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Proverbe Chinois.

INTRODUCTION

I. De l'importance du choix du site de ponte chez les insectes.

a. Le choix du site de ponte est il soumis à la sélection naturelle ?

En 1859, Charles Darwin publie « *L'origine des espèces* » où il développe la théorie de l'évolution des espèces par sélection naturelle. Cet ouvrage est devenu la pierre angulaire des recherches en biologie évolutive. Il est désormais admis que pour être soumis à la sélection naturelle un caractère qui présente des variations interindividuelles doit répondre à deux conditions (Sterns & Hoekstra 2000):

1. être héritable
2. être associé à une différence de succès reproductif.

Le choix du site de ponte répond-il à ces deux exigences ?

1. *Existe-il une hérédité concernant les préférences pour le choix du site de ponte ?*

Si les relations entre les gènes et le comportement sont mal connues, la composante génétique dans le comportement animal est certaine. Toutefois, les exemples de cas où un gène unique correspond à un comportement sont rarissimes (Rothenbuhler 1964a, 1964b). Dans la majorité des cas, c'est un ensemble de gènes qui va influencer un comportement. Or, comme le soulignent Aron & Passera (2000), il n'est pas nécessaire que les comportements soient directement déterminés par des gènes pour être soumis à la sélection naturelle, il suffit que ces caractères soient influencés par des différences d'ordre génétique. Barker & Starmer (1999) par exemple ont montré que la préférence pour le choix du site de ponte chez la drosophile *Drosphila buzzatii* Patterson & Wheeler était héritable, or cette décision est soumise à de nombreux stimulus.

2. *Quelle est l’influence du site de ponte sur la valeur sélective d’un individu ?*

Comme c’est le cas chez la majorité des insectes non-sociaux, les larves de coccinelles ne bénéficient pas de soins parentaux. Par ailleurs, chez ces insectes holométaboles, les larves sont aptères. Leur dispersion est donc limitée, même si elle n’est pas nulle (Cottrell & Yeargan 1999; Barrigossi et *al.* 2001). De ce fait leur survie dépendra de la quantité de nourriture, de la présence d’ennemis naturels et/ou des conditions environnementales du lieu de ponte choisi. Pour les larves de coccinelles, il existe une réelle pression sélective dès le premier stade. Une jeune larve doit pouvoir trouver sa première proie très rapidement après la sortie de l’œuf, car sa survie est limitée à moins de 24h (Majerus 1994, Hemptinne *et al.* 2000b). En plus de la disponibilité immédiate en nourriture, il faut également prendre en compte la durabilité de la ressource puisque quatre semaines au moins sont nécessaires entre le moment de la ponte, et celui où le jeune adulte émerge. Enfin, la particularité des coccinelles est de présenter un cannibalisme intense des larves entre elles et sur les oeufs (Dixon 2000). Le taux de cannibalisme est supposé être modulé par la quantité de la ressource alimentaire (Agarwala & Dixon 1992), mais aussi par la densité de prédateurs présents (Pervez *et al.* 2006). La présence ou l’absence de compétiteurs est donc un élément de plus pour caractériser la qualité d’un patch. Le choix du site de ponte par la femelle est donc essentiel pour maximiser son succès reproductif, et ce choix se fera en réponse à des signaux informant d’une part sur la qualité et la quantité de nourriture présente, mais également sur l’importance de la compétition.

Le choix du site de ponte aura donc une influence cruciale sur la survie des jeunes (Paukku & Kotiaho 2008), et comme tout comportement il est soumis à une influence génétique (Barker & Starmer 1999), et donc à la sélection naturelle. Dès lors la question se pose de savoir quelles caractéristiques définissent un bon site de ponte, et quels attributs décisionnels ont été sélectionnés.

b. Facteurs orientant le choix de ponte.

1. Influence de la quantité de nourriture

La quantité de nourriture est bien entendu capitale, car dans peu de cas les larves auront la possibilité de changer de site pour trouver un environnement plus favorable. Chez de nombreux insectes prédateurs, on a pu montrer une préférence particulière pour les sites contenant un nombre important de proies (Evans 1976, Nakashima & Hirose 2003, Hemptinne *et al.* 1992, Scholz & Poehling 2000, Sigsgaard 2004). Les prédateurs sont souvent attirés par des signaux chimiques, dont la quantité est corrélée au nombre de proies. Ces signaux peuvent êtres produits par la proie (Boo *et al.* 1998, Dunkelblum *et al.* 1996) comme pour le scarabée *Osmoderma eremita* Scopoli dont la phéromone sexuelle attire également les femelles de son prédateur *Elater ferrugineus* L. (Elateridae) (Svensson & Larsson 2008). Il peut également s'agir d'une production de la plante induite par l'attaque d'un ravageur (Krips *et al.* 1999, Tatemoto & Shimoda 2008, James 2005). L'oviposition elle-même peut aussi être sous le contrôle d'un stimulus comme c'est le cas avec le miellat produit par les pucerons en ce qui concerne les femelles de syrphes (Budenberg *et al*. 1992), les filaments de cire que produisent les cochenilles (Merlin et *al.*1996) pour *Cryptolaemus montrouzieri* Mulsant, une coccinelle coccidiphage ou la ponte de la mite *Plodia interpunctella* Hübner qui est stimulé par les huiles alimentaires (Uechia *et al.* 2007).

2. L'influence de la qualité de la nourriture.

Si la densité de proies est un facteur important dans le choix du site de ponte, la qualité des proies est elle aussi essentielle. L'hypothèse de la préférence et de la performance prédit que des femelles devraient préférer pondre sur des patches dont la ressource alimentaire permet le meilleur développement. Cette théorie avait été développée pour les insectes phytophages par

Jaenike (1978) qui proposait qu’une plante soit sélectionnée si elle a un fort potentiel pour le développement larvaire. Une plante de qualité inférieure peut être choisie si la probabilité de trouver un meilleur hôte est rare ou que sa densité varie dans le temps. Comme pour les phytophages, chez les insectes prédateurs la corrélation entre préférence des femelles et performance des larves est très variable selon les études, puisqu’elle peut être forte (Omkar & Mishra 2005), faible (Sadeghi & Gilbert 2000a et 2000b) ou inexistante (Frechette *et al.* 2006, Petersen & Hunter 2002). Ces résultats tendent à montrer que ce facteur n’est pas toujours déterminant dans le processus décisionnel d’une femelle. La raison est peut-être à trouver dans les travaux de Bernays (2001) qui souligne que si les insectes sont capables de recevoir de multiples stimuli, une sélection s’opère afin de n’utiliser que les signaux les plus essentiels et favoriser des décisions rapides. De plus d’autres facteurs peuvent rentrer en compte, et la plante ou la proie optimale pour le développement larvaire peut présenter des contraintes importante : par exemple une faible présence dans le milieu ou une plus grande compétition (Paukku & Kotiaho 2008).

3. *L’influence de la compétition inter et intra spécifique.*

Finalement un élément important influençant le comportement de ponte est la présence de compétiteurs dans l’environnement. Lorsque les insectes exploitent une nourriture limitée dans le temps ou en faible quantité le risque est que cette ressource vienne à manquer si le nombre de consommateurs est trop important. À cela s’ajoute le risque de cannibalisme chez certains insectes prédateurs ou l’élimination des compétiteurs chez les parasitoïdes solitaires. Chez les parasitoïdes, les femelles procèdent soit en reconnaissant une phéromone déposée lors de la ponte par une compétitrice (Vandijken *et al.* 1992; Visser *et al.* 1992a, Gauthier *et al.* 1996; Field & Keller 1999, Santolamazza-Carbone *et al.* 2004), soit par des sondages de l’hôte (Agboka *et al.*

2002; Yamada & Ikawa 2005). Certaines espèces sont capables de discriminer si l'hôte a déjà été parasité par un congénère ou par elle-même (Ueno 1994; McKay & Broce 2004).

La présence de compétiteurs va donc grandement influencer le comportement des femelles, car la qualité du site de ponte va être modifiée. Ainsi en cas de compétition très élevée, on peut assister à des changements de stratégie : chez les parasitoïdes solitaires, le comportement généralement observé dans un environnement contenant de nombreux hôtes libres est d'éviter le superparasitisme (Godfray 1994). Toutefois, au fur et à mesure que le milieu est exploité et que le nombre d'hôtes libres diminue, il devient plus avantageux d'accepter ceux déjà occupés, tout en continuant à éviter ceux que l'on a soit même parasités (Vanhalphen & Visser 1990,Visser 1992a, 1992b). Enfin, s'il y a de nombreuses femelles dans le site, la probabilité que des hôtes contiennent à la fois leurs propres larves et celles de compétitrices augmente. Dès lors, pondre dans ces hôtes permet d'augmenter la probabilité que l'adulte qui sortira de l'hôte soit le sien. Chez *Leptopilina heterotoma* Thomson, par exemple, on constate que dans un site contenant un faible nombre d'hôtes libres et en présence de compétitrices, une femelle pond avec la même fréquence dans des hôtes parasités par elle même que par les autres femelles (Visser 1993).

Chez les coccinelles, les larves déposent via leur disque anal une substance qui inhibe la ponte (Doumbia *et al.* 1998, Laubertie *et al.* 2006). Une femelle cherchant un site de ponte va éviter de pondre lorsqu'elle rencontre ces traces. Cet effet fut attribué à une phéromone d'inhibition de la ponte (ODP) qui y serait contenue. Cette phéromone constitue le fil rouge de cette thèse, dont l'objet va être d'en expliquer l'évolution et les conséquences sur les traits d'histoire de vie des coccinelles.

II. Particularités des Coccinelles en tant que prédateurs de pucerons.

a. Les pucerons : cycle et histoires de vie.

Les colonies de pucerons (Heteroptera, Aphidoïdea) sont des ressources éphémères. Au printemps lorsque les individus de la nouvelle génération sortent des œufs, ils commencent à fonder de nouvelles colonies en produisant des descendants par parthénogenèse. Cette reproduction asexuée est très largement dominante sur la reproduction sexuée, qui n'intervient qu'à l'automne (Dixon 1998, Simon *et al.* 2002). La conséquence de cette reproduction asexuée est une multiplication très rapide de la population de pucerons, un phénomène accentué par le fait que les générations sont dites télescopées (Dixon 1998, Simon *et al.* 2002) ; c'est-à-dire que dans une femelle on trouve des embryons de première génération (les *filles*) qui contiennent eux mêmes les embryons de seconde génération (les *petites filles*). Cette phase correspond au développement exponentiel de la colonie, qui aura un temps d'existence de six à huit semaines, (Dixon 1998) en réponse à la courte période pendant laquelle la sève de la plante hôte est riche en azote (Throop & Lerdau 2004). Les générations télescopées permettent une adaptation rapide de la population grâce à un dialogue hormonal entre mère et petites-filles qui deviendront ailées dès que les conditions environnementales seront défavorables, leur permettant de chercher une nouvelle plante hôte. Ainsi, la disparition d'une colonie de puceron sera aussi rapide que son apparition.

Si une colonie de pucerons est une ressource localisée et limitée dans l'espace, sa taille et le nombre d'individus qui la composent n'est pas fixe. La plante hôte et les conditions environnementales, comme la température ou l'hydrométrie, peuvent jouer un rôle important sur la densité de pucerons dans une colonie. Pour une même espèce, la population peut ainsi varier d'une dizaine à plus d'une centaine d'individus (Agele et *al.* 2006).

b. Contraintes imposées aux coccinelles aphidiphages par leurs ressources alimentaires.

1. *La qualité du site de ponte détermine la stratégie reproductive des femelles.*

Contrairement au modèle proies - prédateurs classiques, les adultes sont moins sensibles à la limitation de nourriture que les larves, et c'est la qualité des sites de ponte qui va déterminer leur stratégie reproductive plus que la quantité de proie présente dans le système. (Dostalkova *et al.* 2002). Outre des besoins alimentaires moindre que les larves, les adultes peuvent se nourrir sur les sites de ponte, y compris ceux qui ne seront pas favorable pour leurs descendant pour cause de trop grande compétition (Frechette 2006).

De plus, toutes les espèces de pucerons ne permettent pas un développement larvaire optimal, certaines peuvent être même toxiques (Hodek & Honek 1996). Comme il a été dit précédemment, l'environnement des larves dépend du choix de la femelle. Cela signifie que le choix des proies sur lesquelles vont se développer les larves est fait par la mère. En conséquence, on constate en laboratoire que les larves ne montrent pas plus de préférence pour une proie optimale que pour une proie de moindre qualité (Ferrer et *al.* 2008).

2. *Un temps de développement long comparé à la durée de la ressource.*

Le temps de développement d'une coccinelle, de l'œuf jusqu'à l'adulte, est proche de la durée d'existence d'une colonie de puceron. En effet, les six à huit semaines d'existence d'une colonie de puceron sont à comparer aux quatre à cinq semaines nécessaires à une coccinelle pour se développer de l'œuf à l'adulte.

Cependant, en début et à la fin de l'existence de cette colonie, la densité de puceron sera trop faible pour soutenir la prédation de plusieurs larves de coccinelles (Dixon *et al.* 1997). De ce fait une ponte effectuée à un moment aléatoire sur une colonie aura peu de chance de donner des survivants car le risque est grand que les larves manquent de nourriture soit au début, soit à la fin de leur développement. En d'autres termes, cela signifie qu'il existe une fenêtre temporelle qui permet de maximiser la survie des futures larves (Hemptinne *et al.* 1992, Kindlmann & Dixon 1993). La limite inférieure de cette fenêtre est déterminée par une densité minimale de pucerons nécessaire pour le déclanchement de l'oviposition. La limite supérieure de la fenêtre, c'est-à-dire le moment où une femelle ne devrait plus pondre sur une colonie est plus difficile à déterminer. Il a été montré que ni l'âge de la plante hôte, ni l'âge de la colonie, qui se traduit par une proportion plus importante d'individus ailés, n'inhibent la ponte (Hemptinne *et al.* 2000a). Jusqu'à présent, seule l'ODP produit cet effet. On peut donc supposer que c'est uniquement la présence d'autres larves qui indique qu'une colonie de pucerons n'est plus un bon site de ponte.

3. *Conséquences d'une trop forte densité de prédateurs : compétition et cannibalisme.*

i. <u>La compétition pour la ressource alimentaire.</u>

Chez les insectes parasitoïdes on parle de superparasitisme lorsque l'hôte contient un nombre de larves supérieur que ce qui peut normalement s'y développer. Les conséquences du superparasitisme peuvent être l'élimination des larves surnuméraires, l'émergence d'adultes de faible taille, ou la mort de l'ensemble des larves (Godfray 1994). Chez les insectes prédateurs de pucerons, le développement a lieu dans un patch et non dans un hôte, c'est à dire sur un espace ouvert où les interactions sont moins directes.

Le désavantage d'une trop grande densité de prédateurs est que le rapport entre le nombre de proies et le nombre de consommateurs va diminuer. Il y a donc un risque de surexploitation des ressources, c'est-à-dire une disparition prématurée de la colonie de pucerons, ou à un degré moindre, un nombre insuffisant de proies pour un développement larvaire optimal. On sait que le nombre de proies consommées pendant la phase larvaire influera directement sur le poids de l'adulte (Dixon, 2000). Or, une femelle investit d'autant plus dans la reproduction que sa taille est grande.

ii. Le cannibalisme

La seconde conséquence d'une forte densité de larves sur une colonie de puceron est la forte occurrence du cannibalisme. Chez les coccinelles, ce comportement est très commun et a un large impact sur les populations. Il a été montré sur le terrain que la mortalité des œufs due au cannibalisme est en moyenne de 50% (Osawa 1993, Schellhorn *et al.* 1999) et peut même atteindre 60 % pour *H. axyridis* (Osawa 1989). S'agissant d'une prédation de larves plus âgées sur des œufs on parle de *non sibling cannibalism*, c'est-à-dire qui se déroule entre individus de pontes différentes et non apparentés. On le différencie du *sibling cannibalism* qui se produit lors de l'éclosion des larves qui consomment les œufs non éclos de la ponte dont elles sont elles mêmes issues. Cette distinction est importante car, pour la mère, ces deux formes de cannibalisme n'ont pas les mêmes conséquences en termes de *fitness*. En intervenant au plus jeune âge, le cannibalisme au sein de la même ponte fournit aux larves les plus compétitives un apport alimentaire immédiat qui augmentera de façon significative leur probabilité de survie (Pervez *et al.* 2006, Roy et *al.* 2007). De ce fait il peut être considéré dans certains cas comme une augmentation de l'investissement reproducteur de la femelle (Osawa 2003; Osawa & Ohashi 2008). En théorie, le cannibalisme au sein d'une ponte peut être augmenté soit en favorisant un décalage dans les éclosions, soit en produisant des œufs trophiques ce qui peut être avantageux sur un site pauvre en proies (Perry & Roitberg 2006, 2005a, 2005b). Toutefois le processus physiologique qui permettrait de stériliser ou de retarder l'éclosion de certains œufs est inconnu. Cependant il semble peu probable que la meilleure stratégie pour une femelle rencontrant un site de faible qualité soit de faire une ponte avec un fort taux de cannibalisme, plutôt que de partir rechercher un site contenant une plus forte densité de proies.

Le cannibalisme entre larves de pontes différentes représente *a contrario* pour la femelle dont les œufs sont sacrifiés une perte nette, car son investissement reproducteur contribue à nourrir les larves d'une autre femelle. Agarwala & Dixon (1992) ont montré que des larves avaient un développement comparable, que ce soit en termes de prise de poids ou de temps de développement, sur une diète composée uniquement de pucerons ou d'œufs conspécifique. Afin d'éviter que son investissement reproducteur soit perdu et utilisé par des larves non apparentées, le *non sibling cannibalism* doit être minimisé. Pour cela des protections chimiques sont présentes sur la surface des œufs pour prévenir le cannibalisme et la prédation intraguilde (Ware et *al*. 2008; Hemptinne et *al*. 2000c; Omkar et *al*. 2004). Cependant, cette protection est imparfaite, et elle n'est plus efficace si les larves prédatrices sont en manque de nourriture. La meilleure façon de diminuer le cannibalisme de sa ponte est donc d'éviter que cette dernière soit découverte par des larves compétitrices.

III. La Phéromone d'Inhibition de la Ponte (ODP) : une adaptation à la contrainte du cannibalisme.

L'utilisation d'un système de marquage est très commun chez les insectes pour signaler la présence de compétiteurs (Roitberg & Mangel 1988). Ce phénomène a été largement étudié chez les parasitoïdes où, dans le cas général, les femelles marquent l'hôte dans lequel elles viennent de pondre (Godfray 1994). La particularité du marquage par les larves des coccinelles est d'abord qu'il intervient sur une zone et non sur un hôte au volume précis. En effet, une colonie de puceron est très étendue, et c'est l'ensemble du patch qui doit être marqué. Il en découle que le marquage par une femelle semble peu probable car il prendrait trop de temps. De ce fait, seules

les larves qui parcourent le site pendant plusieurs semaines sont capables d'émettre un signal susceptible d'être informatif pour les femelles. En 1998 Doumbia *et al.* ont montré que des femelles se retenaient de pondre lorsqu'elles étaient en présence de traces larvaires. À l'inverse, ils ont montré que les traces laissées par les adultes n'étaient pas inhibitrices. Les analyses chimiques ont montré que les traces larvaires étaient composées très majoritairement d'alcanes à longues chaînes carbonées peu ramifiées (Hemptinne *et al.* 2001, Magro *et al.* 2007). Ces molécules ont la particularité d'être peu volatiles et donc d'avoir une grande stabilité. Contrairement aux marquages des parasitoïdes dont la durée n'excède pas quelques heures (Visser 1992a, Godfray 1994), l'effet inhibiteur des traces larvaires de coccinelles est conservé jusqu'à un mois en condition de laboratoire (Doumbia 1998, Ruzicka 2002).

L'existence de l'ODP a été montrée pour de très nombreuses espèces de coccinelles (Yasuda *et al.* 2000, Ruzicka 2001 & 2003, Oliver *et al.* 2006, Magro *et al.* 2007, Michaud & Jyoti 2007) et on a pu mettre en évidence des sensibilités inter-spécifiques qui pourraient jouer un rôle de diminution de la prédation intraguilde au sein des coccinelles aphidiphages (Magro *et al.* 2007). Tout comme chez les parasitoïdes, on observe une plasticité de la réponse à l'ODP en fonction de l'environnement et de l'âge de la femelle. Si les patches libres sont peu nombreux, ou que la coccinelle est âgée et arrive en fin de vie, la probabilité de pouvoir pondre dans un site libre peut être très faible. Dans ces circonstances, il devient plus avantageux de pondre malgré tout dans un site occupé (Frechette *et al.*, 2004).

IV. Le conflit entre femelles et larves comme conséquence du cannibalisme et de la reconnaissance de la phéromone d'inhibition de la ponte.

Les cas où c'est la larve qui synthétise le marquage avertissant de l'occupation d'un site ou d'un hôte est rare. On le rencontre par exemple chez certains parasitoïdes où la larve cherche son hôte (Fournet *et al.* 2001). Les conséquences évolutives de la perception par les femelles d'un signal émis par des larves sont différentes de celles découlant d'interactions directes femelle - femelle car les intérêts des larves et des femelles peuvent diverger, conduisant à un conflit évolutif.

Roitberg & Mangel (1988) proposent deux scénarios évolutifs concernant l'apparition d'un marquage : (1) Il apparaît au sein d'une population sans système de marquage des doubles mutants, c'est-à-dire des individus qui vont à la fois produire cette phéromone et la reconnaître. (2) L'ensemble des individus laissent derrière eux des traces de leur passage. Celles-ci sont toutefois faibles car elles ne sont pas destinées à véhiculer une information. Les mutants qui apparaissent dans la population vont produire ce signal avec une plus haute intensité que le reste de la population. Alors, l'ensemble des individus reconnaît ce signal mais seuls les mutants le produisent en grande quantité.

Ces deux hypothèses évolutives s'adaptent bien à un système où le récepteur et l' émetteur de l'information trouvent chacun un intérêt à la production de ce signal. Qu'en est-il lorsque seul le receveur de l'information y tire un avantage ?

De façon simple, on peut séparer les systèmes de marquage en deux groupes (Nufio & Papaj 2001): ceux pour lesquels le marquage est apparu et a évolué afin de transmettre l'information d'occupation du site, et ceux pour lesquels le marquage est apparu de façon indirect, le signal étant à l'origine synthétisé pour un autre raison physiologique. C'est dans ce dernier groupe que l'on va trouver les signaux produit par des insectes phytophages, comme des hormones sexuelles, et qui ont un effet attractif sur leur prédateur .

Dans notre cas, le but de la femelle est de diminuer la probabilité que des larves non apparentées rencontrent sa ponte afin de la préserver du cannibalisme. Une femelle qui recherche un site de ponte ne rencontrera pas obligatoirement une larve lorsqu'elle visitera un site occupé. Il faut donc qu'elle soit capable de s'assurer de la présence ou de l'absence de larves sans avoir à les rencontrer. Le message de présence de larves passera par voie chimique, via l'ODP. La synthèse de ce message chimique par les larves pose à première vue un problème évolutif. La synthèse de molécules chimiques a un coût énergétique, or si cette dépense est largement compensée lorsqu'il s'agit d'une phéromone sexuelle permettant de trouver un partenaire, ou lorsqu'il s'agit de protéger sa ponte, ici ce n'est pas le cas. Au contraire, la production d'ODP par les larves diminue la probabilité qu'une femelle vienne pondre a proximité et donc la possibilité de pouvoir bénéficier de nourriture supplémentaire par le biais du cannibalisme. La synthèse d'ODP par les larves bénéficie *a priori* uniquement au récepteur, c'est-à-dire aux femelles, et devient un inconvénient pour les larves émettrices puisqu'elle limite leur apport alimentaire.

V. Présentation des différentes parties de la thèse.

L'objectif principal de cette thèse est de construire un contexte théorique qui explique l'évolution du choix des sites de ponte des coccinelles aphidiphages, et des conséquences que ce choix sur l'évolution du cannibalisme. Pour atteindre cet objectif, la thèse est structurée en trois chapitres, le premier est un traitement mathématique du problème et les deux suivants relatent des expériences réalisées pour valider des prédictions obtenues produite par le modèle mathématique.

a. Évolution du cannibalisme et de la Phéromone d'inhibition de la ponte

Comme le but de cette thèse est d'explorer de façon théorique les raisons qui ont permis au système de production d'ODP par les larves et leur reconnaissance par les femelles d'évoluer et de se maintenir, un modèle mathématique a été construit. Une attention particulière a été portée afin de le structurer selon les différents stades de développement du prédateur : œuf, larve et adulte, car ces trois stades ont des implications très différentes en matière de cannibalisme. En partant d'un système simple, nous l'avons complexifié par étapes pour finalement aboutir à un modèle qui autorisait le polymorphisme tant du point de vue de la production de la phéromone, qu'au niveau de la reconnaissance de ce signal par les femelles. Ce modèle nous a permis de formuler des prédictions quant à la reconnaissance des larves apparentées par les femelles et à l'intérêt du cannibalisme que nous avons testé dans les deux chapitres suivant de cette thèse.

b. Étude comparative de la sensibilité des femelles aux traces de leur descendance.

L'objet du deuxième chapitre de cette thèse fut d'explorer la sensibilité des femelles aux traces produites par leurs propres descendants. L'hypothèse alternative étant que, puisque le cannibalisme est avantageux pour les larves qui le pratique, une femelle pourrait avoir intérêt à pondre sur un site déjà occupé par ses descendants afin de leur apporter un surplus alimentaire. En effet dans un environnement appauvri, une femelle dont la probabilité de survie de sa future ponte est faible aurait intérêt à pondre à proximité de ses propres traces, plutôt que sur un site occupé par des larves non apparentées.

c. De l'intérêt du cannibalisme et de sa pratique sur par les larves de coccinelles.

Le troisième chapitre de cette thèse a trait au cannibalisme des œufs par les larves. Nous avons voulu explorer l'avantage physiologique de l'apport du cannibalisme au sein du régime alimentaire des larves. Contrairement aux études déjà effectuées qui suivent le développement complet de larves nourries de diètes exclusivement constituées d'œufs ou de pucerons, nous avons souhaité nous rapprocher d'une situation naturelle en testant un régime mixte d'œufs et de pucerons. De plus, nous avons voulu tester l'hypothèse *meet and eat* proposée par Kindlmann & Dixon (2003) selon laquelle le taux de cannibalisme est proportionnel au taux de rencontre entre des larves et des œufs. L'augmentation du cannibalisme observée en laboratoire lorsque la densité de proies diminue ne serait en fait due qu'à une diminution du taux de rencontre entre les larves et les pucerons et ne résulterait pas d'un choix des larves (Agarwala & Dixon 1992). Grâce à un protocole expérimental original, nous avons testé le choix des larves, en fixant la probabilité du taux de rencontre entre des œufs et des pucerons.

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PREMIER CHAPITRE

… On s'aperçoit, à méditer le travail mathématicien, qu'il provient toujours d'une extension d'une connaissance prise sur le réel et que, dans les mathématiques mêmes, la réalité se manifeste en sa fonction essentielle : faire penser.

Gaston Bachelard. *Le nouvel esprit scientifique*, 1934.

Premier Chapitre

Évolution du cannibalisme et de la reconnaissance des femelles à la phéromone d'inhibition de la ponte chez les coccinelles aphidiphages.

Ce chapitre a fait l'objet en 2009 d'une publication dans le *Journal of Animal Ecology*,

Sous le titre suivant :

Evolution of cannibalism and female's response to oviposition-deterring pheromone in aphidophagous predators.

Xavier Martini, Patsy Haccou, Isabelle Olivieri, Jean-Louis Hemptinne.

Résumé

Dans le premier chapitre de cette thèse, nous construisons un modèle où la population de prédateurs est divisée en trois classes : œufs, larves, et adultes, car chacun de ces stades a une implication différente dans la reproduction et le cannibalisme. Dans ce système, nous montrons que le cannibalisme est favorisé. En d'autre terme, une mutation qui augmente le taux de cannibalisme par rapport à celui de la population devrait pourvoir s'y fixer.

Or le modèle montre également que l'augmentation du cannibalisme engendre une meilleure survie des larves, l'augmentation du nombre d'adultes tout comme la production d'œufs, ce qui compense, voir même surpasse les pertes dues au cannibalisme. Cette situation rend le système instable, et l'apparition de cycles est favorisée, ce qui dans la nature peu se traduire par une augmentation du risque d'extinction.

La diminution du taux de rencontre par l'intermédiaire de l'ODP permet de rééquilibrer ce système. En parallèle à l'augmentation du cannibalisme, l'inhibition de la ponte des femelles par la reconnaissance des traces larvaires est favorisée.

Dans le cadre d'un conflit entre larves et adultes, le signal ne devrait pas être conservé à l'identique au cours de l'évolution. Nous avons donc intégré dans notre modèle la possibilité de polymorphisme pour la production de traces larvaires et pour la reconnaissance des femelles. Ce polymorphisme permet d'obtenir des oscillations entre des phases de cannibalisme intense où la phéromone est peu reconnue, et des phases d'évitement maximum des sites occupés, grâce à la dominance d'un phénotype qui reconnaît mieux ses descendants. À l'équilibre, le modèle montre que ce sont ces phénotypes avec la meilleure reconnaissance de leurs descendants qui sont dominants.

De ce modèle, nous avons pu en ressortir un certain nombre de prédictions : (1) Le polymorphisme au niveau de la production d'ODP permet d'expliquer le maintien de ce système (2) Le comportement de cannibalisme par les larves doit être favorisé, et ne devrait pas être

influencé par la densité de proies. (3) Les femelles doivent être plus sensible à leurs descendants qu’aux larves non apparentées.

EVOLUTION OF CANNIBALISM AND FEMALE'S RESPONSE TO OVIPOSITION DETERRING PHEROMONE IN APHIDOPHAGOUS PREDATORS

I. Introduction

For non-social Arthropods that do not provide parental care to their offspring, the survival of larvae is strongly dependent on the quality of the oviposition sites selected by gravid females. Since larvae usually have low dispersal capacity, it is unlikely they will be able to find a better place if they hatch in a poor quality site. The choice of oviposition sites is therefore crucial and has a large affect on the fitness of females (Resetarits 1996). Many insect species, whose food supplies are temporally limited, avoid the risk of competition between conspecific offspring by marking the resource (Gabel & Thiery 1992; Ruzicka 1996 and 1997; Dempster 1997; Ruzicka & Havelka 1998; Anbutsu & Togashi 2001; Addesso *et al.* 2007; Liu, Yu & Li 2008). For instance, parasitoids avoid superparasitism by probing potential hosts (Agboka *et al*. 2002; Yamada & Ikawa 2005) or marking them with pheromones, which facilitates the detection of conspecifics within a host (Vandijken, Vanstratum, & Vanalphen 1992; Visser *et al.* 1992; Gauthier, Monge & Huignard 1996; Field & Keller 1999, Santolamazza-Carbone, Rodriguez-Illamola & Rivera 2004). With the exception of cases where larvae forage to find a host (Fournet *et al*. 2001) the females usually mark the hosts that they have just parasitized.

Aphidophagous predators face the same problems as parasitoids. This is particularly well studied in the case of ladybird beetles. Resources are regularly limited at particular periods of time, due to the ephemeral nature of aphid colonies (Dixon 1998). Whereas larvae need 4 to 5 weeks to develop, aphid colonies only last for 6 to 8 weeks, and are thus a short-lived resource. For ladybirds, colonies of aphids are only suitable as oviposition sites during the “egg window” (Dixon 2000). This window opens when a minimum critical density of aphids is reached (Dixon 1959; Honek 1980). Below this threshold aphids are so rare that larvae have a low probability of catching their first prey and are therefore likely to die from starvation. Another risk of starvation occurs if the abundance of aphids in the patch declines before larvae complete their development. Thus, each colony support an optimal number of eggs , which predators should not exceed even though the numbers of aphids are still increasing (Kindlmann & Dixon 1993). Females stop laying additional eggs when they discover tracks of conspecific larvae (Doumbia, Hemptinne & Dixon 1998; Yasuda, Takagi & Kogi 2000). After searching occupied patches and determining that they are unsuitable for oviposition females eat some aphids and fly away (Fréchette *et al.* 2004). Because of this adaptation to the ephemeral nature of their prey the individual aggregative response of ladybirds to aphid density can be strong, but their numerical response is weak or restricted to a narrow range of aphid densities (Hemptinne, Dixon & Coffin 1992; Ives, Kareiva & Perry 1993).

Empirical evidence suggests that the evaluation of egg windows by adult females could be a response to the occurrence of egg cannibalism by larvae. Cannibalism has a great effect on the survival of eggs and young larvae in Coccinellidae (Osawa 1992, Yasuda & Shinya 1997, Snyder *et al.* 2000; Pervez, Gupta & Omkar 2006) and is commonly observed both under laboratory conditions and in the field (e.g. Osawa 1989, Hironori & Katsuhio 1997, Schellhorn & Andow 1999). It is also strongly density-dependent (Mills 1982).

At this point it is important to differentiate the consequences of sibling cannibalism from those of non-sibling cannibalism. Sibling cannibalism can in theory be advantageous both for larvae and their mothers. When it occurs within the same egg batch, it provides the first meal for the larvae and contributes to a faster increase in body mass (Omkar, Pervez, & Gupta 2007) and reduction in the duration of the first larval stage (Michaud & Grant 2004). As after dispersing from the eggs larvae can suffer from starvation, egg cannibalism increases their survival and searching time for aphids (Majerus, 1994).

Non-sibling cannibalism incurs a fitness cost for females. Therefore we expect that strategies that mitigate the risk of non-sibling cannibalism have been selected for. For example, the two-spot ladybird *Adalia bipunctata* (L.) refrains from laying eggs on plants infested by aphids but contaminated by conspecific larval tracks (Doumbia *et al.* 1998; Fréchette *et al*. 2004). They are deterred by the presence of an oviposition deterring pheromone (ODP) deposited on the plant by the anal disk of the larvae (Laubertie *et al.* 2006). This ODP is a mixture of long aliphatic molecules, mainly alkanes (Hemptinne *et al.* 2001, Magro *et al*. 2007). Field observations indicate that aphidophagous ladybirds start laying eggs in aphid colonies quite early in the colony development and cease laying eggs as soon as colonies are marked by foraging first instar larvae. That is, the presence of ODP closes the egg window (Doumbia *et al.* 1998; Hemptinne *et al.* 2001). As the recognition of and reaction to ODP are a good means of preventing non-sibling egg cannibalism, many ladybird species developed this system. Although ODPs are commonly produced by insects dependent on ephemeral resources (Nufio & Papaj 2001), they are usually direct signals, i.e. the foraging females mark the resource and eventually use this information on a later visit to avoid a second exploitation (Godfray 1994). In the Coccinellidae however, it is an indirect system. Larvae produce the ODP and this signal is detected by females. Whereas the importance of this marking pheromone for females is easily understood, the advantage for larvae is less clear.

Ladybirds have always interested theoretical biologists, who have been mostly concerned with their use as pest biocontrol agents (Dixon, Hemptinne & Kindlmann 1997; Dostalkova, Kindlmann & Dixon 2002). However, evolutionary studies on their life histories are rare (Dixon & Hemptinne 2001; Kindlmann & Dixon 1999). Furthermore, theoretical studies on oviposition strategies mainly focus on parasitoids. The main questions addressed are the duration of foraging bouts in patches, or the time at which females should start to super-parasitize, in relation to resource availability or competition. Aphidophagous predators differ from parasitoids in the occurrence of cannibalism, in that the larvae have to find and catch their prey, and in that they produce the signal that is used by foraging females to assess the quality of oviposition sites. In this paper we study the evolution of ODP in aphidophagous predators by means of an evolutionary invasion analysis, which evaluated the selective advantage of mutants with different preferences for egg-cannibalism or sensitivity to ODP. In the last part we numerically investigate the occurrence of polymorphism in ODP produced by larvae and its recognition by females.

II. Description of the models

a. Modelling Strategy

We model the population dynamics of aphidophagous ladybirds and their resource, the aphids, with an age-structured system of differential equations. For reasons of tractability, we neglect seasonal dependence of ladybird-aphid dynamics and use a continuous-time model. We first consider the dynamics of ladybird-aphid populations in the absence of cannibalism. Then we consider the effects of cannibalism and the conditions for this behaviour to evolve. Subsequently we consider the evolution of ODP synthesized by larvae. Finally, we study the effects of diversity in the composition of the ODP.

b. No-cannibalism model.

The structure of this model is illustrated in Fig.1. We assume three life-cycle stages for the ladybirds: eggs, larvae and adults, and only one stage for the aphids. The density at time *t* for each class is *x, y, z* and *r,* respectively. The parameters used in the models are listed in Table 1. The equation for the change in egg density is:

$$\frac{dx}{dt} = \beta \cdot \eta \cdot r \cdot z - \lambda \cdot x - m \cdot x \text{, (eqn 1)}$$

where $\beta \cdot \eta \cdot r \cdot z$ denotes the production of eggs by adults, depending on the number of aphids they eat. λ and *m* refer to the death and maturation rates, respectively. Changes in the density of larvae are given by:

$$\frac{dy}{dt} = m \cdot x - \gamma \cdot \mu \cdot r \cdot y - \xi \cdot y \text{ , (eqn 2)}$$

where $\gamma \cdot \mu \cdot r \cdot y$ refers to the development of adults, which depends on the number of aphids the larvae eat, as shown by Dimetry (1976).

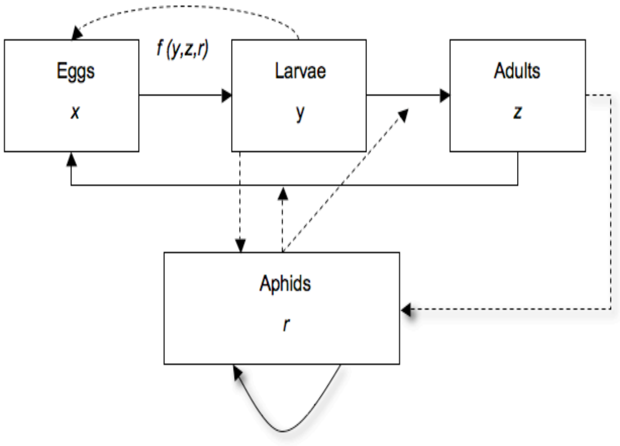


Fig. 1. Schematic diagram of the stage structure used in the models. The letters in each box represent the name of the corresponding state variable. $f(y,z,r)$ refers to the cannibalism function. In the first model we assume the absence of cannibalism, so $f(y,z,r) = 0$.

Scaled parameters	Description	In terms of original parameters	Value
β	Conversion rate (aphids to eggs) for adults	β	5
η	Predation rate of larvae	$\frac{\eta k}{\alpha}$	1
μ	Predation rate of larvae	$\frac{\mu k}{\alpha}$	1
m	Maturation rate of eggs	$\frac{m}{\alpha}$	1
γ	Conversion rate of larvae	γ	5
λ	Death rate of eggs	$\frac{\lambda}{\alpha}$	1
ξ	Death rate of larvae	$\frac{\xi}{\alpha}$	1
φ	Death rate of adults	$\frac{\varphi}{\alpha}$	1
α	Grow rate of aphids	1	-
k	Carrying capacity of aphids	1	-
$f_{(y,z,r)}$	Function of the cannibalism of larvae.	-	-
c_i	Constant of the cannibalism function	-	1
ρ	Rate of acceptance of occupied patches by females	-	0.5

Table 1. In order to simplify calculations, some parameters have been rescaled (third column), but for simplicity we use the original notations in the rest of the paper. The last column shows the default values of the parameters that are used in simulations (unless specified otherwise).

The death rate of the larvae that hatch from the eggs is ξ. The dynamics of adult density is given by:

$$\frac{dz}{dt} = \gamma \cdot \mu \cdot r \cdot y - \varphi \cdot z \text{ , (eqn 3)}$$

with φ the death rate of adults. Finally, we assume that in the absence of predators aphid populations grow logistically. We assume that larvae and adults of ladybirds have different predation rates, denoted by μ and η, respectively:

$$\frac{dr}{dt} = \alpha \cdot r \cdot \left(1 - \frac{r}{k}\right) - \mu \cdot r \cdot y - \eta \cdot r \cdot z \text{ (eqn 4)}$$

To improve the efficiency of the analysis the model is rescaled in dimensionless parameters and densities. We rescale time from *t* to α*t*, i.e. relative to the growth rate of the aphids, and all densities to *density/k*, i.e. relative to the carrying capacity of the aphids. For ease of notation we do not introduce new symbols for the scaled parameters, but refer to them by the original symbols, as introduced in eqn. (1) to (4) (an overview is given in Table 1). This implies that the differential equations are the same as before, except for the population dynamics of aphids, (eqn 4), which becomes:

$$\frac{dr}{dt} = r\left(1 - r\right) - \mu \cdot r \cdot y - \eta \cdot r \cdot z \text{ , (eqn 5)}$$

This dynamical system can have three equilibria. The trivial equilibrium, where all densities are zero, is unstable for all positive parameter values. In the second equilibrium, the ladybirds are extinct and the aphid density is at its carrying capacity. In the third the aphids and ladybirds coexist. It can be shown that in this case (see Annex 1):

$$\hat{r} = \frac{1 + \sqrt{1 + 4\left(\dfrac{\dfrac{\beta \cdot \eta}{\varphi}\dfrac{m}{(\lambda + m)}}{\dfrac{\gamma \cdot \mu}{\xi}}\right)}}{2\left(\dfrac{\beta \cdot \eta}{\varphi}\dfrac{m}{(\lambda + m)}\right)}, \qquad \text{(eqn 6)}$$

This equilibrium only exists if $\hat{r}$ is less than 1, since otherwise the aphid density equals its carrying capacity, and there can be no coexistence. This leads to the condition:

$$2\left(\frac{\beta \cdot \eta}{\varphi}\frac{m}{(\lambda + m)}\right) > 1 + \sqrt{1 + 4\left(\dfrac{\dfrac{\beta \cdot \eta}{\varphi}\dfrac{m}{(\lambda + m)}}{\dfrac{\gamma \cdot \mu}{\xi}}\right)}, \text{ (eqn 7)}$$

which can be written as:

$$\frac{\beta \cdot \eta}{\varphi} > \left(1 + \frac{\lambda}{m}\right) \cdot \left(1 + \frac{\xi}{\gamma \cdot \mu}\right) \text{ (eqn 8)}$$

It can be concluded that β and η need to be high enough, and φ low enough, to make coexistence possible. In words, ladybird larvae have to eat many aphids and adults have to survive well and efficiently convert the aphids they eat into eggs. Fig. 2.a shows the maximum of the real part of the eigenvalues of the Jacobian matrices for the second (ladybirds extinct, aphids at carrying-capacity) and the third equilibrium (coexistence) as a function of β, the rate of conversion of aphids into eggs by adult ladybirds. From this figure it can be seen that as long as inequality (8) is invalid, the second equilibrium is stable. As soon as the third equilibrium exists, this non-coexistence equilibrium becomes unstable. Initially the third coexistence equilibrium is then stable, but at very high values of β it also becomes unstable. In that case none of the equilibria are stable. Numerical analyses show that in this region of the parameter space there are stable limit cycles (see Fig. 2.b and 2.c).

In biological terms it simply means that ladybirds have to produce sufficient eggs to ensure coexistence. If egg production is larger, the model predicts limit cycles (Fig 2.b. and 2.d). Indeed increase in egg production leads to an increase in the number of larvae and of their predation rate, so the number of aphids per larva goes down. As we assume that the growth rate of larvae depends on the number of prey consumed, larvae will take longer to develop. This results in a decrease in adult recruitment.

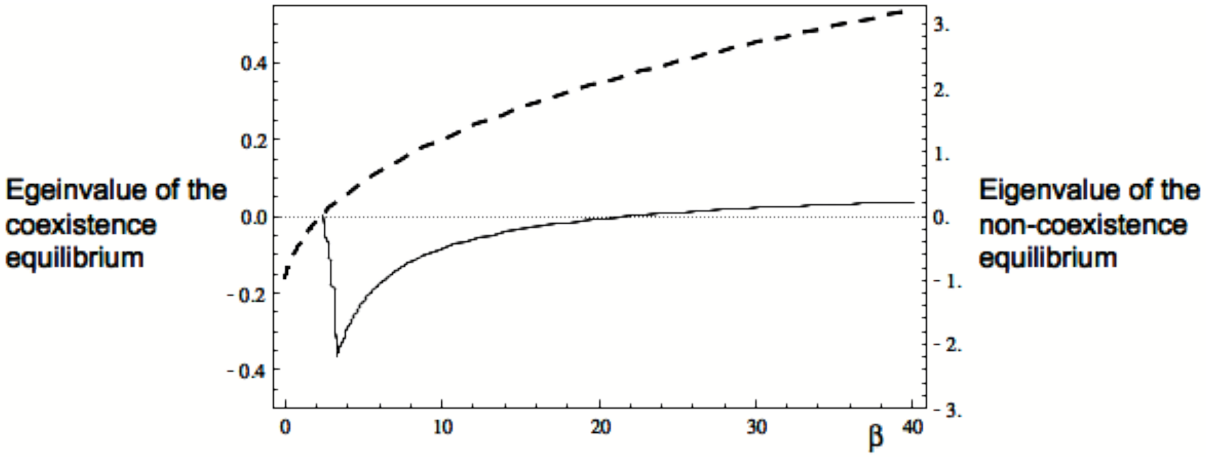


Fig. 2.a Maximum real parts of the eigenvalues of the non-coexisting equilibrium (dashed line) and the coexistence equilibrium (thick line). As long as inequality (8) is invalid, the co-existence equilibrium does not exist and the non-coexistence equilibrium is stable. This equilibrium becomes unstable as soon as inequality (8) holds, and at that point the coexistence equilibrium comes into existence and is initially stable. For large values of β this equilibrium too becomes unstable and the system shows stable limit cycles.

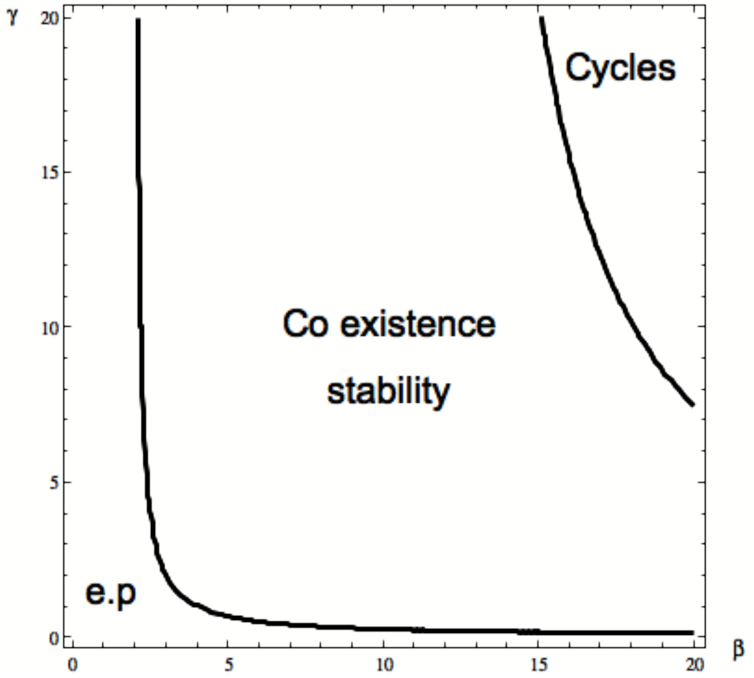
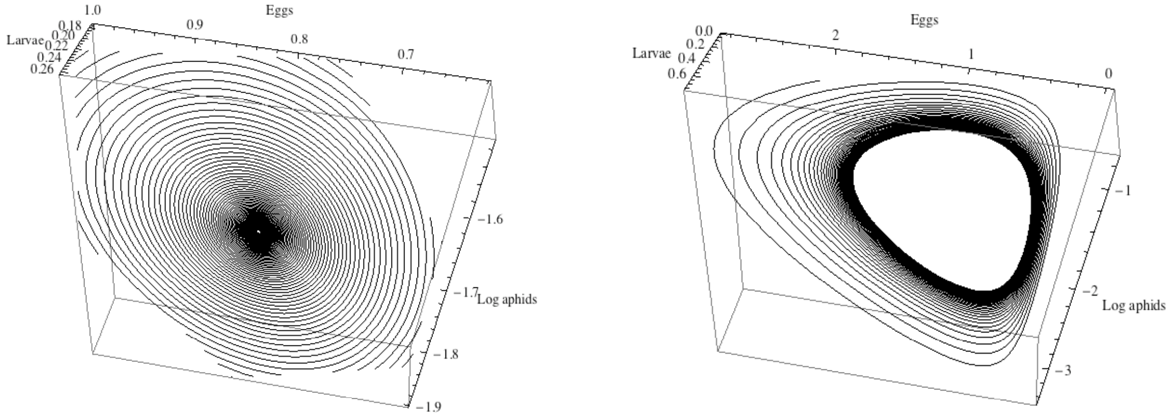


Fig. 2.b Bifurcations of the system. e.p.: Extinction of predators. In this region aphid density is at its carrying capacity. At large values of β and γ stable limit cycles occur.



(c) (d)

Fig 2.c Example showing stability after damped cycles. Parameter values: γ=15, **β=14; Fig 2.d.** Increase of fertility leads to stable cycles. Parameter values: γ=15, **β=17**

c. Cannibalism Model

Next, we consider a model where larvae also eat conspecific eggs (Fig.1) In this case the egg density changes as follows:

$$\frac{dx}{dt} = \beta \cdot \eta \cdot r \cdot z - f(y,z,r) \cdot x \cdot y - \lambda \cdot x - m \cdot x \quad \text{(eqn 9)}$$

Where *f(y,z,r)* is the cannibalism function, defined by:

$$f(y,z,r) = c_1 \cdot \left(1 - e^{-c_2 \cdot (y+z)}\right) \cdot e^{-c_3 \cdot r} \quad \text{(eqn 10)}$$

c_1 is a constant that refers to the cannibalism tendency of the population. The term $\left(1 - e^{-c_2 \cdot (y+z)}\right)$ models the effect of adult and larval densities on cannibalism. We assume that high adult and larval densities increase the risk of egg cannibalism, as the distribution of egg-batches becomes more aggregated due to the number of females that forage in the patch. Finally $e^{-c_3 \cdot r}$ refers to the influence of aphid density on cannibalism. We assume that at high aphid densities there is less cannibalism, due to satiation of larvae and decreased probability of meeting eggs. For eggs, cannibalism can be seen as an increase in the death rate, but it is a source of energy for the larvae. Accordingly, the dynamics of larval density is given by:

$$\frac{dy}{dt} = m \cdot x - \gamma \cdot \left(\mu \cdot r + f(y,z,r) \cdot x\right) \cdot y - \xi \cdot y \quad \text{(eqn 11)}$$

That is, the more conspecific eggs larvae eat, the more energy they accumulate and the greater their growth rate. As a consequence, the equation for changes in adult density becomes:

$$\frac{dz}{dt} = \gamma \cdot \left(\mu \cdot r + f(y,z,r) \cdot x\right) \cdot y - \varphi \cdot z \quad \text{(eqn 12)}$$

That is, the more conspecific eggs larvae eat the higher the proportion that become adult. Egg-cannibalism results in an increase in food supply and consequently decreases the time needed for larval development. Consequently, cannibalism first reduces the density of larvae (Fig 3. b), but this loss is not due to death but to an increase in adult recruitment (Fig 3. c). The resultant increase in egg production (Fig 3. a) is counterbalanced by cannibalism, which allows the system to reach equilibrium.

The conditions for the extinction of the predator do not change when cannibalism is added to the model. However cannibalism destabilizes the system, as it increases the parameter range over which cycling occurs (Fig. 4). Still the area of stable cycles remains limited, since a severe increase in the cannibalism rate does not lead to the disappearance of a stable coexistence area. In the following, only parameter combinations where stable coexistence occurs are considered.

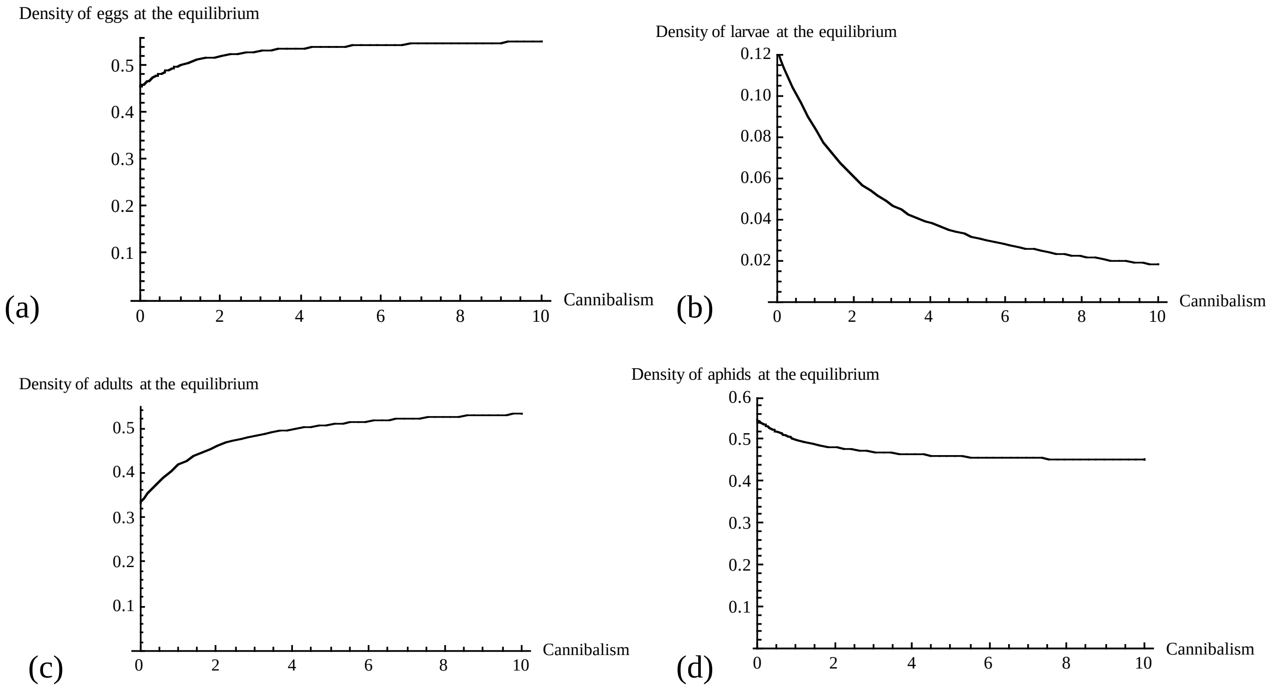


Fig. 3. Effect of cannibalism rate *f(y,z,r)* on the steady states of the three stages of the predator and aphid density.

The evolution of cannibalism

In this part we examine by means of adaptive dynamics how cannibalism might have evolved. We consider a resident ladybird population at equilibrium with a fixed level of cannibalism, and study whether a mutant with a slightly different tendency to cannibalize can invade the population. By determining which types of mutant can invade different types of resident populations, we can infer the direction of evolution (see e.g. Otto & Day 2007).

In this analysis we use the tendency to cannibalise as the decision variable that varies between mutant and resident. This implies that the parameter c_1 of the cannibalism function (cannibalism tendency, see eqn 10) will change for the mutant and this will affect the invasive capacity of the mutant. We consider a resident population at equilibrium, with a cannibalism function, denoted by f_r. The dynamics of the egg density of a rare mutant appearing in this population is given by:

$$\frac{dx_m}{dt} = \beta \cdot \eta \cdot \hat{r} \cdot z_m - f_r(\hat{y}, \hat{z}, \hat{r}) \cdot x_m \cdot \hat{y} - \lambda \cdot x_m - m \cdot x_m \quad \text{(eqn 13)}$$

where $\hat{r}, \hat{y}, \hat{z}$ denote the equilibrium densities of aphids, larvae and adult ladybirds in the resident population. Dynamics of mutant larva and adult densities are given by:

$$\frac{dy_m}{dt} = m \cdot x_m - \gamma \cdot \left(\mu \cdot \hat{r} + f_m(\hat{y}, \hat{z}, \hat{r}) \cdot \hat{x}\right) \cdot y_m - \xi \cdot y_m \quad \text{(eqn 14)}$$

$$\frac{dz_m}{dt} = \gamma \cdot \left(\mu \cdot \hat{r} + f_m(\hat{y}, \hat{z}, \hat{r}) \cdot \hat{x}\right) \cdot y_m - \varphi \cdot z_m \quad \text{(eqn 15)}$$

where $\hat{x}$ is the resident equilibrium egg density. Numerical analyses show that any resident population can be invaded by more cannibalistic mutants, that is, when $f_r(\hat{y}, \hat{z}, \hat{r}) < f_m(\hat{y}, \hat{z}, \hat{r})$. We have seen that despite the increase in cannibalism the parameter range for coexistence of predators remains the same, as the loss of eggs due to cannibalism is counterbalanced by a better recruitment of adults (Fig. 3.c). However, it can be seen from Fig. 3.b and Fig. 4 that without limitation the evolutionary increase in cannibalism would lead to a dramatic reduction in the density of ladybird larvae and the occurrence of cycles, which with the stochasticity occurring under natural conditions, will increase the risk of extinction.

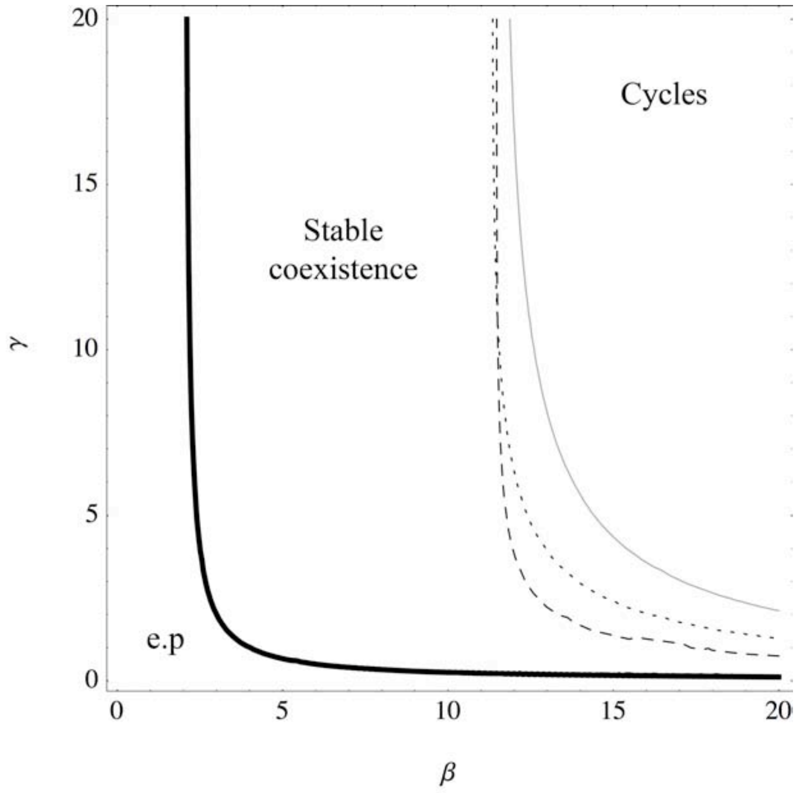


Fig. 4. Bifurcation diagram for the cannibalism model. As cannibalism increases, the area with stable limit cycles grows. But the range of parameter values that lead to the extinction of the predator remains the same. e.p. : Extinction of predators. Solid line: *f(y,z,r)=0.2*; Dotted line: *f(y,z,r)=0.5*; Dashed Line: *f(y,z,r)=2*

d. The ODP model

We now add the possibility of adult female predators responding to the presence of conspecific larvae and avoid laying eggs in such patches. The differential equations for the densities of the three predator stages become:

$$\frac{dx}{dt} = \beta \cdot \eta \cdot r \cdot z - \rho \cdot f(y,z,r) \cdot x \cdot y - \lambda \cdot x - m \cdot x \quad \text{(eqn 16)}$$

$$\frac{dy}{dt} = m \cdot x - \gamma \cdot \left(\mu \cdot r + \rho \cdot f(y,z,r) \cdot x\right) \cdot y - \xi \cdot y \quad \text{(eqn 17)}$$

$$\frac{dz}{dt} = \gamma \cdot \left(\mu \cdot r + \rho \cdot f(y,z,r) \cdot x\right) \cdot y - \varphi \cdot z \quad \text{(eqn 18)}$$

With ρ the rate of acceptance of occupied patches, so $\rho<1$, and should decrease when females become more sensitive to ODP. It can be seen that the incorporation of ODP in the relationship corresponds to a reduction in the cannibalism function. Therefore, the effect of ODP is opposite to cannibalism.

Evolutionary Invasion Analysis: adding ODP

We have seen that ODP can be considered as a decrease of the cannibalism function. To study its evolution, we proceed as before, and consider the initial growth rate of a rare mutant in a resident population fixed for a certain level of ODP. We suppose for physiological reasons that all larvae produce the molecules that compose the ODP, and that these molecules signal the presence of larvae. That is, a mature female will avoid laying eggs near larvae when they are able to detect them. The equations for the dynamics of rare mutants are

$$\frac{dx_m}{dt} = \beta \cdot \eta \cdot \hat{r} \cdot z_m - \rho_m \cdot f(\hat{y},\hat{z},\hat{r}) \cdot x_m \cdot \hat{y} - \lambda \cdot x_m - m \cdot x_m , \text{ (eqn 19)}$$

where ρ_m is the rate at which mutant females lay eggs in occupied patches,

$$\frac{dy_m}{dt} = m \cdot x_m - \gamma \cdot \left(\mu \cdot \hat{r} + \rho_r \cdot f\left(\hat{y},\hat{z},\hat{r}\right) \cdot \hat{x}\right) \cdot y_m - \xi \cdot y_m , \text{ (eqn 20)}$$

where ρ_r is the rate at which resident females lay eggs in occupied patches, and

$$\frac{dz_m}{dt} = \gamma \cdot \left(\mu \cdot \hat{r} + \rho_r \cdot f\left(\hat{y},\hat{z},\hat{r}\right) \cdot \hat{x}\right) \cdot y_m - \varphi \cdot z_m . \text{ (eqn 21)}$$

Numerical analyses show that mutants with a better recognition of ODP can invade a resident population. If the level of recognition can improve indefinitely during evolution, this will eventually lead to a perfect avoidance of occupied patches by females, reducing the level of cannibalism to zero.

e. **Diversity model**.

From the previous analyses we can conclude that there can be an arms race between the larvae and adult females. The best strategy for larvae is to mask their presence from gravid females and benefit by eating any eggs they lay. Thus, when adult females can detect the pheromone produced by larvae, there is a selective pressure towards changing the chemical composition of the pheromone. This situation gives the opportunity for polymorphism in ODP, since it is advantageous to produce a rare pheromone that cannot be detected by the majority of the females.

On the other hand, the best response for adult females would be to recognize a mixture of molecules rather than only one, potentially at the cost of being less efficient at recognizing each molecule.

In order to explore this possibility, we consider a model with two versions of ODP and 4 phenotypes: *AA*, *AB*, *BA*, *BB*. The first letter refers to the version of ODP produced by larvae, the second to that recognized best by adult females. As before, ladybirds have three-age classes. When we add the dynamics of the aphid population, this results in a system of 13 differential equations. For example, the dynamics of the density of eggs of type *AA* are given by:

$$\frac{dx_{AA}}{dt} = \beta \cdot \eta \cdot r \cdot z_{AA} - \left(\lambda + m + f\left(x_{tot,} y_{tot}, r\right) \cdot \left(\Gamma_{aa} \cdot \left(y_{AA} + y_{AB}\right) + \Gamma_{ba} \cdot \left(y_{BB} + y_{BA}\right)\right)\right) \cdot x_{AA}$$

(eqn 22)

where e.g. Γ_{ba} denotes the rate of acceptance of patches with tracks of type *B* by females that are best at recognizing type *A*, and Γ_{aa} , Γ_{ab} , and Γ_{bb} are defined analogously, with:

$$\Gamma_{aa} = \Gamma_{bb} \leq \Gamma_{ab} = \Gamma_{ba} \quad \text{(eqn 23)}$$

Now, we can write the equation for the dynamics of larval density of type *AA*:

$$\frac{dy_{AA}}{dt} = m \cdot x_{AA} - \gamma \cdot \left(\mu \cdot r + f\left(x_{tot}, y_{tot}, r\right) \cdot \left(\Gamma_{aa} \cdot \left(x_{AA} + x_{BA}\right) + \Gamma_{ab} \cdot \left(x_{BB} + x_{AB}\right)\right)\right) \cdot y_{AA} - \xi \cdot y_{AA} \text{(eqn 24),}$$

and for the adults:

$$\frac{dz_{AA}}{dt} = \gamma \cdot \left(\mu \cdot r + f\left(x_{tot}, y_{tot}, r\right) \cdot \left(\Gamma_{aa} \cdot \left(x_{AA} + x_{BA}\right) + \Gamma_{ab} \cdot \left(x_{BB} + x_{AB}\right)\right)\right) \cdot y_{AA} - \varphi \cdot z_{AA} \quad \text{(eqn 25).}$$

Analysis of the model shows four kinds of stationary behaviour:

(1) An equilibrium where the densities of all the phenotypes are the same. (2) An equilibrium where the densities of types *AA* and *BB* are equal and smaller than those of types *AB* and *BA*, which are also equal. (3) An equilibrium where the densities of *AA* and *BB* are equal and larger than those of *AB* and *BA*, which are also equal to each other. (4) Stable limit cycles, where the densities of all types fluctuate.

Equilibria (1) and (2) are unstable. Depending on initial conditions (and provided the starting conditions are not exactly equal to equilibrium (1) or (2)) the system converges to either case (3) or (4). Cycles are due to the alternation of advantage due to cannibalism, and recognition of the ODP. That is, the sequences of the peaks are $AB \rightarrow AA \rightarrow BA \rightarrow BB \rightarrow AB$.

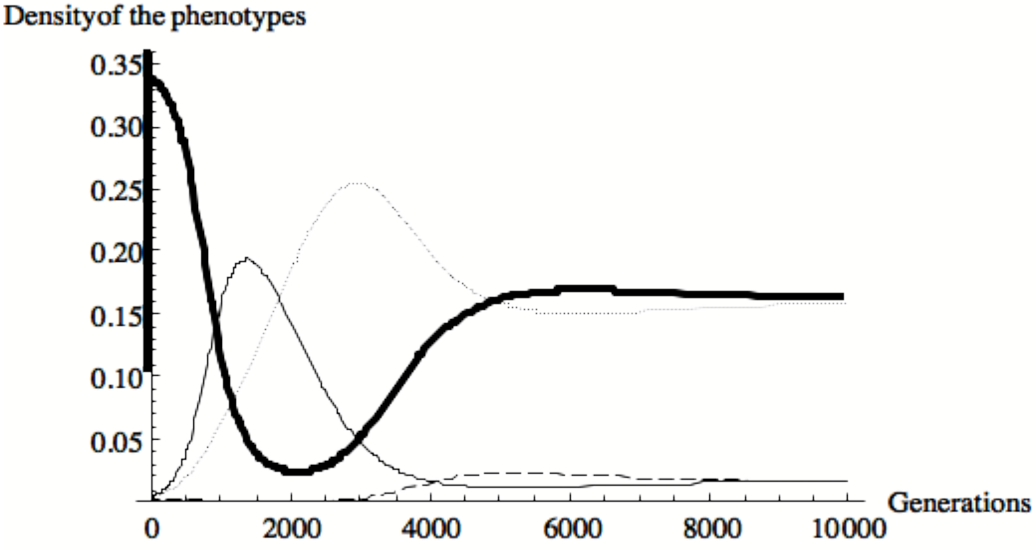


Fig. 5. Adult densities of *AA*, *BB* and *AB*. When we start with a high relative density of *AA* the system reaches an equilibrium where *AA* and *BB* are dominant,. Starting values: *AA* =0.1, *AB*=0.001, *BA*=0.001, *BB*=0.001; $\Gamma_{AA}=\Gamma_{BB}=0.5$; $\Gamma_{AB}=\Gamma_{BA}=0.75$. Thick line: *AA*, thin line: *BA*, dotted line: *BB*, dashed line: *AB*.

Alternation of peaks is the result of phases of high cannibalism alternating with phases of high recognition of ODP. When *AB* is dominant it means that tracks are mainly of the kind *A*, but the recognition of ODP is not optimal. In this case, densities of type *AA*, that is best at recognizing tracks of kind *A* increase, due to the avoidance of conspecifics. Phenotype *BA* is also better at recognizing *A* tracks, but it produces offspring that synthesize *B* tracks. Therefore, they are not recognized by their own group and are at a disadvantage compared to *AA*. When type *AA* is dominant, phenotype *BA*, whose larvae produce *B* tracks, are less likely to be recognized by the majority of the adult females and will benefit from eating eggs they lay. In the same way, *BB* and *AB* finally become successively dominant, and close the cycle.

To obtain cycles, “mixed strategies” i.e. *AB* (resp. *BA*), need to be frequent enough to increase at the time *BB* (resp. *AA*) dominates. Otherwise the system produces damped oscillations that go to the equilibrium (3) where both *AA* and *BB* are the main phenotypes. The higher the initial densities of *AA* or *BB*, the fewer oscillations. It means that in a scenario where ODP is well established, the model predicts the maintenance of a higher recognition rate for ODP when a mutant with new larval track is added in the system (Fig. 5).

III. Discussion

The models described in this paper were used to study the evolution of cannibalism in the context of the oviposition behaviour of aphidophagous insects. Although the models are clearly simplifications, this study leads to some interesting conclusions about the life- history evolution of aphidophagous predators.

Survival when there is a lack of food that would result in extinction is often cited as the reason for the evolution of cannibalism (Cushing 1991; Claessen, de Roos & Persson 2004). This study, however, indicates that in our case, a low density of aphids is not necessary for the evolution of cannibalism. The speed at which cannibalism evolved was probably greatly influenced by the ephemeral nature of aphid colonies as suggested by Wagner *et al.* (1999). Furthermore, our mutant invasion analysis shows that egg cannibalism should always be favoured by evolution. In nature, egg-cannibalism mostly occurs when aphids are relatively scarce, at the beginning and the end of an aphid colony's existence. Moreover some laboratory studies have shown that cannibalism increases when aphid density is low. It is suggested that this simply results from the increased probability of larvae meeting conspecific eggs or larvae (Agarwala & Dixon, 1992; Dixon, 2000). So, we predict that in the field larvae will eat eggs whenever possible, whatever the availability of aphids. This prediction can explain for instance sibling-cannibalism in which the first larva to hatch first eats its egg shell and then those eggs that have not yet hatched (Michaud *et al.* 2004; Perry & Roitberg 2005). Gagné, Coderre & Mauffette (2002) show that neonate *Coleomegilla maculata lengi* Thimberlake prefer to eat eggs than aphids. Moreover, *A. bipunctata* fed a diet consisting exclusively of conspecific eggs have the same development time and weight gain as those fed only aphids (Agarwala *et al.*, 1992; Michaud, 2003). As larvae readily eat conspecific eggs, it is interesting to consider whether mothers could be selected to increase the food supply to first instar larvae by laying trophic eggs in unfavourable environments, as suggested by Perry *et al.* (2005).

Although the loss of all the eggs to cannibalism is unlikely in the real world, too high a loss due to cannibalism could result in cycles. This result agrees with the prediction of some models that specifically study the influence of cannibalism on age structured populations (see e.g. Claessen *et al* 2004 for a review). Under natural conditions, cycles might increase the risk of extinction. Consequently, in a persistent system other factors not considered here might decrease the probability of larvae encountering eggs. Possible factors are migration or selection at a metapopulation level, including extinction and recolonization. In addition, certain aspects of the behaviour of aphidophagous ladybirds may decrease encounter rate. For instance, synchronous hatching of the eggs in clusters would restrict sibling cannibalism mostly to infertile eggs (Osawa & Ohashi 2008).

More generally, a female should detect the presence of larvae and so avoid ovipositing in colonies of aphids already being exploited. The sensitivity to these tracks should be under directional selection whatever the level of cannibalism. This explains why ODPs are recorded for many species of Coccinellidae and other aphid predators. Our model predicts that the evolution of ODP recognition should lead to the avoidance of occupied patches, implying the disappearance of cannibalism, due to lack of opportunity. However, a mutant that would practice cannibalism and produce a different pheromone could invade a non-cannibalistic population.

Since there is a conflict between larvae and adults in this respect, there is a selective pressure on the larvae to change the composition of their tracks in order to become less easily recognized by adults. This may lead to further diversification of the ODP. The *diversity* model with two types of ODP predicted that this could lead to a polymorphic equilibrium in which the mutant that is best at recognizing its own phenotype is the most frequent. This implies that adult females should be better at recognizing and avoiding the tracks of larvae of their own type. This result is counterintuitive since kin selection arguments lead us to expect that the best strategy for females is to avoid patches with larvae of the other type but not their own larvae. Indeed, as egg-cannibalism is a source of food for the cannibals, it is more advantageous for females to have their eggs eaten by their own larvae than non-related ones. However, the probability of a female finding by chance a patch with its own larvae is probably weak because the residence time of a ladybird at a specific location in the field is on average not longer than 5 to 7 days in spring, and about 3 days in summer (Osawa, 2000). Moreover during this time, ladybirds tend to frequently move within the habitat. In fact the emergence of larvae that produce a track that differs from that recognized by resident females would reduce the effect of the ODP, and as discussed above a system with a low recognition rate of the ODP can be invaded by a mutant with a higher sensitivity. Therefore, we predict that females should be more sensitive to the tracks of closely related than to those of more distantly related larvae. The balance between the intensity of egg-cannibalism, the sensitivity of females to ODP and changes in the chemical composition of this signal can account for the 50% egg cannibalism recorded in the field (Osawa 1993, Schellhorn *et al.* 1999).

The following scenario is proposed for the evolution of ODP in Coccinellidae. On one hand, cannibalism has been favoured and has probably contributed to the success of sib-families as it has allowed higher reproductive rate at the steady states. On the other hand, assuming cannibalism, females which could detect the presence of larvae and avoid occupied patches are likely to have had a selective advantage. Females could potentially respond to any chemical produced for any purpose by larvae and so avoid occupied patches. Such chemicals could for instance be produced by larvae to adhere to plant surfaces, or act as a waterproofing barrier (see Hadley 1981 for a review). As the avoidance of conspecific larvae results in a decrease in cannibalism, and egg cannibalism by the larvae should always be selected for (at least under the assumptions of our model), we can hypothesize that selection favoured quantitative or qualitative modifications of the mixture of molecules, as long as their function was maintained. As a result, the rate of recognition by females would have decreased and the probability of egg cannibalism would have increased. In the end, once different types of ODP had evolved, selection probably gave an advantage to those females able to recognize a mixture of hydrocarbons rather than a single molecule. We thus predict that females should be able to recognize mixtures of hydrocarbons, and that there should be genetic variability in the type of chemical profile recognized, rather than in the ability to recognize a single compound. Our model also predicts that there should be frequent changes in the profile of larval tracks in populations and that females should be more sensitive to their own larval tracks than those of the larvae of other females.

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SECOND CHAPITRE

La famille est plus importante que les individus qui la constituent

Moses Isegawa. *Chroniques abyssiniennes*, 1998.

Second Chapitre

Influence de l'apparentement génétique sur la réponse des femelles à la phéromone d'inhibition de la ponte chez *Adalia bipunctata* L.

Influence of relatedness on the response to oviposition deterring pheromone by females of *Adalia bipunctata* L.

Résumé

Dans le modèle du premier chapitre, l'ajout de polymorphisme au niveau de la production et de la reconnaissance des traces larvaires a pour conséquence une meilleure sensibilité à l'ODP produite par des apparentés. Cette nouvelle partie rend compte des expériences menées pour tester cette hypothèse. Nous comparons le temps de ponte de femelles soumises à trois traitements : (1) Absence d'ODP (contrôle), (2) Traces de larves non apparentées, (3) Traces de leurs propres larves. Ces différents traitements sont ensuite soumis à l'influence de l'âge et de l'expérience des femelles afin d'étudier leur influence sur la sensibilité des femelles à l'ODP.

Les résultats montrent que les femelles *d'Adalia bipunctata* pondent moins en présence de traces de leurs descendants que des larves non apparentées. Si une femelle s'est déjà trouvée en présence d'ODP, cette différence de sensibilité en fonction de l'apparentement est conservée. A l'inverse, l'âge des femelles rend ces dernières insensibles aux traces larvaires, quelles qu'elles soient.

Cela implique un polymorphisme au niveau de la production de l'ODP, une molécule seule ne pouvant aboutir à de tels résultats. C'est la première fois que l'on a pu montrer l'effet de l'apparentement au niveau de la phéromone d'inhibition de la ponte dans la famille des Coccinellidae.

INFLUENCE OF RELATEDNESS ON THE RESPONSE TO OVIPOSITION DETERRING PHEROMONE BY FEMALES OF *ADALIA BIPUNCTATA* L.

I. Introduction

Many insect species that exploit time and size limited resources mark oviposition sites to avoid competition (Roitberg & Mangel 1988, Gabel & Thiery 1992, Ruzicka 1996 and 1997, Ruzicka & Havelka 1998, Anbutsu & Togashi 2001, Nufio & Papaj 2001, Addesso *et al.* 2007, Liu *et al.* 2008). Solitary parasitoids, for example, mark host they parasite with a pheromone that prevents superparasitism (Vandijken *et al.* 1992; Visser *et al.* 1992; Gauthier, Monge & Huignard 1996; Field & Keller 1999, Santolamazza-Carbone et *al.* 2004).

In aphidophagous ladybirds, females refrain from laying eggs when they detect an oviposition deterring pheromone (ODP) produced by larvae (Ruzicka 1997, Doumbia *et al.* 1998; Yasuda *et al.* 2000). The larvae mark substrates on which they walk by a secretion released through the anal disk (Laubertie *et al.* 2006). The ODP consists of a mixture of long chain hydrocarbons, mainly alkanes (Hemptinne *et al.* 2001, Magro *et al.* 2007).

For ladybirds, avoiding competition when they search sites for oviposition is crucial due to non-sibling egg cannibalism by larvae. It is commonly observed under laboratory and field conditions (Osawa 1989). Therefore, it has a great impact on female fitness, and predator density (Hironori & Katsuhiro 1997). Non-sibling egg cannibalism is a source of conflict between females and larvae. On the one hand larvae eliminate competitors and access to new alimentary supplies because eggs are rich in lipids and proteins and ensure the development of larvae (Sloggett & Lorenz 2008). A number of studies have found that ladybirds exclusively fed conspecific eggs complete larval development and become adults (Agarwala & Dixon 1992; Gagné *et al.* 2002; Michaud 2003). Consequently, cannibalism can be beneficial and occurs even in the presence of aphids (Martini *et al.* 2009, Khan *et al.* 2003). On the other hand, as egg cannibalism can reach to very high level, females evolved the ability to assess the risk of intraspecific competition by reacting to larval tracks. Therefore, the ODP is beneficial to females but not to larvae.

A model on the origin and the evolution of this ODP proposes a solution to this conflict (Martini *et al.*, 2009). Larvae started producing a substance that probably improved adherence to plant surfaces. Mutant females that refrained to lay egg when they detected those substances gained an evolutionary advantage, because they decrease the risk of non-sibling cannibalism. In response there was a selection pressure on larvae that led to the chemical evolution of the ODP. If the tracks of some larvae differed from the rest of the population, those tracks would not be recognized and that would increase the probability of cannibalism. The conclusion of Martini *et al.* (2009) is that larval tracks should be chemically more similar with kin than non-related larvae. Therefore there is a possibility of a higher inhibition of females to their offspring larval track due to a phenotypic similarity, which is an important mechanism in kin discrimination (Villavicencio *et al.* 2009).

The objective of this paper is to test the hypothesis that females of the two spot ladybird *Adalia bipunctata* L. are more sensitive to their offspring's ODP than those of non-related larvae. Many species of parasitoids are able to discriminate a self-parasited host from a non-related parasited one (e.g. Ueno 1994; McKay & Broce 2004). The females of the predator mites *Iphiseius degenerans* Athias-Henriot, can discriminate conspecific and heterospecific eggs (Faraji *et al.* 2000). In the Coccinellidae family, kin discrimination has been observed for larvae and females that prefer cannibalizing unrelated eggs or larvae than related ones (Agarwala & Dixon 1993; Jospeh *et al.* 1999). To the authors' knowledge kin preference for ODP has never been studied in Coccinellidae. Furthermore, as several marking systems are depending on environmental factors (Visser, 1993; Fréchette *et al.*, 2004), we want to know how this behaviour changes with age and when females have previously experienced ODP.

II. Material and methods

a. Ladybird Culture

The two-spot ladybirds, *A. bipunctata*, used in this study came from a laboratory stock culture. Adults of this stock culture were reared at 20±1°C, LD 16:8, in 5-litre plastic boxes, which contained a piece of corrugated filter paper on which the females laid eggs. Three times a week the ladybirds were fed an excess of pea aphids, *Acyrthosiphon pisum* Harris. Two stems of broad bean, *Vicia faba* L. were added to each box to improve the survival of the aphids.

b. Ladybirds used in the experiments.

The ladybirds used in the experiments were obtained by incubating eggs from the stock culture in 175cm^3 plastic boxes under the conditions described above. The larvae were fed 3 times a week an excess of pea aphids until pupation. Freshly emerged adults were kept in a large plastic box during 48h, then their sex determined. Couples consisting of a male and a female were formed and each pair placed in a 90 mm Petri dish containing a piece of corrugated paper and kept at 20±1°C, LD 16:8. Each day these couples were transferred to clean Petri dishes and fed pea aphids in excess. Eggs were removed and counted daily. Ladybirds selected for the experiments were between 15 and 45 day old and had laid at least one batch of eggs daily over the previous 5 days. In order to standardize hunger and oviposition drive, females were deprived from food and isolated for 16h prior to the beginning of the experiment. Females that have laid more than 10 eggs during these 16h were excluded from the experiment.

c. Filter paper contaminated with ODP.

Contaminated filter papers were obtained by placing a 90-mm diameter Whatmann® filter paper at the bottom of a 90-mm diameter Petri Dish in which five fourth-instars larvae of *A. bipunctata* from the stock culture were kept for 24 hours with an excess of *A. pisum* at 20±1°C, LD 16:8. After 24h the larvae and aphids were removed, the filter paper was carefully brushed to remove faeces and aphid remains. Then, the filter papers were kept in darkness at 20C°± 1C° for a maximum of one month.

d. Sensitivity of females to the ODP of their offspring: a non-choice test

We wanted to know if females refrain from ovipositing with the same strength if they encounter larval tracks deposited by their offspring or by other female larvae. In addition, we were interested in the interaction of age and experience of females with relatedness. Indeed, Frechette *et al.* (2004) showed that these two factors decrease the female's response to ODP. Therefore, we worked with three groups of females: (1) naive and young, (2) experienced and young and (3) naive and old. Naive individuals never encountered larval tracks before the experiments. Females became *experienced* after being placed 24 hours in a 90 mm Petri Dish containing a filter paper contaminated with larval tracks the day prior to the experiment. Females are *young* when they are less than 40 day old. Old females were between 45 to 70 day old. Females of these three groups were either offered (i) a clean filter paper (Control), (ii) a filter paper contaminated with tracks of non related larvae or (iii) a filter paper contaminated with tracks of their offspring. Therefore, there were 9 different treatments with 17 to 24 replicates (Table 1).

At the beginning of an experiment, a female was placed in a 90 mm Petri Dish lined with one of the three kinds of filter paper just presented above. There were about 50 aphids of all developing instars in the Petri dish. Experiments ran at 20°C ±1°C and started between 9 to 10 AM. In the laboratory, females refrain from ovipositing in the presence of larval tracks for 9 h (Doumbia *et al.* 1998; Fréchette *et al.*, 2004; Laubertie et *al.*, 2006). Each hour the Petri dishes were observed and it was recorded which females had laid eggs. After 9 hours we counted the number of eggs in dishes. After 9 hours some females did not laid eggs. Therefore, we had censoring data that we chose to analyse by a Cox's proportional hazard model with filter paper, age and experience of the females as covariables. The model was formulated in term of hazard rate. In our case, the hazard rate was the probability per unit time that oviposition occurred.

Moreover, the effect of the nine treatments was also assessed by comparing the proportions of females that had laid eggs and the number of eggs laid by each females 9 hours after the beginning of the experiment. The numbers of females that laid eggs at the 9th hour were compared by a logistic model with filter paper, age and experience of the females as categorical explanatory variables. The numbers of eggs laid in each treatment were analysed by a three-way ANOVA with filter paper, age and experience of the females as independent factors. Statistical analyses were computed using R and SAS®.

	Experience	Age	Filter	N	Egg batch size	*n*
1	Naive	Young	Clean	21	13.21 ± 1.51	19
2	Naive	Young	Non Related	21	12.70 ± 1.92	10
3	Naive	Young	Related	21	19.60 ± 4.05	5
4	Experienced	Young	Clean	24	10.23 ± 1.46	21
5	Experienced	Young	Non Related	24	13.37 ± 1.68	16
6	Experienced	Young	Related	24	14.40 ± 1.56	13
7	Naive	Old	Clean	21	11.61 ± 1.76	13
8	Naive	Old	Non Related	17	12.12 ± 1.61	8
9	Naive	Old	Related	18	13.58 ± 2.19	12

Table 1. The nine treatments of the non-choice experiments. “Young” means aged less than 40 days. “Experienced” means that females were placed during 24 hours in presence of ODP the day prior experiment. Egg batch size: mean number of eggs in a batch (± SE) when it occurs in the nine hours of the experiment. N refers to the number of female for each treatments. *n* refers to the number of females that laid eggs after 9 hours.

III. Results

The Cox model shown that age and experience did not influence the probability of oviposition of females (P= 0.68 and P= 0.075, respectively, figures 1b and 1c, table 2a). The females on non-related tracks had a lower probability of laid eggs than female on clean papers ($P < 0.001$; figures 1 a, b and c; table 2a). However Females on related tracks are more inhibited than those on non related tracks ($P < 0.05$; figures 1 a, b and c; table 2a). We found an interaction between age and filter: old females are significantly less inhibited by related filter paper ($P<0.05$; figure 1c; table 2a).

After 9 hours there was no interaction between the quality of the filter papers and the experience of the females (χ^2=2.01, d.f.= 2, P=0.365).Therefore, it was removed from the analysis. However, there was a significant interaction between female age and the quality of the filter paper (χ^2=8.616, d.f.=2, P=0.013).The quality of the filter papers had a significant influence on the proportion of females that oviposited at the end of the experiment (χ^2=20.025, d.f.=2, P<0.001, table 2b). The contrast tests showed that the proportion of females that oviposit after 9 hours on clean filter paper was significantly higher than the proportion on paper contaminated by tracks of their offspring (χ^2=13.25, d.f.=1, P<0.001) or on paper marked by tracks produced by larvae of other females (χ^2=10.65, d.f.=1, P=0.001). Finally, The proportion of females that laid eggs on paper marked by tracks of their offspring was significantly smaller than on filter paper on which non related larvae deposited tracks (χ^2=4.14, d.f.=1, P=0.042).

Finally, the number of eggs laid by the females that oviposited after 9 h was not influenced by their age or their experience but by the quality of the filter papers (Table 1 & 3). Females on paper contaminated by related tracks laid significantly more eggs than those on clean paper (Table 1 & 3).

	ß	S.E (ß)	exp (ß)	P
Young	0.000	0.000	1.000	-
Old	-0.179	0.426	0.836	0.68
Naive	0.000	0.000	1.000	-
Experienced	0.408	0.229	1.504	0.075
Filters:				
Non-Related	0.000	0.000	1.000	**-**
Clean	0.888	0.262	2.431	< **0.001**
Related	-0.615	0.307	0.541	< **0.05**
Filters x Age :				
Clean x Old	-0.303	0.520	0.739	0.56
Related x Old	1.440	0.497	3.128	< **0.05**

Table 2a: Estimated regression coefficient (ß), standard errors (S.E.) and hazard ratios exp(ß) of covariates on the tendency of females to laid eggs during experiment. Interaction between age and filter was removed from the analyse because it was not significant

Source	d.f.	χ^2	P
Age	1	1.896	0.169
Experience	1	3.781	0.052
Age x Filter	2	8.616	**0.013**
Filter	2	20.025	**< 0.001**
Related vs. Control	1	13.25	**< 0.001**
Non Related vs. Control	1	10.65	**=0.001**
Non Related vs. Related	1	4.14	0.0417

Table 2b: The general linear model with contrast tests, for the number of females that oviposit after nine hours, when placed on one of three types of filter paper: control, marked with related tracks, marked with non-related tracks. The interaction Experience x Filter was removed from the analyse because it was not significant

Source	df	F	P
Age	1	0.13	0.72
Experience	1	1.94	0.17
Filter	2	3.80	**0.026***
Related vs. Control	1		**0.023***
Non Related vs. Control	1		0.405
Non Related vs. Related	1		0.343
Error	38		

Table 3 The analyse of variance with Tukey test for the number of eggs laid by females after 9 hon one of three types of filter paper: control, related tracks, non related tracks. The interactions Age x Experience; Filter x Age; Filter x Experience and Age x Filter x Experience were removed from the analyse because they were not significant.

IV. Discussion

The choice of egg-laying sites is important for non-social insects because of the absence of parental care. In Coccinellidae, to protect their offspring from non-sibling cannibalism females avoid laying eggs in patches occupied by larvae. It is the presence of larval tracks that induces the inhibition of oviposition (Doumbia *et al.*1998; Frechette *et al.* 2004). However, older larvae take advantage of egg cannibalism as it gives them energy and constitutes an alternative resource in case of prey scarcity. Therefore, there is a conflict between female and larva interests as the response of females to larval tracks decreases the probability of egg cannibalism. This situation leads to an arm race between females and larvae, and that there is a selective pressure on the later to change the composition of their tracks. Therefore it is predicted, that females should be more sensitive to tracks produced by their own offspring (Martini *et al.*, 2009).

Our experiment confirms this hypothesis as females on filter paper contaminated by their offspring's ODP are significantly more inhibited than females on non related larval tracks. This result is counterintuitive as the obvious strategy in a highly competitive environment should be to lay eggs on colonies already occupied by related larvae. In terms of fitness, females would benefit more if the cannibals are their kin. However, the probability that females find by chance a patch occupied by their own offspring is unknown but probably weak. It was shown that a ladybird stay no more than 5 to 7 days in the same field in spring and move a lot during this period (Osawa, 2000). Therefore, there is no interest for a female to be more inhibited by larval tracks of their offspring rather than those of non-related ones. We suggest that this is the result of the arm race between females and larvae. As larvae are selected to change the composition of their tracks, females are more sensitive to those of their offspring due to phenotypic similarity. Therefore, we can hypothesis that this result is due to genetic constraints.

The fact that discrimination between kin and non-related track is lost with age is consistent with our hypothesis that this difference of response is due to genetic constraint. If recognition of kin brings advantage to female through the avoidance of competition for offspring, this character should been maintained with age. The effect of age suggests a degeneration of the sensitive system due to senescence. This could be due to either a lower selection or an adaptation to age. Theory says that the strength of natural selection declines with advancing age (Wilson, Charmantier & Hadfield 2008) because the reproductive success of younger organisms will be greater than of older ones (Sterns & Hoekstra 2000). In ladybirds egg production declines with age (Dixon & Argawala 2002). Therefore, we can expect a lower selection on old females for responding to the ODP. An alternative hypothesis is that the absence of response could be adaptive. At the end of life it may be advantageous for a female to be less selective for oviposition site (Mangel 1989, Frechette *et al.* 2004). There is a trade-off between a low benefit for ovipositing in a poor site and the risk of dying before discovering a better environment.

Our results suggest that experienced females need a stronger signal to being inhibited. But the quality of the signal perception remains as they still discriminate between kin and non-related. One unanticipated finding is that females laid more eggs on related tracks than on the control. It might be an artefact due to the intensity of the inhibition because the females with the higher egg load would be unable to refrain from ovipositing for a long period of time.

Our results imply a high polymorphism in the composition of tracks laid by larvae. Magro *et al.* (2007) have shown that the composition of larval tracks change more in quantity than in quality between three species of ladybirds, and recently Magro *et al.* (2010) demonstrate a strong relationship between phylogeny of ladybirds and the chemical composition of larval tracks. Our result implies that the females are able to recognize a mixture of hydrocarbon rather than a single molecule. It advocates a change of larval tracks at the species level. Isolated molecules that show inhibition properties (Klewer *et al.* 2007) should be therefore a part of the message. Our study is the first to show effect of relatedness on the ladybird female response to larval tracks.

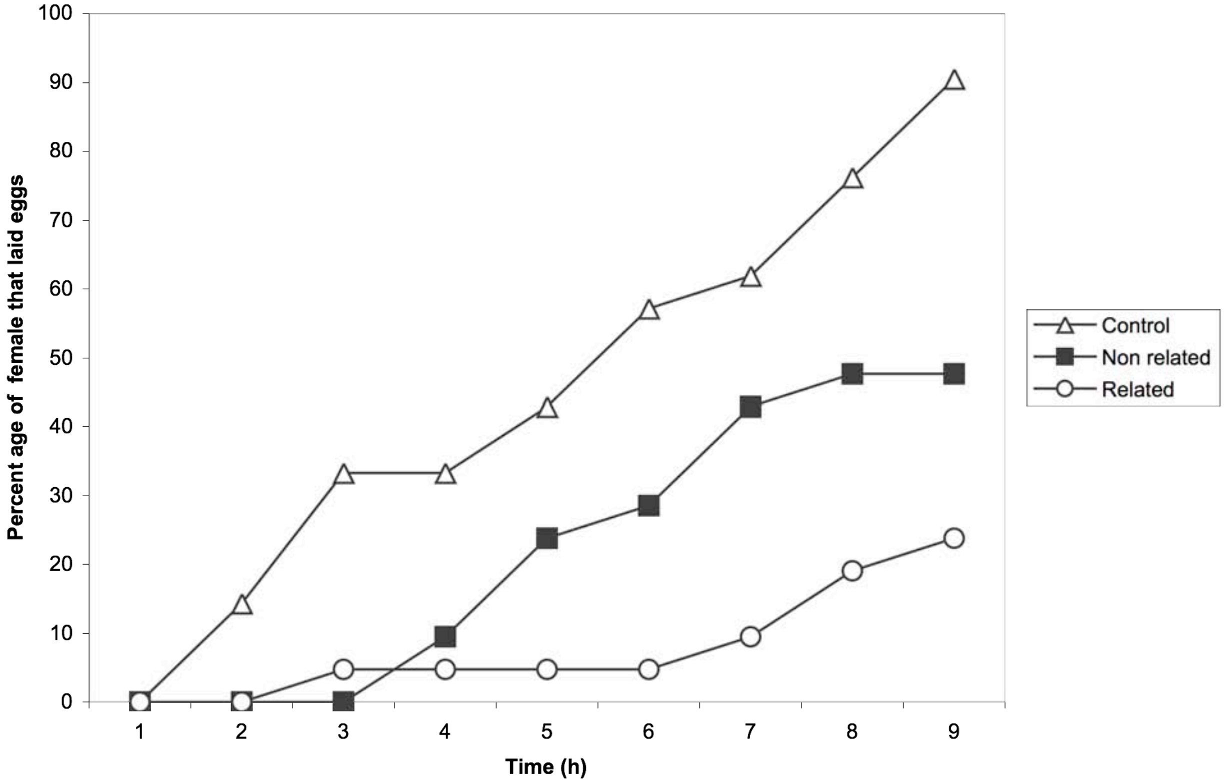

Fig. 1. a. The cumulative percentages of naives and young females that laid eggs during the nine hours of the non-choice experiment.

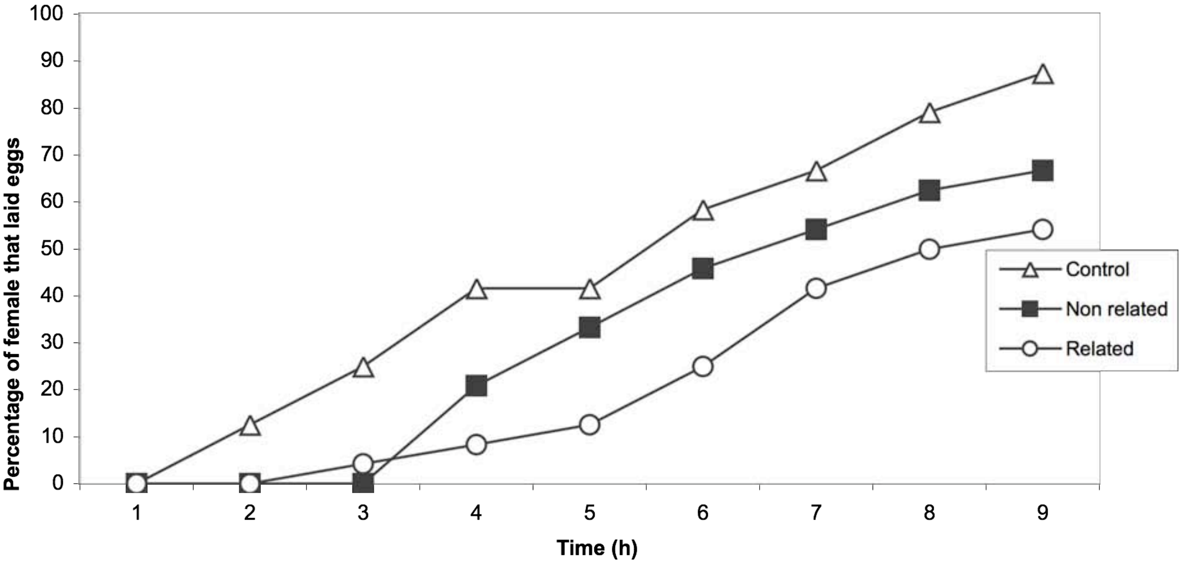

Fig. 1. b. The cumulative percentages of experienced and young females that laid eggs during the nine hours of the non choice experiment.

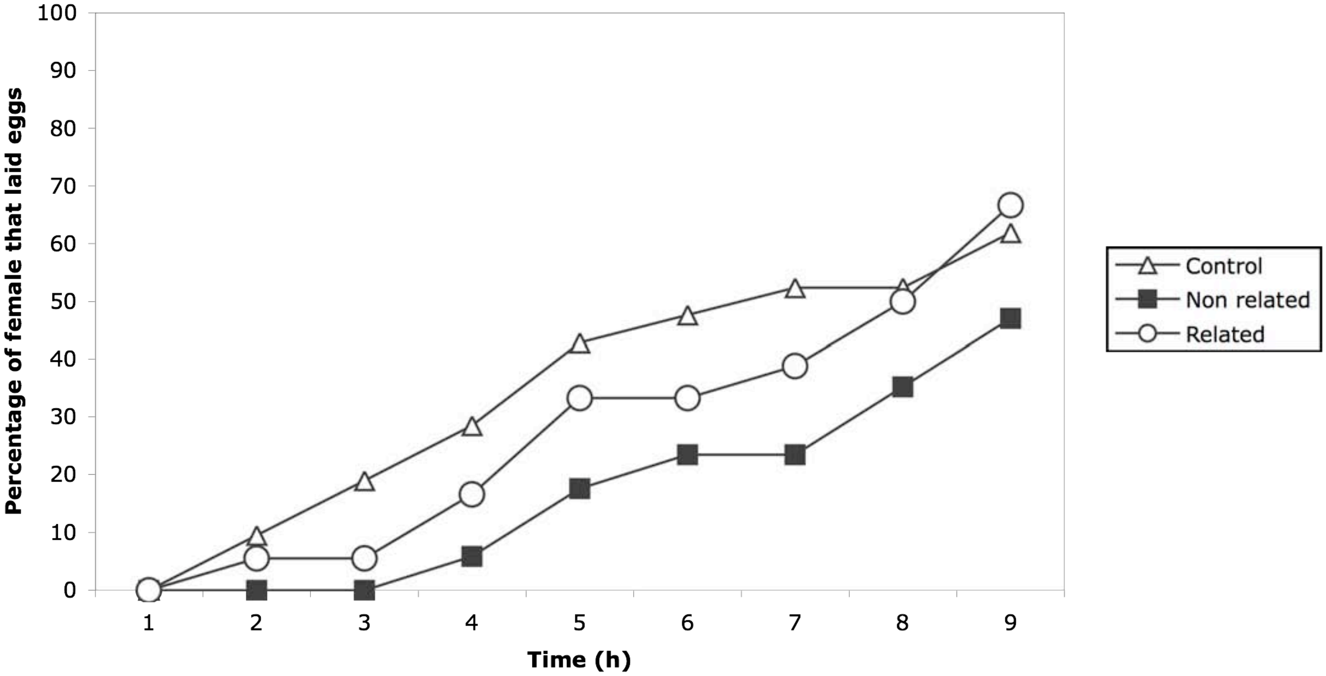

Fig. 1. c. : The cumulative percentages of naives and aged females that laid eggs during the nine hours of the third experiment.

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TROISIÈME CHAPITRE

Chaque année, il y a plus de naissances que de survies; le plus petit grain dans la balance doit à la longue, avoir un effet sur celui que la mort abattra et celui qui survivra

Charles Darwin. *Ebauche de l'origine des espèces*, 1844.

Troisième Chapitre

Cannibalisme chez les Coccinelles : Bénéfice d'une diète mixte, influence de l'expérience et de la densité de proie.

Cannibalism in Coccinellidae:

Benefit of a mixed diet, influence of experience and prey density

Résumé

Le cannibalisme est un comportement couramment observé chez de nombreuses espèces. Il est souvent décrit comme une adaptation au manque de nourriture, et permet à des communautés de perdurer même en cas de pénurie alimentaire. Toutefois dans le premier chapitre de cette thèse (Martini *et al.* 2009) nous montrons que le cannibalisme des œufs chez les coccinelles aphidiphages devrait être avantageux même en présence de proies. Cela implique un comportement où les larves consommeraient sans distinction pucerons et œufs conspécifiques. De plus, si le cannibalisme est très commun on s'attend à ce que les individus se développant le mieux sur une diète intégrant des œufs conspécifiques aient été sélectionnés. Dans ce chapitre nous conduisons une série d'expérience afin de vérifier si les œufs conspécifiques sont une bonne nourriture en cas de stress alimentaire.

Ainsi, nous montrons que si des larves nourries avec des pucerons ont une meilleure croissance, celles nourries avec des œufs conspécifiques perdent moins de poids lorsqu'elles sont privées de nourriture.

Dans un deuxième temps nous comparons le développement de larves nourries d'une des deux diètes pures (œufs ou pucerons) et d'une diète mixte (œufs et pucerons). Le résultat de cette expérience est que les larves nourries avec une diète mixte atteignent un poids plus important à l'âge adulte. Cependant, la survie ou le temps de développement ne sont pas affectés par les différentes diètes.

Finalement, la troisième partie de ce chapitre s'intéresse au comportement d'attaque des larves, lorsqu'elles sont dans un environnement où oeufs et pucerons couvrent la même surface. Dès lors, nous montrons qu'à taux de rencontre égal les larves préfèrent nettement consommer des pucerons plutôt que des œufs conspécifiques. Toutefois, si les larves ont déjà

expérimenté le cannibalisme ou si les molécules présentes sur les œufs sont retirées, cette différence disparaît.

CANNIBALISM IN COCCINELLIDAE: BENEFIT OF A MIXED DIET, INFLUENCE OF EXPERIENCE AND PREY DENSITY

I. Introduction

Cannibals kill and eat conspecific individuals. Polis (1981) recorded 1300 different species that actively practice cannibalism. They are encountered in a wide range of taxa such as fishes, insects or mammals. Cannibalism is advantageous as it provides energy, eliminates a competitor and a potential aggressor (Getto *et al.* 2005). On the down side it is disadvantageous because it transmits pathogens (Boots 1998; Williams & Hernandez 2006), and can result in the loss of inclusive fitness if cannibals eat genetically related individuals (Polis 1981; Dixon 2000). Therefore, we can expect that the intensity of cannibalism is linked to the balance between benefits and costs. For example, there are several cases where cannibals avoid eating related conspecifics (Agarwala & Dixon 1993; Joseph *et al.* 1999; Pervez *et al.* 2005; Green, Mirza & Pyle 2008; Markman *et al.* 2009). Moreover, the risk of injuries when cannibalising can deter small predators from attacking conspecifics (Mayntz & Toft 2006). Cannibalism is known to be highly density-dependent (Mills, 1982; Hopper *et al.* 1996, Wagner & Wise 1996, Yamamura *et al.* 2001, Buddle *et al.* 2003) and victims of cannibalism are mainly eggs, young or small individuals. Improvement of survival is probably the main reason for the evolution of cannibalism (Cushing 1991, Diekmann *et al.* 2003, Claessen, de Roos & Persson 2004, Getto *et al.*2005). However, Martini *et al.* (2009) have shown that cannibalism can be beneficial and promoted even in the presence of sufficient food. Some empirical support for this theoretical prediction exists. For instance, Gagné *et al.* (2002) found that neonate larvae of the ladybird *Coleomegilla maculata* De Geer prefer to eat conspecific eggs rather than aphids. In those species where cannibalism is common, there should be selection for increased survival on conspecific eggs. The aim of the present paper is to study the interest of eating conspecifics, compared to heterospecific food, and the factors that shaping the cannibalism behaviour.

Ladybirds are a good model for studying cannibalism because they attack conspecifics both in the field and in the laboratory (e.g. Osawa 1989; Cotrell & Yeargan 1998 a, b; Snyder *et al.* 2000; Pervez, Gupta & Omkar 2006). In the field egg cannibalism by larvae is the most common and can reach very high levels (Osawa 1993, Hironori & Katsuhiro 1997, Schellhorn & Andow 1999). Cannibalism has a strong influence on the survival of larvae because aphid colonies, which constitute their essential source of prey, collapse in about 5 to 8 weeks whereas ladybird larvae require about 4 to 5 weeks to complete development (Dixon 2000). It has been shown that females maximise their lifetime reproductive success if they lay eggs for a short period of time when colonies start to rise exponentially. This period has been named the “reproductive window” (Hemptinne & Dixon 1997) the existence of which has been shown by field observations (Hemptinne, Dixon & Coffin 1992, Osawa 2000), laboratory experiments (Hemptinne *et al.* 1992) and a mathematical model (Kindlmann and Dixon 1993). If eggs are laid too early, that is before the reproductive window, first instar larvae are unlikely to find rare aphids and will die from starvation. If eggs are laid too late, that is after the reproductive window, there will remain too few aphids to sustain the development of fourth instar larvae. Therefore, oviposition should occur before the peak of aphid abundance. However, aphid colonies will collapse prior to the completion of ladybird development if several females lay their eggs in the same colonies. There will be too many larvae hunting in the same patches and such a situation will again promote cannibalism.

Several mechanisms have evolved to reduce the incidence of cannibalism in ladybirds. First, hydrocarbons present at the surface of chorions deter larvae and adults from attacking readily eggs unless they are becoming desperate for food (Hemptinne *et al.* 2000; Omkar *et al.* 2004*;* Ware *et al.* 2008). Second, females refrain from ovipositing in aphid colonies where they detect smears of an oviposition deterring pheromone (ODP) deposited by larvae (Hemptinne *et al.* 1997, Doumbia *et al.* 1998, Laubertie *et al.* 2006). The presence of this signal indicates that patches are unsuitable for oviposition and females fly away (Frechette *et al.* 2004). However, if unmarked patches are rare due to a high density of predators or a low number of aphid colonies, it could be advantageous for females to oviposit in colonies already occupied by conspecific larvae. In such a context, taking its chance is more rewarding than searching for an unlikely free patch of prey (Frechette *et al.* 2004). Senescent females also may lay eggs in marked colonies. They balance the assurance of low benefit, as eggs production declines with age (Dixon & Agarwala 2002), against the likely risk of dying before exhausting their egg load while trying to oviposit in a better environment (Frechette *et al.* 2004).

Recently Martini *et al.* (2009) proposed that the elimination of competitors and energetic gain from egg-cannibalism are sufficient factors for the evolution of cannibalism, even in the presence of aphids. This particularly applies when egg cannibalism is free of cost, and when larvae can cannibalize on genetically unrelated eggs. Therefore, larvae should have no particular preference for aphids or eggs. This prediction agrees with the “meet and eat” hypothesis (Dixon & Kindlmann 1993), according to which hungry larvae should always eat conspecific when they meet them so that the rate of cannibalism is proportional to the probability of encountering eggs and aphids (Agarwala & Dixon 1992; Dixon 2000). As a consequence, the rate of egg cannibalism increases when the relative abundance of aphids is reduced (Agarwala & Dixon 1992) but persists even when prey are abundant (Khan, Khan & Hussein 2003).

In the present paper we report on three experiments. In the first experiment we ask whether a diet made of conspecific eggs allows larvae to recover as well from starvation than a diet made of aphids. We compare the recovery of weight following a long starvation event of ladybirds larvae fed with either aphids or conspecific eggs, as well as the loss of weight following a second, shorter, starvation event for both types of larvae. In the second experiment we ask whether a diet made of either conspecific eggs, aphids, or a mixture of both, allow larvae and adults to reach similar sizes. We also study the effect of these diets on survival, development time and the number of ovarioles. Finally, in a third experiment, we study the choice of larvae between aphids and conspecific eggs under conditions of equal encountering probabilities, depending on past experience of larvae (whether or not they encountered conspecific eggs prior to the experiment, whether or not they were first fed under high or low density of aphids, and whether or not the eggs were still protected by the chemicals present on their surface). This allows us to accept or reject the “meat and eat” hypothesis depending on past experience, and chemical defences on eggs.

II. Materials and Methods

a. Insect cultures

The pea aphid *Acyrthosiphon pisum* Harris was reared on broad bean *Vicia faba* (L.) grown in compost at 20±1°C and a photoperiod of 16:8 LD. Three times a week broad beans were sown, watered and two–week old plants were shaken in order to dislodge aphids that fell in a tray and were collected to feed ladybirds.

The two-spot ladybird, *Adalia bipunctata* (L.) used in this study came from the laboratory stock culture. Adults were reared at 20±1°C and a photoperiod of 16:8 LD, in 5 litre plastic boxes, which contained a piece of corrugated filter paper on which the females usually lay eggs. Three times a week the ladybirds were fed pea aphids in excess. Two stems of broad bean were added to each box to improve the survival of the aphids until the following rearing. When ladybirds were fed, the filter papers were removed from the boxes and new papers provided. The paper was cut with fine scissors around the egg masses, which were either used to perpetuate the laboratory culture or for the experiments. The eggs used as food for the experiments were placed in plastic boxes kept in the darkness at 4°C ± 1°C to prevent incubation and were at a maximum 6 day old when used in an experiment.

b. Experiment 1: Are eggs good alternative food in case of starvation?

In this experiment we wanted to firstly check the potential of cannibalism in case of aphid scarcity. Our hypothesis was that eggs could be a better food to cope with starvation. Eggs from the stock culture were incubated at 20±1°C and a photoperiod of 16:8 LD. After hatching first instar larvae were isolated in small Petri dishes and fed with A. pisum three times a week. Forty-height hours after moulting in the fourth instar larvae were weighed. In order to standardize the experimental larvae only those between 6.5 to 11mg were used for the experiment, which resulted in a mean of 8.82 mg (S.E = 0.30). Larvae were isolated in Petri dishes without food for 18 hours in order to standardize their drive for eating. Then, they were weighted again, and randomly sorted out into two groups according to the regime they received for the next 3 hours: (1) pea aphids ad libitum that had been collected less than one hour before the experiment, or (2) conspecific eggs ad libitum. Time of feeding was fixed to 3 hours to see a significantly weight gain, without the risk that larvae will spend too much time without eating. There were 14 individual larvae in each group. To avoid biases in the results due the fact that some larvae might not eat, we checked continuously the Petri dishes during the first ten minutes and only larvae that have been seen eating were considered for the statistical analysis. Later on, we periodically checked the Petri dishes to ensure that larvae never ran out of food. If necessary, eggs or aphids were added to the dishes depending on the treatment. At the end of these 3 hours, the larvae were again weighed and transferred to a new Petri dish where they starved for 3 hours. Then, they were weighed once again. We analysed the relative growth rate of larvae after the 3 hours of feeding on eggs or aphids, and the relative loss of weight after the 3 hours of starvation with student t tests.

c. Experiment 2: Is cannibalism advantageous?

Eggs from the laboratory stock culture were incubated at 20±1°C and under a photoperiod of 16:8 LD. Twenty-four hours after hatching first instar larvae were weighed and isolated in small Petri dishes. Then, they were daily fed with *A. pisum* in excess. At the time of feeding the dishes were searched for the presence of a skin as an indication that the larva moulted in the previous 24 h. This allows determining when larvae entered their third instar of development. Then, third instar larvae were weighed the day they moulted. In order to standardize the experimental larvae, we selected those weighing between 1.5 and 2.5 mg and randomly sorted them in three groups according to the food they will receive every day until becoming adult: (1) 20 adults of *A.pisum*; (2) 10 adults of *A. pisum* and 40 (± 4) conspecific eggs, or (3) 80 (± 8) conspecific eggs. The quantities of the pure diets (1) and (3) were determined to make sure the larvae are fed *ad libitum* (personal observation). The mixed diet was determined by giving half of the quantities of the two pure diets. In this diet the quantities of aphids and eggs alone were not enough to satiate a third instar larvae. The aim of this procedure was to force the larvae to eat both eggs and aphids. There were 32 replicates for each diet.

The dishes were checked every day and larvae moved to clean dishes. After pupation, adults were weighed and sexed the day they hatched. The females were fed for 2 weeks an excess of *A. pisum*, then they were dissected and their ovarioles counted. The consumption of eggs was analysed by a Student t test. We made a survival analysis with a parametric model and we compared the number of ovarioles by a one-way analyse of variance (ANOVA). Because of the non-normal distribution of the data (Shapiro test, W=0.819, P<0.001) the development time was analysed using a Kruskal-Wallis test. The maximum weight reached by the larvae, the weight at adult size and the relative loss of weight during the pupal stage were analysed by two-way ANOVA, with diet and sex as the two independent factors. Whenever diet and sex interaction was not significant at 0.05 level, it was removed from the analysis (Crawley 2007). We then compared by Tukey's honest significant differences test.

d. Experiment 3: Factors shaping cannibalism behaviour.

In this experiment we studied the "meet and eat" hypothesis in a 8 x 8 cm square in a circular arena. On this square there were 25 patches of about 16 mm² separated by 2 cm from each other along the square sides. The patch at the centre was used to introduce larvae. A cluster of 15 to 20 eggs or two adult aphids of *A. pisum* that had been frozen for 10 minutes at -78°C just before the beginning of the experiment were randomly assigned to one of the remaining 24 patches. There were 12 patches with eggs and 12 with frozen aphids. The quantities of aphids and eggs in patches were chosen to make sure that the same surface was covered by theses two kinds of food. At the beginning of the experiment, a 48 h old larva was gently deposited in the central patch. The larva was observed until it had attacked its first prey. Then it was removed, the prey attacked was replaced and the patches randomly mixed. Then a new larva was placed in the arena. Remaining eggs and frozen aphids were not used more than five times.

Larvae used in this experiment came from eggs collected from the laboratory stock culture and incubated at 20±1°C, LD 16:8. After hatching larvae were isolated in a small Petri dish and sorted out into four treatments. There were 25 larvae per treatment.

(1) Control group. Larvae were fed three times a week with pea aphids in excess.

(2) Low prey situation group. To explore the effect of prey density without a bias due to starvation, larvae fed three times a week an artificial diet rich in proteins and sugar and 4 adults of *A. pisum*.

(3) Experimented group. To study the possibility of learning larvae were fed three times a week pea aphids in excess and eggs of *A. bipunctata* the day prior to the experiment.

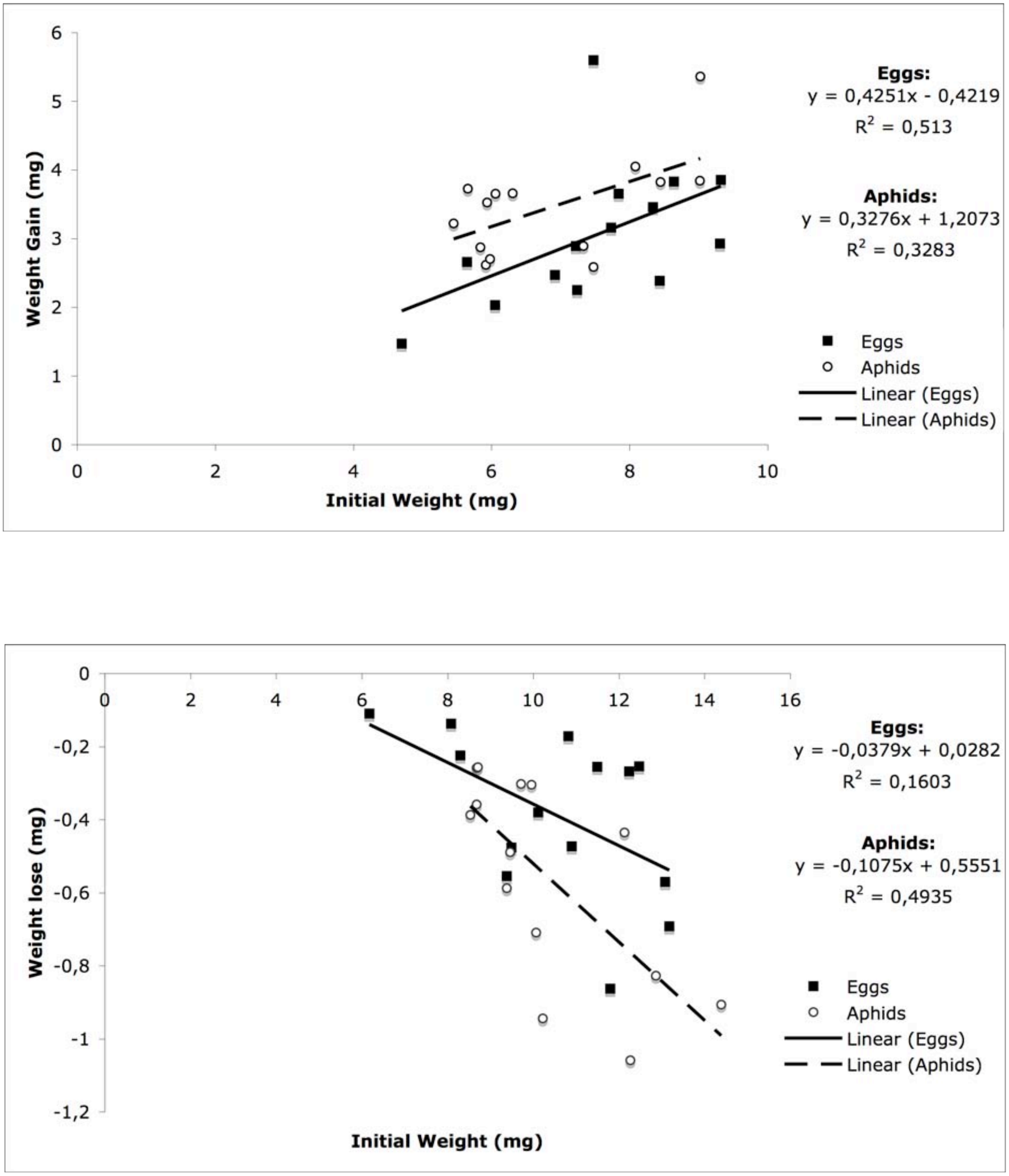
(4) Washed eggs group. Larvae were fed like those of the control group. However, chemicals present on the surface of the eggs in the arena were removed in order to study their role in the protection against cannibalism. Eggs were washed with n-hexane prior to the experiment (Hemptinne *et al.* 2000). Eggs to be washed were first removed from the filter paper on which they were laid with a fine paintbrush watered with distilled water. They were then immersed with n-hexane in groups of about 300 in a 200ml glass beaker for 2 min. Then the eggs were dried for 30 min and gently put on a piece of filter paper in groups of 15 to 20 before being placed into the arena. Larvae used in this treatment were fed three times a week with an excess of *A. pisum*

Prior to this experiment, we tested that frozen aphids were as attractive for larvae as living aphids. In a choice test, we isolated 28 larvae in small Petri dishes in presence of two frozen aphids and two living aphids. Every 30 minutes, the Petri dishes were checked until a first prey was attacked. Data of the fourth treatments and of the preliminary experiment were analysed by a binomial test, where the null hypothesis was a 50% of attack for the two kind of preys presented. To compare effect of each of these treatments we secondly built and analysed a general linear model with density, washing with hexane, and experience of larvae as three explanatory variables.

III. Results

a. Experiment 1: Are eggs good alternative food in case of starvation?

After fasting for 18 hours, larvae lost on average 18.89% (S.E.= 0.01%) of their weight. There was no relationship between their initial weight and the relative loss of weight (r=0.06, n= 28, P= 0.20). After 3 hours of feeding the relative grow rate was significantly higher for the larvae fed with aphids compared to larvae fed with eggs (t= 2.78, d.f.: 26, P = 0.01, Fig. 1.a). However, after a second fast of 3 hours the larvae fed eggs lost significantly less weight (t= 2.52, d.f.: 26, P < 0.05, Fig 1.b). Finally, there was a slight difference in the relative growth rate of the two groups of larvae after 3 hours of different feeding and the second fast of 3 hours (0.35 ± 0.029 S.E. for larvae fed with eggs; 0.43 ± 0.028 S.E. for larvae fed with aphids; t=1.85, d.f.:26, P =0.075).



(a)

(b)

Figure 1: (a) The weight gain in relation to the initial weight of fourth instar larvae fed conspecific eggs or aphids for 3 hours after a fasting period of 18h. (b) The loss of weight of the same larvae starved 3 hours after fed conspecific eggs or aphids.

b. Experiment 2: Is cannibalism advantageous?

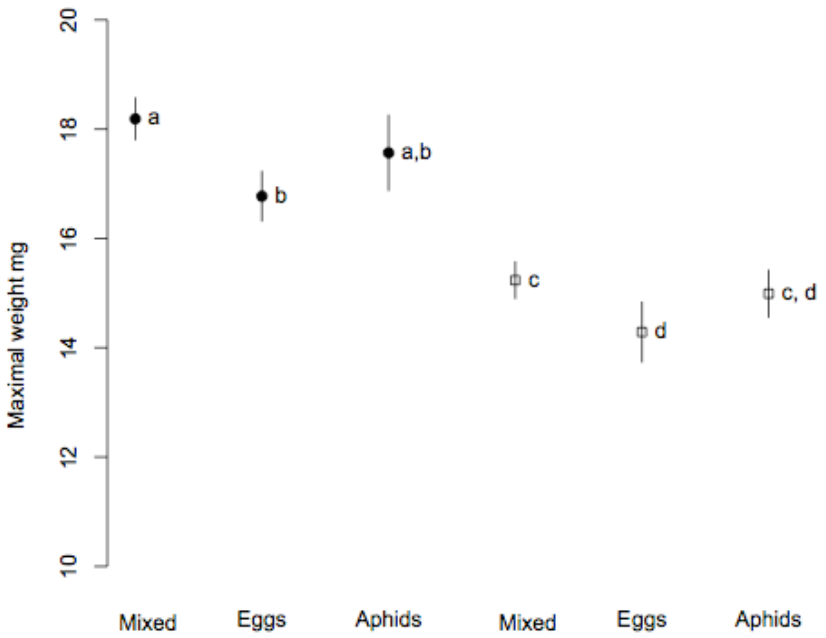
Survivorship was not significantly affected by the three treatments (χ^2= 1.46, d.f. =2, P=0.46, Table 1). In the mixed group 5 larvae ate only aphids during the 3rd instar but all ate eggs during the 4th instar. Third and fourth instar larvae ate significantly less eggs in the mixed group that in the pure eggs diet (t tests: t = 7.39, d.f.: 57, p < 0.001; t = 15.146, d.f.: 57, p < 0.001; respectively, Table 2).

	n	Survivor to adult	Nb.f.	Number of ovarioles
Aphids	32	27 (84.4%)	12	46.82 ±0.79[1] (S.E.)
Eggs	32	30 (93.7%)	17	45.40 ±1.31[2] (S.E.)
Mixed	32	29 (90.6%)	16	45.37 ±0.82 (S.E.)

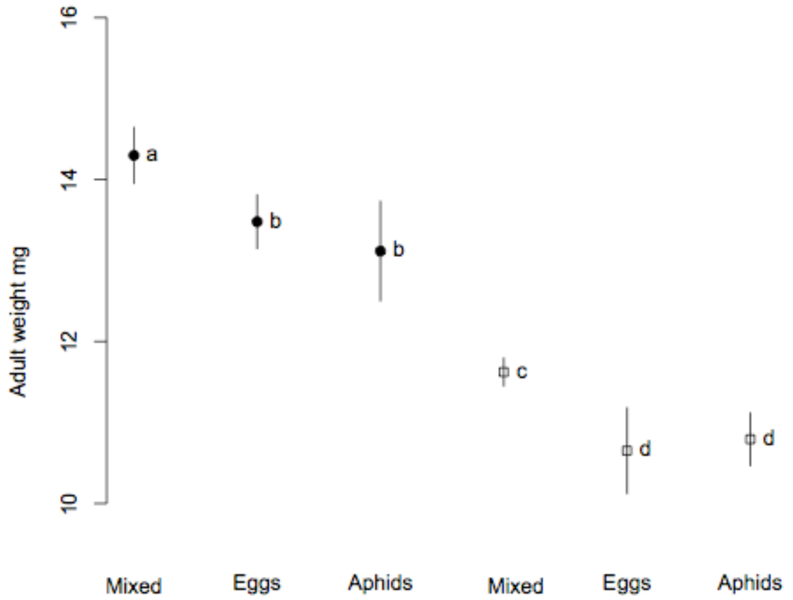
Table 1. The influence of a diet of aphids, conspecific eggs or a mixture of both on the number of larvae surviving to adulthood and the mean number of ovarioles per females (*n*: Initial number of individuals per treatment; Nb.f: the number of females). [1] Due to the death of 1 female before dissection, mean was calculated on 11 individuals. [2] Due to the death of 2 females before dissection, mean was calculated on 15 individuals.

Treatment	Mean number of eggs eaten per day during the 3rd instar	Mean number of eggs eaten per day during the 4th instar
Eggs	21.07 (± 1.16)	43.22 (± 1.14)
Mixed	8.73 (± 1.20)	18.47 (± 1.18)

Table 2. The mean number of eggs eaten per day by 3rd and 4th instar larvae reared either on a mixed or a diet made of eggs (± S.E.).



(a)



(b)

Figure 2. (a) The average of the maximal weight reached by larvae of both sex, depending of the diet. (b) Mean of adult weight for both sex depending of the diet during the larval development. Black circles: females, open squares: males. For each sex, diets labelled by the same letter are not significantly different ($\alpha = 0.05$)

The analysis of the maximum weight reached by the larvae showed no interaction between sex and diet ($F_{2, 86}$=0.13, P=0.88; Fig. 2.a), which was therefore excluded from the analysis. There was a significant effect both for sex and diet, ($F_{1. 86}$=46.01, P<0.001; $F_{2.86}$ =3.11, P=0.050, respectively). The Tukey test indicated that larvae reared with aphids reach a similar weight, whether or not conspecific eggs were part of their diet (P=0.29). Conversely, larvae fed with only conspecific eggs reached a lower weight compared to larvae with at least some aphids in their diet (P = 0.04). Finally we found no difference between larvae fed only conspecific eggs or only aphids (P= 0.63)

For adult weight, there was no interaction between sex and diet ($F_{2, 86}$=0.19, P=0.820), which was therefore excluded from the analysis. Both sex and diet had a significant effect on the adult weight ($F_{1,86}$=63.83, P<0.001; $F_{2, 86}$=5.21, P<0.01; respectively). Post hoc tests indicated that the ladybirds fed with the mixed diet as larvae were significantly heavier than those fed with only aphids (P < 0.05). We also found a difference with conspecific eggs (P < 0.05). Conversely, the final weight of adult larvae fed with either aphids or eggs was the same (P=0.53).

For the relative weight loss during the pupal stage there was no correlation between sex and treatment ($F_{1, 86}$=1.38, P=0.26) Males lost more weight than females (P < 0.01, $F_{1,86}$=10.13; Figure 3). The diet had a significant effect on the loss of weight during the pupal stage ($F_{2, 86}$ = 6.66, P < 0.01). Larvae fed aphids lost proportionally more weight than those fed either conspecific eggs (P < 0.01) or with both eggs and aphids (P < 0.01), while there was no difference between the two diet containing some eggs (P=0.98).

Finally, there was no difference in the number of ovarioles per females between the three diets ($F_{1, 86}$=0.59, P=0.561, Table 1). The development times of the 3rd and 4th instar or nymphs were not significantly different either (Table 3).

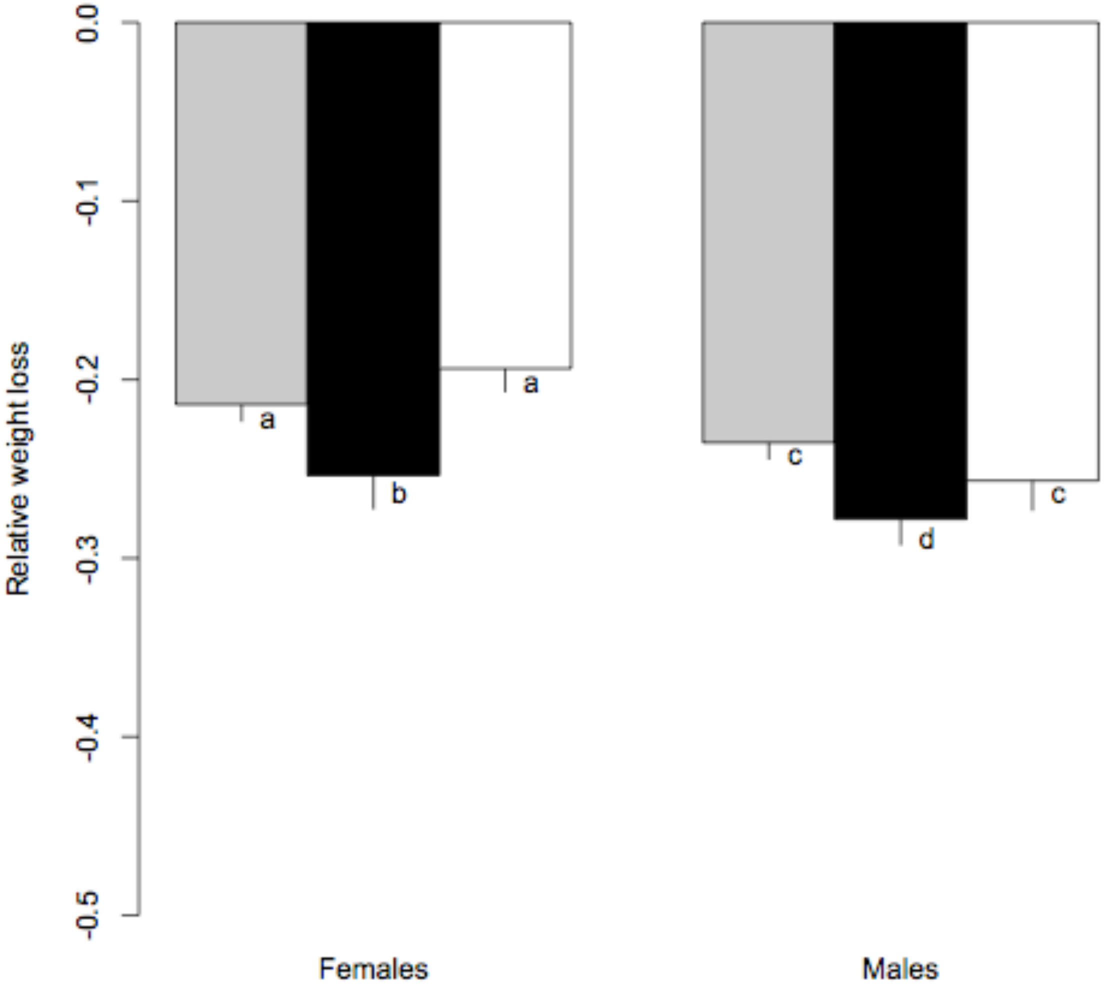


Figure 3: The average relative weight lost during nymphal stage after a regime constituted of either aphid, conspecific eggs or a mixture of both during the larval development. For each sex, diets labelled by the same letter are not significantly different ($\alpha = 0.05$). Grey: mixed, black: aphids, white: eggs.

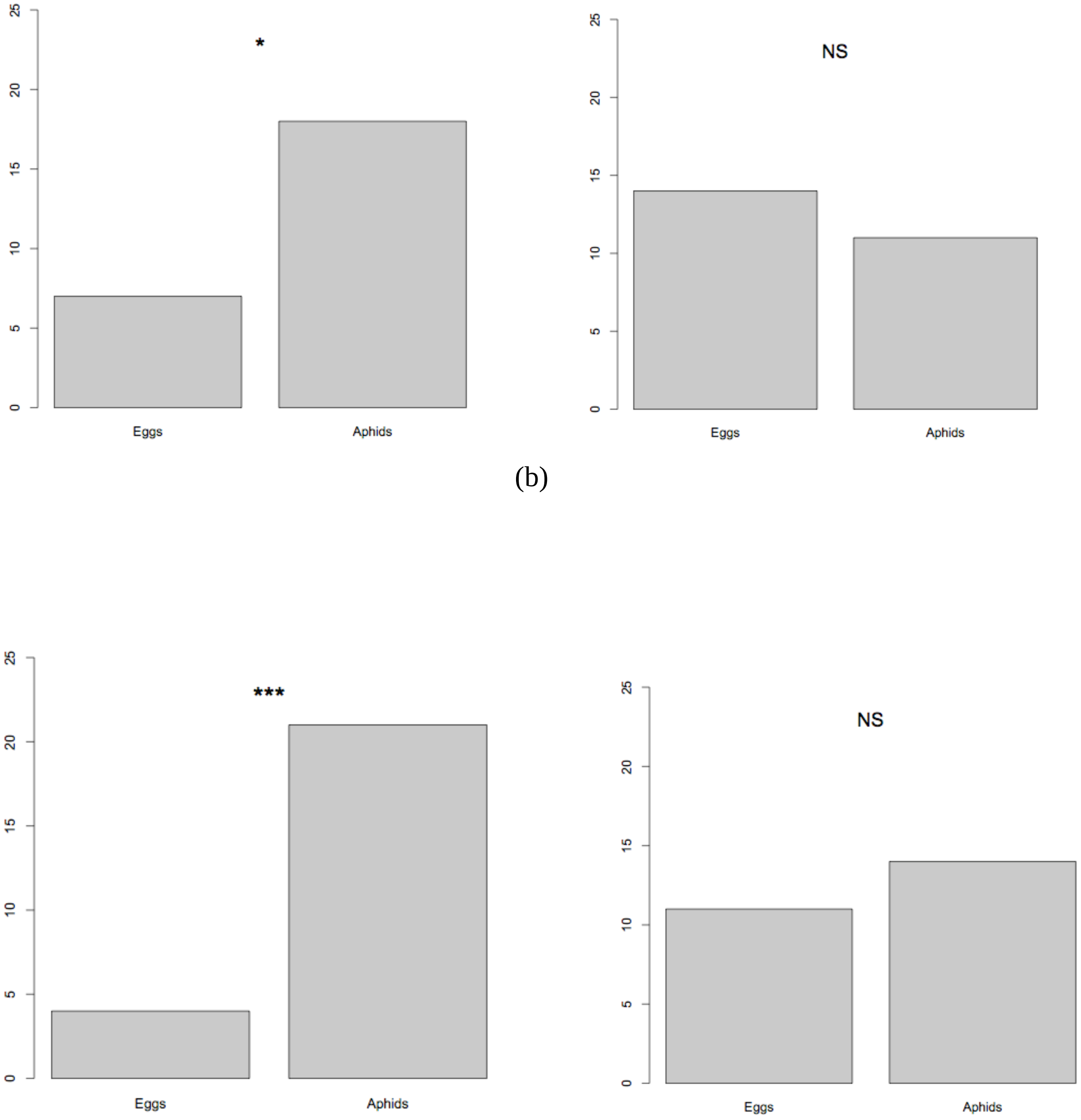
Treatment	Third instar	Fourth instar	Nymph
Mixed	2.36 ± 0.10	3.81 ± 0.10	6.83 ± 0.09
Eggs	2.35 ± 0.08	4.10 ± 0.09	6.87 ± 0.10
Aphids	2.43 ± 0.1	3.79 ± 0.1	6.7 ± 0.1
	$\chi^2=1.93$, d.f.=2	$\chi^2=4.47$ d.f.=2	$\chi^2=1.71$, d.f.=2
	P=0.38	P=0.11	P=0.42

Table 3: The mean developmental time (± S.E.) expressed in days of third, fourth instar larvae and nymphs fed either aphid, conspecific eggs or a mixture of both.

c. Experiment 3: Test of the meet and eat hypothesis under various conditions.

The preliminary test indicated that the proportion of larvae attacking frozen aphids (16 out of 28) did not differ from the proportion attacking fresh aphids (12 out of 28), (p=0.57). The larvae from the control treatment significantly preferred aphids over conspecific eggs (p= 0.043, fig 4.a). In contrast the larvae that have cannibalized before the experiment did not show any preference (p=0.69 fig 4.b). Larvae that have been reared at a low density of aphids showed a high preference for aphids over eggs (p<0.001, fig. 4.c). Finally, when the molecules present on the surface of the eggs were removed larvae showed no preference (p=0.69, fig 4.d).

When we analysed the general linear model we found that density was not significant, so we removed it from analysis. Experience showed a significant effect (P < 0.001), but the hexane treatment only a slightly one (P= 0.052).



(a) (b)

(c) (d)

Figure 4: The number of larvae attacking aphids or eggs eat as the first choice (a) in the control group (b) in the group that have experimented cannibalism (c) in the group reared at a low prey density (d) the washed eggs group.

IV. Discussion

Adaptation to food starvation is often cited as the main reason for the occurrence, evolution and persistence of cannibalism. Other factors can affect cannibalism tendency such as sociality that decreases sexual cannibalism in spider (Pruitt & Riechert 2009) or proximity between related individuals that decreases profitability of cannibalism (Lion & Van Baalen 2009). Martini *et al.* (2009) showed that the physiological advantage of eating conspecifics and the elimination of competitors select for cannibalism in aphidophagous ladybird even in the presence of prey.

In the first experiment described here we found that, following a long period of starvation, the growth rate of larvae fed with aphids was superior to that of larvae fed with conspecific eggs. However, after fasting for a second, short period, larvae fed with eggs lost less weight compared with larvae fed with aphids. These results suggest that under some conditions conspecific eggs are better to cope with starvation. Similarly, we also found, based on our second experiment, that during the pupal stage, those larvae which had been fed either solely conspecific eggs or a mixture of eggs and aphids lost less weight compared to larvae which had been fed with aphids only. These results could be explained by the fact that conspecific eggs are more lipid-rich than *A. pisum*: they represent 10% of weight / fresh weight (Slogett & Lorenz 2008) compared to 2.5% weight / fresh weight in aphids (Febvay *et al.* 1992).

In our second experiment, we also found that larvae fed solely with conspecific eggs performed similarly to larvae fed solely with aphids, in terms of survivorship, potential fecundity (number of ovarioles), larval weight and adult weight. Furthermore, larvae fed a mixture of eggs and aphids performed similarly to (survivorship, fecundity, larval weight) or better than (adult weight) larvae solely fed aphids. Thus, overall, we find that a mixed diet of conspecific eggs and aphids is similar to or better than a pure diet of either conspecific eggs or aphids. The effects of mixed diets on fitness have been studied for generalist predators and found highly variable in terms of survival and reproductive success (Adler 2004, Toft 2005). When mixed diets have been found advantageous over pure, as in spiders, single food types alone were often of low-quality (Toft & Bilde 2002). However, our results suggest that conspecific eggs and aphids both constitute a high quality food. Unlike generalist predators such as spiders, ladybird larvae have only two kinds of prey available on a colony: aphids and conspecifics. When aphids are at low densities cannibalism is the only alternative food. Moreover, unlike spiders (Wagner, 1997) larvae have a limited ability of dispersal (Dixon 2000, Sato *et al.* 2003, but see Cottrell & Yeargan 1999), partly because they need to find quickly food to complete development. Thus under aphid limitation, cannibalism is the only solution. Moreover, Martini *et al.* (2009)'s model suggested that for aphidophagous ladybirds, egg cannibalism might be advantageous even in the presence of aphids. Therefore, it is not surprising that evolution has favoured individuals which develop well on a diet made of conspecific eggs. In ladybirds, three other studies have compared fitness components of individuals fed with either aphids or a mixed diet. It was found that a pure diet of aphids was better than a mixed diet. However in two of these studied, the mixed diet consisted of aphids and another low quality, hardly accepted prey (larvae of alfafa weevils (Evans et al. 1999) or eggs of Colorado potato beetle (Snyder *et al.* 2004)). In the third study, in which a mixed diet of aphids and conspecific eggs were given to *A. bipunctata* or *Harmonia axyridis* Pallas, Ware *et al.* (2009) found a lower fitness on the mixed diet. However the amount of food in the mixed was too low compared to the pure aphid diet. Indeed, in this paper the fourth instar larvae on mixed diet fed eggs alternatively with aphids one day and only 12 eggs the next day. In our experiment fourth instar larvae on a pure diet of eggs ate an average of 43 eggs per day before being satiated, and 18 eggs per day in the case of the mixed diet (table 2).

Our third experiment provides new insights in the understanding of cannibalism in ladybirds. Indeed, in formerly published experiments on cannibalism, the rates of encounter between aphids and eggs were different (Agarwala & Dixon 1992, Khan *et al.* 2003). With our experimental design we controlled the surface covered by each prey, and immobilized aphids to ensure the same rate of encounter of the two preys. This allowed us to test the prediction of the "meet and eat hypothesis" that consumption rate of either prey should be equal to the encounter rate under various conditions. We found that this prediction does not hold for naive larvae. Instead larvae with no former experience of conspecific eggs had a low rate of cannibalism and preferred to feed on aphids rather than on conspecific eggs. This result suggests a switching in foraging strategy, *i.e.* the proportion of eggs which are attacked increases instead of staying fixed. The main reason for switching is learning, as the number of egg-batch attacked significantly increased when larvae were experimented. It is likely that the level of hunger is an important factor for motivating the first cannibalistic event. Moreover, unlike what has been observed in honey bees or syrphids (Kunin 1993, Goulson, Ollerton & Sluman 1997), the low density of the preferred food did not have any influence on switching, as satiated larvae reared on low aphid density were still reluctant to eat conspecific eggs. It is interesting to find that after having cannibalized once, the larvae did not reduce their consumption of eggs despite the fact that eggs and aphids were offered in the same quantity. First instars larvae usually experiment cannibalism after hatching (e.g. Michaud & Grant 2004). Therefore, it seems that the memory of cannibalism experience in these early times of life was lost when larvae were fed with aphids until fourth instar. Molecules on the surface of eggs are likely to play a major role. When we removed these molecules, we found that, even naive larvae no longer discriminated between conspecific eggs and aphids, as it attacked both at the same rate, in agreement with the "meet and eat hypothesis". These results suggest that an arm race must be occurring between females and larvae. The following scenario can be suggested for the evolution of egg cannibalism and egg protection in ladybirds. First, eggs cannibalism by larvae evolved firstly because it is the only alternative food in absence of aphids, and secondly because it can be advantageous even in the absence of preys (Martini *et al.*, 2009). In response, females evolved to produce antifeeding chemicals on the surface on eggs. But larvae were then selected to learn this signal and switch to eat eggs at high frequencies. Once a larva has started to eat eggs, the chemicals no longer deter larvae from cannibalism, and can actually benefit from prolonged cannibalism.

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DISCUSSION

Mon dessein n'est pas de faire un gros livre, et je tâche plutôt de comprendre beaucoup en peu de mots.

René Descartes, *La Geométrie* 1637.

I. Rappel de la problématique

a. La Phéromone d'inhibition de la ponte et son implication en lutte biologique

Dans la famille des Coccinellidae, la ponte est inhibée par une phéromone secrétée par les larves. L'étude de cette phéromone d'inhibition de la ponte (ODP) revêt un intérêt à la fois théorique et appliqué. Ainsi, l'évitement des traces larvaires par les femelles a permis d'expliquer en partie les échecs de la lutte biologique contre les pucerons utilisant des coccinelles (Hemptinne, Dixon & Coffin 1992 ; Doumbia, Hemptinne & Dixon 1998). Pourtant, le premier essai concluant date de 1888 avec l'introduction de la coccinelle coccidiphage, *Rodolia cardinalis* Mulsant sur les citronniers de Californie afin de lutter contre la cochenille *Icerya purchasi* Maskell, originaire d'Australie. *R. cardinalis* a depuis montré son efficacité dans différents pays du globe comme la France, le Portugal, l'Argentine, la Turquie ou la Georgie (Kobakhidze 1965, Oztemiz *et al.* 2008, Rocca *et al.* 2009). Au-delà de cet exemple frappant, les réussites de contrôle des populations de ravageurs par des coccinelles sont rares, particulièrement quand il s'agit de pucerons (Dixon et *al.* 1997). Il avait été proposé que la différence de succès des coccinelles coccidiphages et coccinelles aphidiphages résulterait d'une satiété trop rapide de ces dernières (Mills 1982). Ainsi, les coccinelles prédatrices de pucerons se nourriraient de façon discontinue, avec des pauses importantes entre chaque proie contrairement à celles s'attaquant aux cochenilles. De ce fait, les premières devraient tuer moins de proies. Cependant, en comparant deux espèces de tailles semblables, *A. bipunctata* et *Cryptolaemus montrouzieri* Mulsant respectivement aphidiphage et coccidiphage, Magro *et al.* (2002) montrèrent que le temps de prédation était plus court chez *C. montrouzieri*, qui serait plus rapidement rassasiée.

Cette piste fut donc écartée, et c'est la découverte de l'ODP qui permit de montrer que les femelles optimisaient la survie de leur descendance en la préservant d'un trop grand risque de cannibalisme. À l'échelle de la population, si l'on constate une agrégation des adultes lors des pics de pucerons, l'évitement des sites occupés aboutit ainsi à ce que la densité des pontes et donc des larves soient indépendantes des densités de proies. On comprend alors que l'intérêt évolutif des femelles s'oppose à celui de l'agriculteur qui souhaiterait au contraire une réponse numérique des prédateurs là où les pucerons sont en grand nombre.

Cet exemple témoigne de l'importance des études sur la biologie et le comportement des coccinelles et des prédateurs de pucerons en général afin d'améliorer sensiblement les stratégies de lutte biologique.

b. Existence d'un conflit entre femelles et larves qui produisent ODP

Cette thèse trouve son origine dans le constat que l'inhibition de la ponte des coccinelles par les traces larvaires aboutit à un conflit évolutif entre adultes et larves. Le marquage des sites de pontes est un comportement que l'on retrouve chez de nombreux insectes qui exploitent des ressources limitées dans le temps ou dans l'espace (e.g. Ruzika 1996, Ruzika & Havelka 1998, Scholtz & Poehling 2000, Adesso *et al.* 2007, Liu *et al.* 2008). Dans de très nombreux cas le signal bénéficie à la foi à l'émetteur et au receveur. Or, nous savons que les larves de coccinelles peuvent manquer de proies à la fin de leur développement, particulièrement quand la colonie de pucerons est en phase descendante (Kindlmann & Dixon 1999, Dixon 2000). Le cannibalisme constitue alors un apport de nutriments qui peut se révéler décisif. Dès lors, l'émission par les larves d'une phéromone d'inhibition de la ponte peut sembler paradoxale car elle conduit à une limitation des ressources alimentaires alternatives dont pourraient disposer les larves. L'intérêt des larves à synthétiser l'ODP est donc posé, tout comme le maintien de cette stratégie. La résolution de ce paradoxe peut se faire par le biais de deux hypothèses.

La première serait que la synthèse de cette phéromone, en éloignant les femelles, permettrait de diminuer la compétition sur une colonie. La trop forte densité de prédateurs pourrait se traduire en effet par une chute plus rapide du nombre de proies (Hemptinne & Dixon 1997) et les nymphes pourraient même être victimes du cannibalisme par des larves plus jeunes (Majerus 1994). Dans ce cas, le bénéfice du cannibalisme des œufs serait inférieur aux coûts de la compétition imposée par des larves plus jeunes. La production d'ODP par les larves serait alors justifiée car elle serait bénéfique à la fois à l'émetteur et au récepteur du signal.

La seconde hypothèse est que l'ODP correspond à une substance produite par les larves pour assurer une toute autre fonction physiologique essentielle et dont se seraient servi les femelles pour détecter leur présence. C'est cette dernière solution que nous avons souhaité explorer pendant cette thèse. En effet, les taux de cannibalisme relevés sur le terrain (Osawa 1993, Hironori & Katsuhiro 1997) semble trop élevés pour s'accorder avec une reconnaissance optimale de l'ODP par les femelles. Par ailleurs, la qualité de la reconnaissance de l'ODP étant variable selon les espèces (Magro *et al.* 2007) et les individus, cela nous éloigne d'un signal qui se serait fixé au cours de l'évolution, ce qui aurait été probablement le cas si larves et femelles trouvaient un avantage commun à l'existence de cette phéromone.

L'ensemble des prédictions induites par les deux hypothèses sont résumées dans le Tableau 1.

II. Résumé des résultats obtenus

a. L'approche théorique

Les questions posées :

- *Comment ce système de production de l'ODP par les larves de coccinelles s'est-il maintenu alors qu'il est désavantageux pour les larves ?*
- *Comment a-t-il évolué, et quelles sont les conséquences pour les autres traits d'histoires de vie des coccinelles ?*

Dans le modèle le plus simple, nous montrons qu'au cours de l'évolution les larves présentant un cannibalisme plus fort que le reste de la population sont sélectionnées. En réponse, la sélection naturelle favoriserait les femelles les plus sensibles à l'ODP car elles diminuent ainsi le risque de cannibalisme de leurs descendants. Ces résultats impliquent une inhibition de la ponte complète par les traces larvaires ce qui ne correspond pas à ce qui est observé sur le terrain et en laboratoire.

Aussi, dans un deuxième temps, nous avons ajouté la possibilité de polymorphisme à la fois dans la production des traces larvaires et dans la reconnaissance des femelles vis-à-vis de ces différents signaux. Nous avons ainsi montré l'importance du polymorphisme dans le maintien de l'ODP. Nous mettons en évidence l'existence de cycles où des périodes d'intense cannibalisme alternent avec des phases où la reconnaissance des larves par des femelles serait augmentée. En conclusion, nous montrons qu'il existe une « course à l'armement » entre larves et femelles. Cette course conduit les premières à modifier leurs traces et les secondes à reconnaître un spectre plus large de molécules.

b. Étude du polymorphisme et de la reconnaissance des apparentés.

- *Dans le premier chapitre, nous prédisons un polymorphisme dans la production et la reconnaissance des traces larvaires. On s'attend donc à une meilleure reconnaissance des femelles envers les larves qui leurs sont apparentées.*
- *S'il existe une meilleure réponse des femelles pour les traces de leurs descendants comment cette discrimination change t-elle en fonction de l'expérience ou de l'âge de la coccinelle ?*

Dans le deuxième chapitre de cette thèse, nous montrons que les femelles sont plus sensibles aux traces déposées par leurs larves qu'à celles de larves non apparentées. La reconnaissance des apparentés avait déjà été mise en évidence dans la famille des Coccinellidae : des larves évitent de cannibaliser d'autres larves apparentées et des femelles sont réticentes à consommer leurs propres œufs (Agarwala & Dixon 1993, Pervez, Gupta & Omkar 2005). Notre expérience est la première, à notre connaissance, à montrer un effet de l'apparentement dans le contexte de la reconnaissance de l'ODP. Ces résultats impliquent une variabilité dans le mélange de molécules constituant les traces larvaires ainsi que dans l'aptitude à reconnaître ces traces par les femelles. Le fait que les femelles répondent mieux à leurs descendants est par ailleurs en accord avec le modèle développé dans le premier chapitre.

c. Étude du cannibalisme chez les coccinelles aphidiphages.

Notre modèle repose sur l'avantage que retirent les larves du cannibalisme. Nous avons donc voulu étudier les questions suivantes :

- *Le cannibalisme des œufs peut-il compenser efficacement l'absence de pucerons ?*
- *Apporte-il un avantage lorsqu'il intervient en même temps que la prédation de pucerons ?*
- *Observe t-on un évitement du cannibalisme ?*

Le troisième chapitre de cette thèse a pour objectif d'étudier le cannibalisme des œufs par les larves de coccinelles aphidiphages. Lors de la première expérience, nous montrons que les œufs et les pucerons sont deux nourritures aux caractéristiques différentes. Alors que les pucerons permettent une croissance rapide, ils préparent moins bien les larves à supporter le manque de nourriture. Le cannibalisme des œufs au contraire, abouti à une croissance plus faible des larves mais permet une meilleure conservation de la masse corporelle en cas de jeûne prolongé.

Dans la deuxième expérience, nous étudions l'effet d'une diète mélangeant pucerons et œufs conspécifiques. En effet, dans la nature, les larves pratiquent le cannibalisme en même temps qu'elles consomment des pucerons. Or, à ce jour, aucune étude n'avait été menée pour évaluer l'effet d'une diète mixte combinant ces deux nourritures sur des larves de coccinelles. Nous confirmons les effets des pucerons et des œufs sur la croissance des larves révélés par la première expérience. Les larves nourries à partir de pucerons atteignent un poids plus important que celles nourries uniquement avec d'œufs. Cependant, lors du jeûne naturel lors de la nymphose, les larves n'ayant consommé que des pucerons perdent plus de poids que les autres. En agissant en synergie dans la diète mixte, ces deux nourritures compensent leurs défauts et permettent d'obtenir des adultes de plus grande taille.

Finalement, l'étude comportementale faite sur les larves de coccinelles a montré que la théorie du « *Meet and Eat* » , c'est-à-dire une consommation de congénères ou de pucerons en fonction de leur taux de rencontre respectif, n'était pas vérifiée. Toutefois, nous soulignons le rôle des molécules présentent sur la surface des œufs dans la protection contre le cannibalisme. Une fois ces molécules retirées, les larves sont capables de consommer les œufs sans restriction. Enfin, cette expérience a permis de dévoiler les capacités d'apprentissage des larves qui, après avoir consommé une première fois des œufs, ne sont plus repoussées par leurs protections. Chez les arthropodes prédateurs, cette capacité a été très rarement décrite mais on peut en trouver un exemple récent dans le travail de Rahmani *et al.* (2009) qui ont montré que les acariens prédateurs *Phytoseiulus persimilis* Athias-Henriot étaient également capables d'apprentissage vis-à-vis du cannibalisme.

III. Interprétation des résultats et perspectives.

a. Le cannibalisme

i. Limites du modèle et implications évolutives.

Pour les populations qui exploitent une nourriture dont la quantité est variable dans le temps, le cannibalisme est une solution lorsque la ressource principale vient à manquer (Cushing 1991, Nishimura & Isoda 2003, Diekmann *et al.* 2003, Claessen, de Roos & Persson 2004, Getto *et al.*2005). Cependant, notre modèle a montré que le gain énergétique ainsi que l'élimination des compétiteurs pouvaient suffire à rendre le cannibalisme avantageux et justifier l'augmentation de son intensité au cours de l'évolution. Toutefois, le cannibalisme étant absent de nombreux groupes taxonomiques, il convient de s'interroger sur les caractéristiques et les limites de notre modèle.

Tout d'abord, nous n'avons pas défini un coût à la pratique du cannibalisme ce qui correspond bien à la situation des larves sur les œufs de coccinelles. Or, le cannibalisme revient à attaquer des individus qui sont capables de se défendre, et pourquoi pas, de retourner la situation à leur avantage. En conséquence, le risque de blessure, voire de mort est souvent bien plus important lors de l'attaque d'un congénère que d'une proie hétérospécifique. C'est pourquoi, on constate que le cannibalisme dépend souvent du rapport de taille entre l'attaquant et sa victime (Mayntz & Toft 2006). Par exemple, le cannibalisme sexuel chez les araignées loup est fortement corrélé à l'existence d'un dimorphisme sexuel entre la femelle cannibale, et le male (Wilder & Rypstra 2008). Dans le même ordre d'idée, nous avons considéré que le taux de cannibalisme dépendait uniquement du choix du prédateur puisqu'il n'y avait pas de défense de la part de la victime.

Enfin, nous n'avons pas intégré de degrés d'apparentement entre larves et œufs car nous estimions que la probabilité qu'une coccinelle retrouve un site sur lequel elle a déjà pondu était quasiment nulle, puisque l'on sait que les femelles dispersent fortement leurs œufs dans leur habitat (Osawa 2000). Or, en termes de fitness relative, le cannibalisme d'un apparenté ou d'un non apparenté ne donne pas le même résultat (Dixon 2000). On a d'ailleurs pu observer chez les coccinelles des systèmes d'évitement du cannibalisme entre larves apparentées (Agarwala & Dixon 1993, Pervez, Gupta & Omkar 2005), particulièrement utile si deux pontes de mères différentes ont été pondues dans un cours laps de temps sur le même site. Ainsi, la dispersion joue probablement un rôle non négligeable dans le bénéfice apporté par le cannibalisme (Lion & Van Baalen 2009). En cas de dispersion, la probabilité de rencontrer des individus non apparentés devient plus importante et rend le cannibalisme plus avantageux. De manière plus large, il est certain que les traits d'histoire de vie, tel que la sociabilité, les soins parentaux ou encore des facteurs extérieurs comme la présence de prédateurs (Chin-Baarstad, Klug & Lindstrom 2009) peuvent changer dans un sens ou dans un autre l'intérêt du cannibalisme.

ii. Conséquences au niveau individuel

Au niveau individuel, cette thèse a permis de préciser l'avantage physiologique du cannibalisme. En effet, un des préalables à notre modèle est l'intérêt supposé du cannibalisme pour les larves. Dans le dernier chapitre, nous montrons que le cannibalisme des œufs contribue à former des réserves dont le métabolisme est moins rapide, permettant une meilleure résistance à l'absence de nourriture. Le cannibalisme est donc particulièrement avantageux avant l'entrée en pupe puisqu'il permet de conserver plus de poids lors du passage de la larve à l'adulte. La bonne réponse métabolique des larves de coccinelles au cannibalisme des œufs a sans doute été sélectionnée en raison des faibles capacités de dispersion des larves. Les œufs conspécifiques devenant alors les seules ressources alternatives disponibles en cas de manque de pucerons. Dès lors, les larves qui peuvent tirer le meilleur parti du cannibalisme ont logiquement été avantagées au cours de l'évolution.

Toutefois, si le bilan pondéral des larves nourries avec des œufs conspécifiques est positif, on constate que les signaux chimiques présents à la surface des œufs constituent un frein important à leur consommation. Ces protections apparaissent comme une réponse au cannibalisme mais il est probable qu'en nature leur efficacité soit plus faible que dans les conditions du laboratoire où nous utilisions des larves bien nourries. En effet, leur absence d'efficacité une fois que la larve a appris à les surmonter, sera dans des conditions naturelles un lourd handicap. Le premier acte de cannibalisme semble en effet influencé par l'état de satiété, et nous avons pu constater que des larves préfèrent consommer des œufs conspecifiques plutôt que de jeûner quand il s'agit de la seule nourriture proposée. Dès lors, il y aura un changement de stratégie et les larves attaqueront avec la même intensité pucerons et œufs. Il semblerait que ces molécules protègent du cannibalisme uniquement lorsque les larves ont à disposition des pucerons en quantité suffisante. L'intérêt serait surtout de diminuer les attaques venant d'autres organismes. Les prédateurs susceptibles de les consommer ont été moins à même de développer des moyens d'apprentissage ou de détoxification puisque l'opportunité de manger ces œufs est inférieure à celui des larves conspécifiques.

b. Variabilité et reconnaissance des apparentés.

La plus grande sensibilité des femelles aux traces produites par leurs larves est en accord avec les prédictions du modèle. Dans le premier chapitre, je montre comment le maintien de l'ODP peut s'expliquer par l'existence d'un polymorphisme, à la fois dans la composition des traces larvaires et dans la réponse des femelles. À l'équilibre, les phénotypes les plus sensibles aux traces de leurs larves devraient être dominants.

Cette situation implique une diversification du signal puisque la reconnaissance d'une seule molécule n'expliquerait pas les différences observées de sensibilité. La pression sélective sur les larves favorise celles dont les traces sont légèrement différentes du reste de la population. L'augmentation en fréquence de ce phénotype au sein de la population avantagera à son tour les femelles qui y seront plus sensibles. Mon travail prédit une succession de phases de haute reconnaissance et des phases de plus fort cannibalisme correspondant aux périodes où un nouveau mélange de molécules peu reconnu par les femelles devient dominant. Les expériences faites sur différentes espèces de coccinelles vont dans le sens de mes résultats. D'abord, il existe une forte corrélation entre la phylogénie des Coccinellidae et la diversification des traces larvaires (Magro *et al.* 2009). Ensuite, on sait désormais qu'il existe une reconnaissance interspécifique des traces larvaires, y compris pour des espèces n'ayant pas évolué ensemble récemment (Magro *et al*. 2007).

Des travaux ont également montrés que l'on était capable de mettre en évidence des variations dans la production de traces larvaire à l'échelle de l'espèce (Hokonique 2008). Après moins de 8 générations il est possible d'obtenir des souches qui se différencient de façon significative quantitativement et non qualitativement.

c. Du cannibalisme à la prédation intra-guilde.

Si les travaux de cette thèse s’intéressent au cannibalisme, il peut être utile de s’interroger sur leurs applications dans le cadre de la prédation intra-guilde (IGP). L’IGP est définie comme la prédation qui se déroule entre espèces qui exploitent les mêmes ou la même ressource (Polis *et al.* 1992). Chez les coccinelles, l’arrivée récente d’ *Harmonia axyridis* Pallas en Europe et en Amérique du Nord a donné un nouvel éclairage à ce phénomène. *H. axyridis* peut effectuer son développement larvaire sur une diète uniquement constituée d’oeufs ou de larves de coccinelles indigènes. De ce fait, les pertes imputables à l’IGP sont très importantes chez les espèces locales et cela même en présence de pucerons (Cottrell & Yeargan 1998; Cottrell 2004) ce qui s’intègre bien à notre modèle. De plus, Magro *et al.* (2007) montrent que des espèces sont plus sensibles aux traces de larves produites par des espèces qui ont évolué dans le même environnement pendant un temps suffisamment long. Un phénomène de coévolution déjà observé pour la toxicité des œufs qui est plus forte entre espèces qui partagent les mêmes habitats (Rieder *et al.* 2008). Les résultats de notre modèle suggèrent que si l’IGP par *H. axyridis* impose une pression sélective suffisamment forte aux espèces locales, on s’attend à ce que ces espèces améliorent leur reconnaissance envers les traces larvaires d’ *H. axyridis.*

IV. Conclusion finale.

Dès sa découverte, il a été fait référence à une phéromone pour qualifier la substance inhibitrice de la ponte des traces larvaires de coccinelles (Ruzicka 1997, Doumbia et al. 1998). D’un point de vue étymologique, le terme phéromone a été formé par Karlson & Lüscher (1959) à partir des racines grecques *Pherein* (transporter) et *Hormon* (exciter). L’article évoquait alors des substances sécrétées par des individus qui, une fois détectés par des membres de la même espèce, induisaient une réaction spécifique. Depuis, la nomenclature des phéromones s’est beaucoup élargie mais contrairement aux composés chimiques ayant une activité interspécifique, les phéromones n’ont jamais été distinguées en fonction de l’intérêt de l’émetteur et du récepteur. Actuellement donc, rien ne s‘oppose à considérer les traces larvaires comme une phéromone. Toutefois, Nufio & Papaj (2001) distinguent les marquages ayant évolué pour véhiculer une information de ceux qui sont produits pour une autre raison et qui ont été détournés de leur utilité primaire et interprétés comme un signal.

Cette hypothèse que j’avais choisi de suivre au début de ma thèse semble se confirmer à la lumière des différents résultats obtenus (Tableau 1). La question de l’utilité des traces larvaires est donc posée. Dans la mesure où l’ODP est produite au niveau du disque anal (Laubertie *et al.* 2006), la première supposition est que les alcanes composant l’ODP permettent l’adhésion de la larve au substrat, c’est à dire aux végétaux. On sait en effet que l’adhésion d’une larve à une plante est rendue difficile par la couche plus ou moins épaisse de cires cuticulaires des feuilles (Eigenbrode & Jetter 2002, Eigenbrode 2004). Par ailleurs, on sait que les hydrocarbures cuticulaires ont un rôle important dans l’imperméabilisation de l’épiderme (Hadley 1981, Montooth & Gibbs 2003). Pour confirmer cette théorie, il semble essentiel de sélectionner des lignées faiblement ou hautement productrices de trace larvaire et de comparer différents traits ayant un effet direct sur leur valeur adaptative. En parallèle, puisque l’on constate une absence de réponse à l’ODP de la part de certaines femelles, il pourrait être intéressant de sélectionner une souche dont la ponte est peu inhibée par les traces larvaires. En plaçant des femelles répondant différemment à l’ODP dans des conditions de compétition, on pourrait mesurer l’effet de l’ODP sur la réduction du cannibalisme des pontes. D’un point de vue plus appliqué, cette souche pourrait représenter une solution en lutte biologique pour augmenter les densités de larves de coccinelles sur les colonies de pucerons.

Prédictions	*Hypothèse de la synthèse de l'ODP pour diminuer la compétition entre larves.*	*Hypothèse de la synthèse des traces larvaires pour une autre raison physiologique*	*Résultats*
Le cannibalisme des oeufs	Le cannibalisme des œufs est peu avantageux pour les larves	Le cannibalisme des œufs permet de compenser le manque de proies	Fort interet du cannibalisme en cas de manque de nourriture et en presence de pucerons (Chapitre 3)
La variabilité du signal	Le signal doit être conservé pour permettre une meilleure reconnaissance	Le signal doit être variable car les larves ont intérêt à le changer.	Existence d'une variabilité quantitative. Variabilité impliquée par la reconnaissance des apparentés (Chapitre 2, Hokonike 2008)
Intérêt de la production de Traces	Les traces larvaires peuvent n'avoir aucun autre rôle que celui de convoyer une information.	Les traces larvaires ont une fonction essentielle.	Nécéssite des experimentations.
Qualité de la reconnaissance	Optimale	Variable	Il existe une forte variabilité individuelle à la sensibilité à l'ODP

Tableau 1 : Principales prédictions induites par les deux hypothèses permettant d'expliquer la production de phéromone d'inhibition de la ponte par les larves de coccinelles.

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Annexe 1 : Chapitre 1 Dérivation jusqu'à l'équation (8) - *Derivation to inequality (8)*.

$$\hat{x} = \frac{\beta \cdot \eta \cdot \hat{r} \cdot \hat{z}}{(\lambda + m)} \qquad \text{(eqn S.1)}$$

$$\hat{y} = \frac{m \cdot \hat{x}}{(\gamma \cdot \mu \cdot \hat{r} + \xi)} \qquad \text{(eqn S.2)}$$

$$\hat{z} = \frac{\gamma \cdot \mu \cdot \hat{r} \cdot \hat{y}}{\varphi} \qquad \text{(eqn S.3)}$$

$$\hat{r} = 1 - \mu \cdot \hat{y} - \eta \cdot \hat{z} \qquad \text{(eqn S.4)}$$

From (2) we get:

$$\hat{y}(\gamma \cdot \mu \cdot \hat{r} + \xi) = m \cdot \hat{x} \Rightarrow \hat{x} = \hat{y}\left(\frac{\gamma \cdot \mu}{m} \cdot \hat{r} + \frac{\xi}{m}\right) \qquad \text{(eqn S.5)}$$

In combination with (eqn S.1) and (eqn S.3) this gives:

$$\hat{y}\left(\frac{\gamma \cdot \mu}{m} \cdot \hat{r} + \frac{\xi}{m}\right) = \frac{\beta \cdot \eta \cdot \hat{r} \cdot \hat{z}}{(\lambda + m)} = \frac{\beta \cdot \eta}{(\lambda + m)} \frac{\gamma \cdot \mu}{\varphi} \cdot \hat{r}^2 \cdot \hat{y}$$

$$\Rightarrow \frac{\gamma \cdot \mu}{m} \cdot \hat{r} + \frac{\xi}{m} = \frac{\beta \cdot \eta}{(\lambda + m)} \frac{\gamma \cdot \mu}{\varphi} \cdot \hat{r}^2 \qquad \text{(eqn S.6)}$$

$$\Rightarrow \hat{r}^2\left(\frac{\beta\cdot\eta}{(\lambda+m)}\frac{\gamma\cdot\mu}{\varphi}\right)-\frac{\gamma\cdot\mu}{m}\cdot\hat{r}-\frac{\xi}{m}=0$$

$$\Rightarrow \hat{r}=\frac{\frac{\gamma\cdot\mu}{m}+\sqrt{\left(\frac{\gamma\cdot\mu}{m}\right)^2+4\cdot\frac{\xi}{m}\left(\frac{\beta\cdot\eta}{(\lambda+m)}\frac{\gamma\cdot\mu}{\varphi}\right)}}{2\left(\frac{\beta\cdot\eta}{(\lambda+m)}\frac{\gamma\cdot\mu}{\varphi}\right)} \quad \text{(eqn S.7)}$$

(Only the positive root is an equilibrium of the system).

We multiply nominator and denominator by *m*/ξ, to obtain:

$$\hat{r}=\frac{\frac{\gamma\cdot\mu}{\xi}+\sqrt{\left(\frac{\gamma\cdot\mu}{\xi}\right)^2+4\cdot\left(\frac{\beta\cdot\eta}{(\lambda+m)}\frac{\gamma\cdot\mu}{\varphi}\frac{m}{\xi}\right)}}{2\left(\frac{\beta\cdot\eta}{(\lambda+m)}\frac{\gamma\cdot\mu}{\varphi}\frac{m}{\xi}\right)}=\frac{1+\sqrt{1+4\left(\frac{\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}}{\frac{\gamma\cdot\mu}{\xi}}\right)}}{2\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)} \quad \text{(eqn S.8)}$$

This equilibrium only exists if it is smaller than 1 (because then the aphid density equals its carrying capacity, and there is no coexistence).

So, if:

$$2\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right) > 1+\sqrt{1+4\left(\frac{\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}}{\frac{\gamma\cdot\mu}{\xi}}\right)}$$

$$\Rightarrow 2\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)-1 > \sqrt{1+4\left(\frac{\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}}{\frac{\gamma\cdot\mu}{\xi}}\right)}$$

$$\Rightarrow \frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)} > \frac{1}{2} \text{ and } \left(2\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)-1\right)^2 > 1+4\left(\frac{\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}}{\frac{\gamma\cdot\mu}{\xi}}\right) \qquad \text{(eqn S.9)}$$

$$\Rightarrow \frac{\beta\cdot\eta}{\varphi} > \frac{1}{2}\left(1+\frac{\lambda}{m}\right)$$

$$\text{and } \left(4\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)^2+1-4\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)\right) > 1+4\left(\frac{\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}}{\frac{\gamma\cdot\mu}{\xi}}\right)$$

the second condition gives:

$$\left(\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)^2-\left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)\right) > \left(\frac{\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}}{\frac{\gamma\cdot\mu}{\xi}}\right)$$

$$\Rightarrow \left(\frac{\beta\cdot\eta}{\varphi}\frac{m}{(\lambda+m)}\right)-1 > \frac{\xi}{\gamma\cdot\mu} \qquad \text{(eqn S.10)}$$

$$\Rightarrow \frac{\beta\cdot\eta}{\varphi} > \left(1+\frac{\lambda}{m}\right)\left(1+\frac{\xi}{\gamma\cdot\mu}\right)$$

If this is satisfied, the first condition also holds, so the coexistence equilibrium exists if and only if:

$$\frac{\beta \cdot \eta}{\varphi} > \left(1 + \frac{\lambda}{m}\right) \cdot \left(1 + \frac{\xi}{\gamma \cdot \mu}\right) \qquad \text{(eqn S.11)}$$

Evolution of cannibalism and oviposition strategies in aphidophagous ladybirds

The framework of this Thesis is the evolution of cannibalism and oviposition strategies in Coccinellidae. The first chapter of is an evolutionary model that deals with the links between egg-cannibalism and female response to oviposition deterring pheromone (ODP).

The second chapter is a behavioral study on female's response to the ODP synthesized by related larvae, compared to ODP synthesized by non-related larvae. As predicted by the model, we show that females are more sensitive to tracks synthesized by kin, but this discrimination do not hold with the experience, and the age of female.

Finally, the third chapter deals with the interest and the decision making of eggs-cannibalism by larvae. We show that cannibalism is particularly advantageous before the end of the larval development, because it brings more reserves than aphids. Moreover, due to chemical protection eggs are less predated than aphids, but we demonstrate the possibility of learning that make this protection useless.

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Évolution du cannibalisme et du comportement de ponte chez les coccinelles aphidiphages.

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Les coccinelles aphidiphages femelles reconnaissent une phéromone d'inhibition de la ponte (ODP) contenue dans les traces que déposent les larves sur leur substrat. La reconnaissance de cette phéromone permet aux femelles de préserver leurs pontes du cannibalisme très présent chez ces insectes. Cependant, pour les larves, le cannibalisme est avantageux puisqu'il constitue un apport alimentaire supplémentaire.
Le premier chapitre de cette thèse est un travail de modélisation qui montre l'intérêt du polymorphisme dans ce système.
Le second chapitre est une étude comportementale qui étudie l'effet de l'apparentement sur la réponse des femelles à l'ODP. Nous montrons une plus grande sensibilité des femelles en présence de traces larvaires produites par leurs propres larves que celles de larves non apparentées.
Finalement le troisième chapitre est une étude des facteurs influençant le cannibalisme des œufs par les larves, ainsi que l'avantage que celles-ci en retirent. Les expériences soulignent notamment l'intérêt du cannibalisme juste avant l'entrée en pupe, ainsi que les capacités d'apprentissage des larves concernant l'évitement des protections présentes sur les œufs.

Mots-clefs : Coccinellidae, cannibalisme, oviposition, Phéromone d'inhibition de la ponte.

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