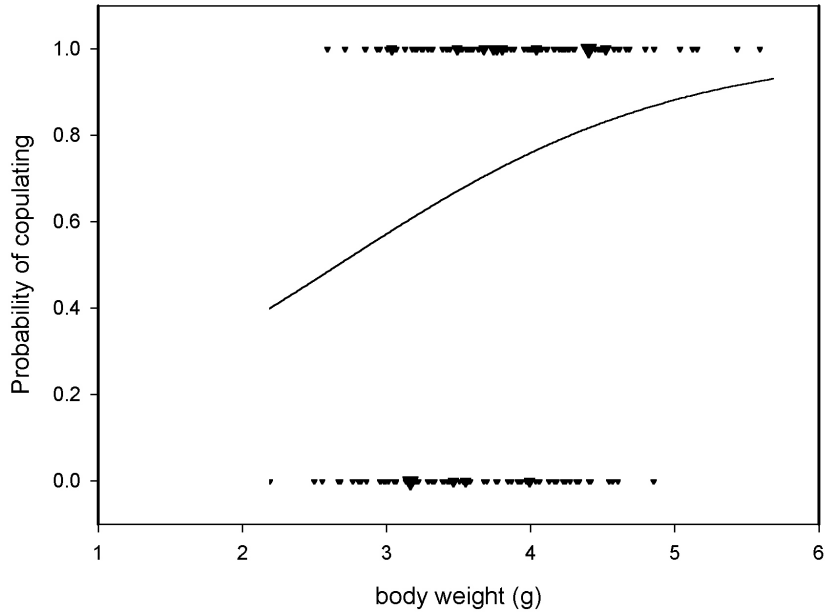
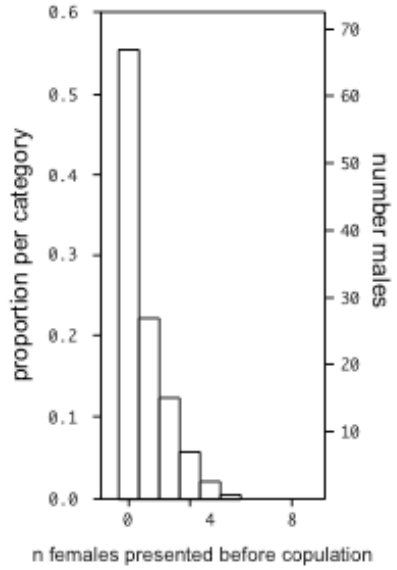


Figure 2. Probability of copulating with a female in relation to body weight. The dot size corresponds to the sample size (smallest dot N = 1; biggest dot N = 3). The line corresponds to the estimated relationship between the body weight and the probability of copulating.



579 Figure 3. Distribution of the number of females a male encountered before copulating with
580 the first female.
581

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**Information socialement acquise chez le lézard vivipare (*Lacerta vivipara*)**

Dans un environnement inconstant et incertain, prendre une décision adéquate est difficile mais néanmoins crucial. Décider de partir de son lieu de vie, de s'installer dans un nouvel habitat, de se reproduire et d'interagir avec d'autres individus, sont autant de décisions inévitables nécessitant diverses informations. Pour acquérir des informations liées aux conditions biotiques et abiotiques de l'environnement, différents systèmes ont été mis en place au cours de l'évolution. Alors qu'une estimation personnelle du milieu environnant est usuellement admise, des études récentes ont mis en évidence une forme plus complexe d'acquisition de l'information : l'information socialement acquise. Cette information, basée sur l'observation de la présence et du comportement des congénères, permet d'accéder à de nombreuses informations par l'intermédiaire d'autrui. Chez les espèces à communication vocale réduite, les mécanismes sous-jacents de cette information socialement acquise restent encore peu étudiés. Utilisant le lézard vivipare comme sujet d'étude, mon travail de thèse a pour but de démontrer l'existence de cette information socialement acquise et les modalités de transmission de cette information. L'association entre des études à l'échelle de la population et des expériences comportementales à l'échelle individuelle révèle qu'une information est acquise au cours d'interactions sociales. Ainsi, les lézards peuvent renseigner leurs congénères sur la densité des populations voisines et sur leurs niveaux de compétition de parentèle, en utilisant des signaux de couleur, des signaux olfactifs et des signaux comportementaux. Les études présentées dans cette thèse montrent également le rôle important de ces informations sur la dispersion natale et, plus généralement, sur la dynamique de la population. Ces études, intégrées dans la globalité des connaissances sur l'information, soulignent l'importance de la prise en compte de mécanismes comportementaux précis dans notre compréhension de la biologie des populations, et donc dans la conservation des espèces.