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Camouflage chez les araignées crabe: Approche sensorielle, comportementale et écologique

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RESUME

De nombreuses interactions interspécifiques de type proie-prédateur font intervenir la manipulation des signaux sensoriels. Certaines espèces sont capables par exemple de produire un contraste chromatique et/ou achromatique suffisamment faible sur leur substrat pour rendre difficile leur détection par les proies ou les prédateurs, une stratégie appelée 'background matching'. Parmi ces espèces, on trouve des araignées crabe, comme *Misumena vatia* (Thomisidae), qui chassent immobiles sur les fleurs et qui sont capables de changer de couleur. Il est supposé depuis plus d'un siècle que ce changement de couleur permet de devenir invisible aux yeux des proies. Mais, comme la plupart des espèces reportées comme camouflées, elles le sont de façon subjective puisque l'appréciation du degré de camouflage est basée sur notre propre vision. Globalement, il existe un décalage entre la quantité de travaux sur l'écologie de *M. vatia*, sa notoriété en tant qu'experte du camouflage, et la connaissance réelle sur le camouflage et le changement de couleur chez cette espèce. L'objectif de cette thèse était d'aborder le camouflage chez *M. vatia* d'un point de vue sensoriel, à une échelle communautaire, avec une approche combinant physiologie et comportement. L'utilisation de la spectroradiométrie et des modèles de vision des couleurs ont permis de quantifier le niveau de contraste chromatique et achromatique de l'araignée sur son substrat dans les systèmes visuels de différentes proies comme les abeilles, les bourdons, les diptères et des prédateurs comme les passériformes. Il a été ainsi démontré que si *M. vatia* était indétectable dans l'achromatique à longue distance, le niveau de contraste chromatique à courte distance était fortement dépendant du substrat et de l'identité du receveur. Des méthodes d'électrophysiologie intra- et extracellulaire combinées à des adaptations sélectives ont permis de révéler que *M. vatia* possédait deux types de photorécepteurs dans chaque paire d'yeux, l'un ayant un pic de sensibilité dans la région des UV-A (environ 340 nm) et le second dans la région verte du spectre (environ 525 nm). Ces résultats impliquent que *M. vatia* possède les bases physiologiques nécessaires à la vision des couleurs, et constituent des éléments importants pour la compréhension des mécanismes visuels à l'origine du changement de couleur. D'un point de vue comportemental, des tests de choix floraux ont suggérés une préférence d'ordre chromatique chez les araignées juvéniles. Cette préférence les rend peu discriminable pour les proies. Les résultats de cette thèse sont finalement replacés dans un contexte évolutif et physiologique plus général.

Mots-clés: *Misumena vatia*, Camouflage, Ecologie sensorielle des communautés, Contraste chromatique, Contraste achromatique, Préférence colorée, Sensibilités spectrales

ABSTRACT

Numerous prey-predator interactions rely on the manipulation of sensory signals. Some species for example are able to produce a low chromatic and/or achromatic contrast on their substrates, making them quite difficult to detect for prey or predators. This specific strategy is known as background matching. Among those species, some crab spiders, as *Misumena vatia* (Thomisidae), hunt motionless on flowers waiting for flower-visiting insects and are able to change its colouration from white to yellow over several days. It has assumed for more than a century that this species changes colour to decrease the risk of detection by prey and predator, such as birds. However, as for the majority of species reported as cryptic, this assumption is based only on our own subjective perception of the degree of crypsis. Overall, there is a discrepancy between the high number of works on its ecology, its fame as an expert of camouflage and the real empirical knowledge about its crypsis and colour change mechanisms. The aim of this thesis was therefore to study crypsis in *M. vatia*, from community sensory perspective, using an approach combining physiology and behaviour. The use of spectroradiometry and colour vision models allowed us to rigorously quantify the chromatic and chromatic contrasts of spiders in the perspective of all receivers. We showed that if *M. vatia* was undetectable at long distance through achromatic vision, the chromatic contrast value is quite dependent of both substrate and receiver identity. Intra- and extracellular electrophysiological recordings combined with selective adaptation have disclosed that *M. vatia* possesses two classes of photoreceptors in each pair of eyes: one in the ultraviolet (around 340 nm) and one in the green region (around 525 nm). *M. vatia* has therefore the physiological basis at the retinal level required for colour vision. Behavioural choice experiments with third instar spiderlings between artificial flowers with different chromatic and achromatic compositions suggested a chromatic preference. This preference induced a low discriminability of spiderlings on their substrate from the perspective of hymenoptera prey. In the final part, we discuss these results in an overall evolutionary and physiological context.

Key-words: *Misumena vatia*, Crypsis, Community sensory ecology, Chromatic contrast, Achromatic contrast, Colour preference, Spectral sensitivities

TABLE DES MATIERES

Liste des tableaux

Liste des figures

Liste des annexes

- INTRODUCTION GENERALE -

De nombreuses interactions interspécifiques, notamment de type proie-prédateur, font intervenir la manipulation des signaux sensoriels. Un organisme peut exploiter les préférences et capacités sensorielles d'un second organisme avec qui il interagit, pour que le résultat de l'interaction lui soit bénéfique en terme de fitness (Haynes & Yeargan, 1999). On distingue deux grandes catégories de stratégies qui permettent de duper une proie ou un prédateur.

La première catégorie concerne les organismes qui possèdent des traits mimétiques c'est-à-dire limitant leur reconnaissance. Certaines espèces parfaitement comestibles ont évolué sous la pression de prédation pour ressembler à un autre organisme toxique ou dangereux à attaquer présent dans leur environnement, et ainsi profiter de leur relative sécurité. Cette stratégie, connue sous le nom de mimétisme batésien, a fait l'objet de nombreuses études (Jeffords et al., 1979; Dittrich et al., 1993; Pfennig et al., 2001; Ruxton et al., 2004). Dans la littérature, on trouve des exemples de couples mime/modèle assez spectaculaires chez de nombreux taxons. En effet, certaines chenilles se mettent à ressembler à des serpents (Robinson, 1969), alors que des lézards juvéniles *Eremias lugubris* ont la manière de se déplacer, la couleur et la taille d'un coléoptère toxique (Huey & Pianka, 1977). Certains organismes mimétiques sont quant à eux capables d'exploiter à leur avantage l'attraction d'une seconde espèce pour un signal spécifique (Jackson & Pollard, 1996). Des araignées de la famille des Araneidae attirent des papillons nocturnes mâles en produisant des cocktails chimiques similaires aux phéromones sexuelles émises par les femelles papillons de la même espèce (Yeargan, 1994; Haynes et al., 2002). Cette stratégie de mimétisme agressif chimique est complémentée par une goutte collante placée à l'extrémité d'un fil de soie pour la capture.

La seconde catégorie regroupe des espèces qui, plutôt que de ne pas être reconnues, ont développé des stratégies leur permettant de ne pas être détectées par les systèmes sensoriels de leur proie et/ou de leur prédateur. Ces stratégies sont regroupées sous le terme de camouflage ('crypsis') (Ruxton, 2009; Stevens & Merilaita, 2009). Il est important de noter que certains organismes sont considérés à la fois comme étant cryptiques et mimétiques. C'est le cas par exemple, de phasmes ou de larves de papillons qui ont non seulement la forme des éléments de leur environnement mais aussi leurs couleurs. Comme pour le mimétisme, un organisme peut être cryptique dans différents contextes sensoriels comme l'olfaction, l'audition et la vision (Ruxton, 2009). Wilson & Hare (2006) ont par exemple démontré un cas de camouflage acoustique chez l'écureuil *Spermophilus richardsonii*. Ces écureuils, qui émettent un chant audible lorsque qu'un prédateur est très proche, utilisent un chant ultrasonique moins efficace pour la communication intra-spécifique mais indétectable

pour le prédateur lorsque celui-ci est plus distant. Ceci permet aux écureuils de communiquer entre eux sans se faire détecter par le prédateur. Plusieurs études ont aussi rapporté des cas de camouflage olfactif chez des larves de papillon ayant la même signature chimique que leurs plantes hôtes, et leur conférant une protection contre les fourmis (Akino et al., 2004; Portugal & Trigo, 2005). Néanmoins, le camouflage dans le système visuel des receveurs est celui qui a reçu la plus grande attention. Le camouflage visuel regroupe à lui seul différentes stratégies, toutes basées sur l'utilisation de motifs, de marques et/ou de couleurs, par sa composante chromatique et/ou achromatique, pour empêcher la détection (Stevens and Merilaita, 2009). Il est donc important pour l'ensemble de la thèse de définir ici la notion de couleur et de rendre compte de la complexité de sa genèse.

Les animaux peuvent extraire de la lumière différents types d'informations comme son intensité (composante achromatique), sa couleur (composante chromatique) ou encore son vecteur électrique (polarisation) (Nilsson & Warrant, 1999; Kelber et al., 2003). Les mammifères semblent incapables de percevoir la polarisation de la lumière à l'inverse de certaines espèces d'oiseaux, reptiles, amphibiens, arthropodes et poissons (Taylor & Adler, 1973; Adler & Phillips, 1985; Hawryshyn, 1992; Munro & Wiltschko, 1995; Dacke et al., 1999; Dacke et al., 2003). Nous partageons par contre avec l'ensemble de ces groupes la capacité de voir la couleur (Kelber et al., 2003). Percevoir la couleur ('True colour vision') est défini comme la capacité à discriminer deux stimuli de composition spectrale différente, indépendamment de leur intensité relative (Menzel, 1979; Kelber et al., 2003). Il est primordial d'avoir à l'esprit que la couleur n'est **pas** une propriété inhérente d'un objet ou d'un organisme mais résulte de plusieurs étapes d'ordre physiques et physiologiques (**Figure 1**).

La lumière qui provient d'un objet ou d'un organisme résulte dans la majorité des cas d'une interaction physique entre une source de lumière, composée de photons, et leur surface. Quelques espèces d'invertébrés sont capables de produire leur propre lumière (Johnsen, 2005; Lewis & Cratsley, 2007), mais pour la majorité des organismes, la source lumineuse émettrice de photons la plus importante est le soleil qui émet, dans la gamme de longueur d'onde comprise entre 380 et 700nm, près de 10^{20} photons.s^{-1}.m^{-2} pendant une journée ensoleillée d'été. A titre de comparaison, la lumière de la pleine lune qui reflète la lumière du soleil envoie vers la surface terrestre un millionième de fois moins de photons (Lythgoe, 1979).

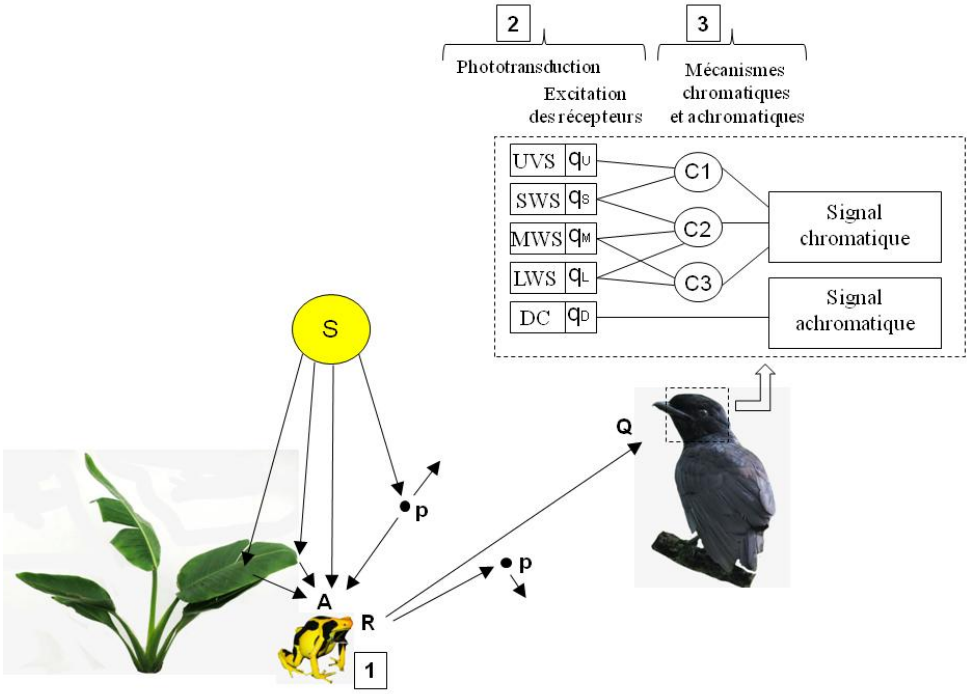

Figure 1: Représentation schématique des étapes de la genèse de la sensation colorée. A est le spectre d'irradiance ambiant. Il est composé de la lumière réflechie ou filtrée par les objets, de la lumière provenant directement de la source de lumière principale (S), et de la lumière absorbée ou dispersée par des particules (p). Etape 1: La fraction des longueurs d'ondes réfléchies (R) est fonction de la composition spectrale de la lumière ambiante (A) et de la réflectance spectrale de la surface de l'objet. Q représente la lumière atteignant l'œil de l'observateur. Etape 2: Les photons vont être absorbés par les différents types de photorécepteurs. Dans le cas des oiseaux, on trouve généralement cinq classes de photorécepteurs. Les récepteurs sensibles aux Ultraviolets (UVS), aux longueurs d'ondes courtes (SWS), aux longueurs d'ondes moyennes (MWS) et longues (LWS) vont être impliqués dans la genèse des signaux chromatiques. Les signaux achromatiques seront quant à eux générés à partir d'une seule classe spécifique, les doubles cônes (DC). Les réponses des cinq types vont dépendre du nombre de photons absorbés (q). Etape 3: Les signaux des différents types de cônes sont intégrés par des mécanismes chromatiques et achromatiques. Les mécanismes chromatiques (C1, C2, C3), ou codage de l'information chromatique, consiste en la comparaison des signaux provenant de différents types de photorécepteurs. Les mécanismes achromatiques consistent en la sommation d'un ou plusieurs types de photorécepteurs. Dans le cas des oiseaux, les signaux achromatiques sont formés à partir des signaux générés par les doubles cônes. (Schéma adapté d'après Endler, 1990; Bradbury & Vehrencamp, 1998 ; Osorio et al., 1999a). Photo du dendrobate *Dendrobates tinctirius* par Klaus Draeby et de l'oiseau par Jose Garcia.

La lumière du jour a une composition spectrale, c'est-à-dire une gamme de longueurs d'ondes émises, et une intensité qui sont bien définies. De nombreuses interactions visuelles entre espèces se déroulent directement sous la lumière du jour. Cependant, certains milieux ont un

environnement lumineux particulier dérivé de la lumière du jour (Endler, 1993). C'est le cas par exemple des océans où la composition et l'intensité de la lumière du jour varient fortement en fonction de la profondeur (Warrant & Locket, 2004). Les photons émis par une source de lumière vont interagir avec la surface des objets ou des organismes. Toutes les surfaces absorbent, transmettent et réfléchissent des longueurs d'ondes spécifiques. La gamme de longueurs d'ondes réfléchies constitue une des propriétés physiques de la surface, la réflectance spectrale. La réflection de la lumière incidente peut être induite soit par des pigments, on nomme alors la couleur résultante de 'pigmentaire' (Oxford & Gillespie, 1998) soit par des microstructures qui vont décomposer la lumière, on parle alors de couleur structurale (Kinoshita et al., 2002; Parker et al., 2003). C'est la diversité des pigments et des microstructures observés naturellement qui explique la grande variété des colorations animales. Pour conclure sur cette première interaction, il est donc important de noter que la lumière réfléchie par une surface est contexte-dépendante car un même objet pourra réfléchir différentes compositions de lumière et apparaître d'une couleur différente pour un observateur selon la composition spectrale et l'intensité de la source lumineuse.

La deuxième étape se déroule au niveau de l'œil de l'observateur. En effet, les photons émis par une surface vont être absorbés par des structures sensorielles spécialisées au niveau de la rétine, les photorécepteurs (Land & Fernald, 1992; Land & Nilsson, 2002). Chaque photorécepteur, qu'il soit cilié ou rhabdomérique, va posséder une partie distale photosensible où se trouvent les pigments visuels. Les pigments visuels sont composés d'une protéine d'opsine et d'un chromophore de type caroténoïde. Aidley (1998) montra notamment que lorsqu'un chromophore absorbe un photon il s'isomérise, entraînant un changement de conformation de l'opsine qui active la phototransduction. Un pigment visuel est caractérisé par une courbe d'absorption spécifique, déterminée par la probabilité relative d'absorber un photon incident en fonction de sa longueur d'onde. Chaque pigment a une absorption maximale pour une longueur d'onde spécifique. Dans la plupart des cas, un seul type de pigment est contenu dans un photorécepteur mais il existe quelques exemples où deux types de pigments coexistent au sein d'un même photorécepteur (Firsov et al., 1994; Kitamoto et al., 1998; Neitz & Neitz, 2001). Le nombre de classes de photorécepteurs au niveau de la rétine peut varier de un jusqu'à seize chez certains crustacés stomatopodes (Cronin & Marshall, 1989; Marshall & Oberwinkler, 1999).

Les étapes suivantes sont post-transductionnelles et permettent le codage des informations provenant des photorécepteurs, à l'origine de la sensation colorée. La présence systématique de neurones à simple antagonisme ('single opponent neuron') a été mise en

évidence à différentes étapes du codage spectral chez de nombreuses espèces qui possèdent la vision des couleurs. Ces neurones tiennent leur nom du fait qu'ils répondent à des différences de signaux provenant de plusieurs classes de photorécepteurs pour une aire spécifique de l'espace visuelle (Thompson, 1995). Ils ont ainsi la propriété de pouvoir recevoir les signaux provenant de différentes classes de photorécepteurs. Ils seront excités (ou inhibés) par des signaux d'une ou plusieurs classes dans le centre de leur champ de réception et inhibés (ou excités) par les autres classes dans la périphérie du champ de réception (Thompson, 1995). Ces neurones et leurs mécanismes ont ainsi été caractérisés par exemple dans les ganglions visuels et le protocerebrum de papillons comme *Heliconus*, *Papilio*, *Epargyreus* (Swihart 1968, 1970, 1972a), les neuropiles visuelles de l'abeille *Apis mellifera* (Kien & Menzel, 1977) ou les cellules ganglionnaires rétiniennes et cellules horizontales chez les macaques (Gouras, 1968; De Monasterio & Gouras, 1975; De Monasterio et al., 1975; De Monasterio, 1978). Le codage des informations chromatiques et achromatiques semble donc impliquer des principes communs chez des groupes aussi éloignés que les primates et les insectes, bien que les structures et circuits nerveux diffèrent entre ces espèces. En général, que ce soit pour les primates ou les insectes, le codage chromatique dépend de plusieurs types de cellules nerveuses qui diffèrent dans leur morphologie, leur densité spatiale, leurs connections synaptiques et leurs propriétés physiologiques (Rodieck, 1998; Dacey, 2000). De plus, le codage chromatique emprunte différents circuits nerveux (Menzel & Backhaus, 1991; Dacey, 2000). La présence de plusieurs types de photorécepteurs ayant des sensibilités différentes au niveau de la rétine n'induit donc pas automatiquement la vision des couleurs chez un organisme. En effet, plusieurs étapes neurales post-transductionnelles sont nécessaires pour que les signaux générés au niveau des différents types de photorécepteurs par un stimulus aboutissent à la **sensation colorée** (Kelber et al., 2003). Il est important de noter, que contrairement au codage chromatique qui est basé sur des interactions antagonistes entres signaux provenant de différents types de photorécepteurs, le signal achromatique d'un stimulus repose sur des interactions additives entre un ou plusieurs types de photorécepteurs. Les circuits empruntés pour le codage achromatique semblent quant à eux indépendants de ceux utilisés pour le codage chromatique (Backhaus, 1991; Chittka et al., 1992). Pour conclure, il est primordial d'avoir à l'esprit que si la vision des couleurs est très répandue dans le règne animal, la sensation colorée d'un stimulus est propre à chaque espèce. Dans la suite de la thèse, je préciserai à quelle composante, chromatique ou achromatique, je m'intéresse. Si le terme 'couleur' est utilisé, c'est que je considère les deux composantes à la fois.

Pour ne pas être détectés, les organismes peuvent exploiter certaines de ces étapes. Une des stratégies les plus répandues de camouflage visuel, appelée 'background matching', consiste à avoir un contraste chromatique et/ou achromatique sur un type de substrat qui rend difficile sa détection pour un receveur. Cette stratégie consiste soit à occuper un substrat qui correspond au mieux à ses caractéristiques chromatiques et/ou achromatiques génétiquement fixées, soit à adapter sa couleur à celle de son substrat. Cette dernière capacité se retrouve chez de nombreux taxons de vertébrés et d'invertébrés, et fascine chercheurs et naturalistes depuis des siècles. On distingue deux grands types de changements de couleur réversibles utilisés par les animaux pour se confondre sur leur substrat (Needham, 1974; Stuart-Fox & Moussalli, 2009). Le changement de couleur dit physiologique ou chromomoteur est dû à une dispersion ou une concentration de granules de pigment au sein de structures spécifiques, les chromatophores. Ce type de changement est généralement sous contrôle neuromusculaire ou neuroendocrinien et peut se réaliser en un temps allant de quelques millisecondes à plusieurs heures (Thurman, 1988; Nery & Castrucci, 1997; Messenger, 2001). Un des modèles les plus étudié est la seiche *Sepia officinalis.* Chez ce mollusque, la vitesse du changement et la gamme de couleurs et de patterns spectaculaires dont il peut se parer lui ont conféré le titre de 'master of camouflage' (Mäthger et al., 2006; Hanlon & Warrant, 2007).

Le second type de changement est dit morphologique ou chromogénique, et implique une synthèse de pigment au niveau du derme. Ce type de changement se déroule sur une période plus longue que le changement de couleur physiologique puisque il peut prendre de plusieurs jours à plusieurs mois. Parmi les espèces qui ont un changement de couleur morphologique, on retrouve certaines espèces d'araignées crabe qui font l'objet d'études et d'observations depuis plus d'un siècle, en particulier *Misumena vatia* (Rabaud, 1923; Gabritschevsky, 1927; Weigel, 1941) (**Figure 2**). Cette espèce est assez commune dans l'hémisphère nord et est une des rares espèces d'araignées qui s'est vue consacrer un livre entier sur son écologie (Morse, 2007). *M. vatia* chasse plus ou moins immobile sur les fleurs, attendant que des insectes pollinisateurs passent à proximité pour tenter de les saisir. La particularité de cette espèce est de changer de couleur du blanc au jaune, et inversement, en quelques jours.

Figure 2: Femelle *Misumena vatia* blanche et jaune chassant sur *Heracleum sphondylium* et *Eschscholzia californica*, respectivement.

L'ontogenie du changement de couleur chez cette araignée a été récemment mise à jour. Insausti & Casas (2008, 2009) ont ainsi décrit très précisément l'anabolisme et le catabolisme des pigments responsables du jaunissement de l'araignée, les ommochromes. Ils ont notamment révélé que la formation des ommochromes se déroule en 3 étapes successives, chacune caractérisée par un type de granules ayant des propriétés optiques et des composés spécifiques (Insausti & Casas, 2008). Comme pour l'anabolisme, la catabolisme est un processus progressif. La dégradation débute par l'autolyse des granules contenant les ommochromes. Certains composants sont évacués hors de la cellule et d'autres sont recyclés via l'autophagie. Le catabolisme et l'anabolisme des granules se déroulent simultanément. En effet, il a été trouvé des granules intactes et à différents stades de dégradation au sein d'une même cellule (Insausti & Casas, 2009).

Ce changement de couleur est influencé notamment par la couleur du fond visuel (Weigel, 1941; Théry, 2007). La coloration jaune de l'araignée est ainsi déclenchée par des substrats de couleur jaune. L'araignée sur sa fleur peut générer ainsi des contrastes chromatiques ou achromatiques très faibles pour les observateurs humains, voir indétectables pour les abeilles (Chittka, 2001). Il est fortement suspecté que la coloration de l'araignée sur sa fleur sert donc au camouflage, à la fois défensif et offensif (Théry & Casas, 2009). Cependant, il existe un décalage chez *M. vatia* entre la quantité de travaux sur son écologie, sa physiologie mais aussi sa notoriété en tant qu'experte du camouflage et la connaissance réelle sur le camouflage. En effet, on ne connaît ni les niveaux de contrastes de cette araignée en milieu naturel dans le système visuel des receveurs, ni les mécanismes visuels qui entrent en jeu dans la stratégie de

camouflage. Au début de cette thèse, à ma connaissance, seule l'étude de Chittka (2001) avait abordé de façon rigoureuse le camouflage chez cette espèce.

L'objectif général de cette thèse fut donc d'étudier rigoureusement le camouflage, et de mettre en lien l'écologie du camouflage, sur le terrain, et des approches de physiologie sensorielle. Plus spécifiquement, le niveau de contraste chromatique et achromatique de *M. vatia* sur les fleurs, en milieu naturel, dans la perspective des proies et des prédateurs est quantifié dans le **chapitre 1** de cette thèse. Le **chapitre 2** traite (i) des sensibilités spectrales des différentes paires d'yeux par des méthodes d'électrophysiologie intra- et extracellulaire. Ce chapitre aborde la question de la présence des bases physiologiques nécessaires à la vision des couleurs, (ii) de la présence de préférence colorée chez les premiers stades juvéniles, et (iii) des contrastes chromatiques et achromatiques qui en résultent dans la perspective des proies. Enfin le **chapitre 3** étudie la présence de la vision des couleurs chez *M. vatia* par l'utilisation de biotests comportementaux.

Les résultats de cette thèse sont discutés dans un contexte évolutif et physiologique plus général, intégrant notamment des résultats d'écologie comportementale portant sur l'interaction proies-araignées crabe (Ings & Chittka, 2008; Brechbuhl et al., 2010a, b, c). Nous discuterons des mécanismes sensoriels et de régulation du changement de couleur, puis aborderons la question de l'interprétation fonctionnelle de la coloration chez *M. vatia*, et enfin de l'apport de cette thèse dans le contexte du camouflage chez les prédateurs généralistes. Nous conclurons grâce à nos travaux sur la nécessité dans l'étude du camouflage d'une approche d'écologie sensorielle des communautés.

- CHAPITRE 1 -

Camouflage chez l'araignée crabe *Misumena vatia*: Une perspective d'écologie sensorielle des communautés

Article 1

Background colour matching by a crab spider in the field: A community sensory ecology perspective

Defrize, J., Théry, M. and Casas, J. (2010)
Journal of Experimental Biology, 1425-1435

Abstract

The question of whether a species matches the colour of its natural background in the perspective of the correct receiver is complex to address for several reasons; however, the answer to this question may provide invaluable support for functional interpretations of colour. In most cases, little is known about the identity and visual sensory abilities of the correct receiver and the precise location at which interactions take place in the field, in particular for mimetic systems. In this study, we focused on *Misumena vatia,* a crab spider meeting the criteria for assessing crypsis better than many other models, and claimed to use colour changes for both aggressive and protective crypsis. We carried out a systematic field survey to quantitatively assess the exactness of background colour matching in *M. vatia* with respect to the visual system of many of its receivers within the community. We applied physiological models of bird, bee and fly colour vision, using flower and spider spectral reflectances measured with a spectroradiometer. We observed that crypsis at long distance is systematically achieved, exclusively through achromatic contrast, in both bee and bird visions. At short distance, *M. vatia* is mostly chromatically detectable, whatever the substrate, for bees and birds. However, spiders can be either poorly discriminable or quite visible depending on the substrate for bees. Spiders are always chromatically undetectable for blowflies. We discuss the biological relevance of these results in both defensive and aggressive contexts of crypsis within a community sensory perspective.

Introduction

Crypsis through background matching has been reported for a wide range of animals, including both vertebrates and invertebrates (Marshall, 2000; Ruxton et al., 2004; Mäthger et al., 2008; Stuart-Fox et al., 2008). Background matching is defined as a strategy preventing detection by changing the colour and patterning of the body to match those of the background (Stevens & Merilaita 2009). Many species have been described as cryptic on the basis of human vision but colour contrast, which involves both chromatic and/or achromatic contrasts, has rarely been tested from the perspective of the usual receiver, and in natural conditions (Stevens & Merilaita, 2009). There are several reasons for this lack of data: (i) the correct prey and/or predators of the 'cryptic' organism may not yet be clearly identified, (ii) the assessment of chromatic and/or achromatic contrast(s) in the prey/predator visual system requires knowledge of the physiological basis of both types of contrasts in the species concerned, particularly in terms of the number and nature of the different photoreceptor types.

These physiological works must be supplemented by (iii) behavioural studies, which are also required to determine not only whether true colour vision and colour blind mechanisms are used by an observer but also the colour discrimination thresholds. True colour vision is the ability to discriminate between two lights of different spectral compositions, regardless of their relative intensity (Kelber et al., 2003), and colour discrimination threshold is defined as the lowest contrast between two stimuli that can be detected by an observer. Spectral sensitivities are known for a wide range of species but both true colour vision and colour discrimination thresholds have been studied in detail in only a few species, including bird and bee species (Menzel & Backhaus, 1989; Vorobyev & Osorio, 1998; Hart et al., 2000). Moreover, cryptic animals are rarely caught in the act of either catching prey (for cryptic predators) or escaping detection (for cryptic prey). As a corollary, the location at which the interaction occurs is known only imprecisely and is described in broad, generic terms (e.g. 'rocks', 'grasses' for example). This may be problematic in cases in which the substrate colour and patterns vary over short distances within the range of habitat use of the cryptic species. A survey of the literature shows that, unlike most background-matching species, crab spiders, including the species we will focus on, *Misumena vatia* (Araneae, Thomisidae), meet the criteria for addressing questions of this kind better than many other models (Théry et al., 2010). They are mainly sedentary and are found in large numbers on flowers. Moreover, one of the main prey of the crab spiders such as *M. vatia*, besides flower-visiting flies, is foraging bees (see Table S1 and Table S2 in Appendix), the colour vision of which has been studied in detail.

Misumena vatia has been studied for more than a century, due to their amazing ability to be the same colour as the colour of some of the flowers on which they hunt (Heckel, 1891; Weigel, 1941; Insausti & Casas, 2008; Insausti & Casas, 2009; reviewed in Théry & Casas, 2009). This apparent colour matching is particularly spectacular because it involves a change in the colour of the entire body from white to yellow (and back) over the space of a few days, depending on the colour of the flower (Weigel, 1941; Théry, 2007). It is widely assumed that this apparent flower matching is not only a form of aggressive mimicry against nectar- and pollen-feeding prey but also a form of defensive mimicry, especially against birds. This is an assumption, as exceedingly few bird attacks have been reported so far, despite intense sampling of gut contents (Bristowe, 1971) and decades of long field work (Morse, 2007). Studies with bee physiological vision models recently revealed that *M. vatia* can produce both chromatic and achromatic contrasts well below the discrimination thresholds of their Hymenopteran prey (Chittka, 2001). At first sight, these results are thus consistent with the

above hypothesis of crypsis against prey. However, chromatic and achromatic matching have been quantitatively assessed in *M. vatia* on two flower species only (*Chaerophyllum temulum* and *Senecio vernalis*; Chittka, 2001) and for two individual spiders only. *Misumena vatia* has been however detected on a much wider range of flower species in the field (Heckel, 1891; Rabaud, 1923; Weigel, 1941). Moreover, crab spiders ambush numerous prey species (**Figure 3**), with different visual abilities.

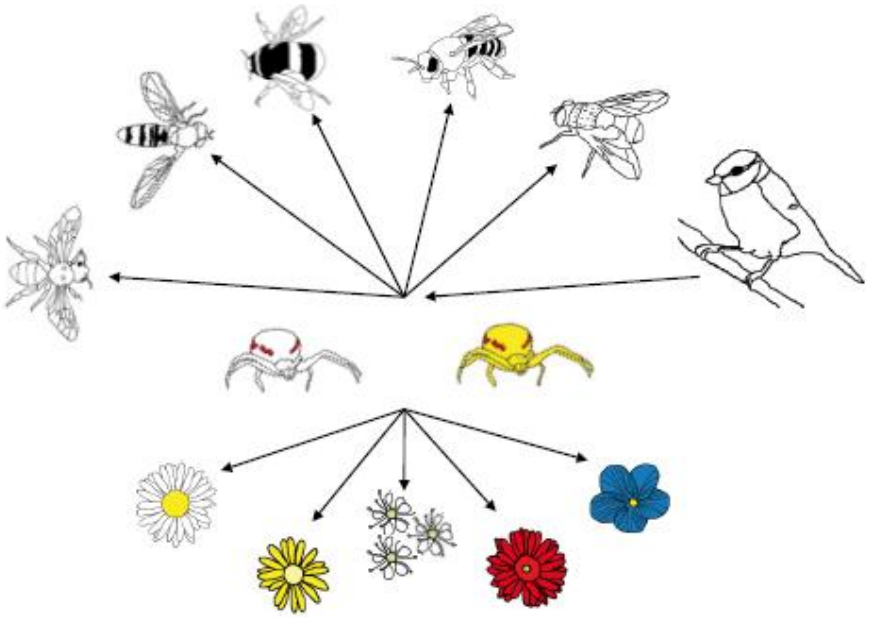

Figure 3: Schematic representation of both multi-substrate and multi-receiver communities considered in this study. From left to right: *Halictus sp.* (solitary bees), *Episyrphus sp.* (Syrphid flies), *Bombus terrestris* (bees), *Apis mellifera* (bees), *Lucilia sp.* (Blowfly) and Blue tit (Passeriformes). At the bottom are represented abstract flower colour types on which *Misumena vatia* can be found.

We therefore carried out a systematic field survey in a given geographical region, using a statistical test, to produce a quantitative assessment of the exactness of the colour matching of *M. vatia* on all flower species on which spiders were observed, with respect to the visual system of not only their main putative predator, insectivorous birds, but also their main prey, bees and flies.

Materials and methods

Spider and flower collection

Juvenile and adult female *Misumena vatia* Clerck 1757 crab spiders were collected from all of the flower species on which *M. vatia* was observed at various sites in the surroundings of Tours (47°20'18" N, 00°42'52" E), France, from April to October, in 2007 and 2008. All of the flowers of each patch were carefully inspected to prevent sampling bias. Once caught, the spiders and the flowers on which they were sitting were placed in a plastic box with a piece of damp cotton wool and transferred to the laboratory. We measured the reflectance of the spiders and the flowers on the same day. We also measured the length of the prosoma to test whether a relationship between the stage of development and the contrasts on the substrate occurred in the field.

Misumena vatia goes through seven juvenile instars, the first of which is spent in the egg sac (Gertsch, 1939). We captured spiders with a prosoma size ranging from 1 mm (fourth juvenile instar) to 3 mm (adults). Total size (prosoma + opisthosoma) varied between 2.5 mm and 12 mm. Second and third instar spiders were not captured, as their abdomen dimensions were smaller than the diameter of the optic sensor. We collected 75 % (110/146) of the spiders studied on 'white' flowers whereas only 18% were caught on 'yellow' flowers and 7% on 'red' and 'blue' flowers. This heterogeneity did not result from a sampling bias. Indeed, large numbers of 'yellow'-flowered species were carefully inspected without the detection of *M. vatia*. Among these 146 spiders, 20 were found only once or twice on a specific flower species. We decided that only flower species on which at least five spiders were found would be included in the analysis. Thus, crypsis in the perspective of the receivers was analyzed on 126 spiders found on 6 flower species. Spiders hunting on *Filipendula ulmaria* Maximowicz 1879 ('Meadow sweet') and *Senecio* sp. ('Ragwort') were collected from homogeneous patches consisting of single flower species whereas spiders found on *Achillea millefolium* L. ('Common yarrow'), *Heracleum sphondylium* L. ('Common hogweed') and *Cleome spinosa* L. ('Spiny spiderflower') were collected from heterogeneous patches, consisting of at least two flower species. *Leucanthemum vulgare* Lamarck 1779 ('Oxeye daisy') was the only plant species from which spiders were collected in both homogeneous and heterogeneous patches. Spiders were caught in 8 different patches. The smallest patch had an area of 20 m x 20 m. All of the spiders collected were found on the flower petals.

Spectroradiometric measurements

We measured the reflectance of both spiders and flowers with a spectroradiometer (Avantes Avaspec 256, Eerbeek, The Netherlands) and a deuterium-halogen lamp (Avantes Avalight D/H-S) emitting light of wavelengths between 215 and 1100 nm. Reflectance was expressed relative to a 99% (300-700 nm) reflectance standard. A reference reading was taken and dark current calibration was carried out before taking the measurements for each spider and each flower. An optic fiber sensor 1.5 mm in diameter and equipped with a quartz window cut at a 45 deg. angle was used. Spiders were anesthetized with CO_2 before recordings of the reflectance spectrum of the abdomen were taken (**Figure 4A**).

Spiders and flowers were placed on a flat mounting stand for measurements. We assessed both chromatic and achromatic contrasts of each spider, by measuring the reflectance of the exact part of the flower on which *M. vatia* was found (**Figure 4B-D**). We obtained three reflectance spectra for each abdomen and for each flower. A mean reflectance spectrum was then calculated for each spider and each flower.

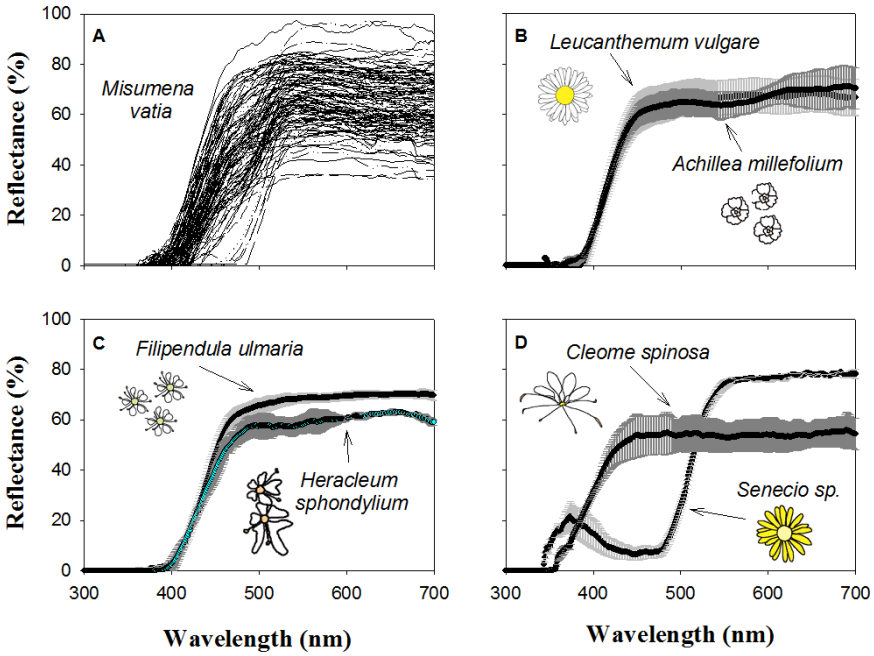

Figure 4: Mean (±s.d.) reflectance spectra of *Misumena vatia* analysed in this study (A), and of the flower species used as substrate by *Misumumena vatia* (B, C, D).

Modeling chromatic and achromatic contrasts in both bee and bird visual systems

We measured the chromatic and achromatic contrasts created by *M. vatia* against its substrate using the physiological model developed by Vorobyev and Osorio (Vorobyev & Osorio, 1998; Vorobyev et al., 2001). The model developed by Chittka (Chittka, 1992) has also been widely used for assessments of the chromatic and achromatic contrasts of crab spiders against their substrates. However, the model of Vorobyev & Osorio (1998) has the advantage of including a powerful colour discrimination threshold, as it includes the total receptor noise. Total receptor noise is the sum of photon ('quantum') noise and internal receptor ('neural') noise. Indeed, this physiological model, based on the observation that the ability to discriminate between colours is limited by total receptor noise, has been shown to predict well the ability to discriminate between colours in animals, including primates, birds and the honeybee *Apis mellifera*. The chromatic and achromatic contrasts between two spectra are measured in units of just noticeable difference (JND). A value of 1 JND between two spectra corresponds to the discrimination threshold under ideal conditions and under which two spectra are considered to be indistinguishable (Wyszecki & Stiles, 1982). The relationship between noise level and light intensity is however not linear (Anderson and Laughlin, 2000; Vorobyev et al., 2001), and this model does not incorporate physiological mechanisms that may affect colour discrimination such as spatial and temporal summation (Dyer & Neumeyer, 2005). Despite these shortcomings, Vorobyev and Osorio' model remains the most efficient colour vision model to date. In the following, we present the colour computation in the bee visual system first, followed by the bird vision system. The fly colour vision model, which is very different, is presented last.

The quantum catch Q for a given spectra in the respective photoreceptor *i*, is calculated as

$$Qi = \int_{300}^{700} Ri(\lambda)S(\lambda)I(\lambda)d\lambda \qquad (1)$$

where R*i* is the spectral sensitivity function of the Ultraviolet (UV), Blue (B) and Green (G) receptors for trichromatic bees with sensitivity peaks at 340nm, 435nm and 540nm, respectively (Peitsch et al., 1992). We used bee templates to obtain absorption curves (Stavenga et al., 1993). S(λ) is the spectral reflection function of spiders or substrates and I(λ) is the illuminating daylight spectrum (CIE D65). Here we assume that almost all visual interactions occur in sunny daylight.

The colour distance ΔS, in JND units, between each spider and its flower, for the trichromatic eyes of bees, is given by

$$(\Delta S)^2 = \frac{E_{UV}^2 (\Delta f_G - \Delta f_B)^2 + e_M^2 (\Delta f_G - \Delta f_{UV})^2 + e_L^2 (\Delta f_{UV} - \Delta f_B)^2}{(e_{UV}e_B)^2 + (e_{UV}e_G)^2 + (e_B e_G)^2} \quad (2)$$

where e_i is the internal receptor noise for each receptor class i of bees (UV, B, G) and Δf_i is the natural log of the quantum catches for receptor i (UV, Blue and Green for bees) between spiders ($_{Sp}$) and flowers ($_F$)

$$\Delta f_i = \ln (Q_{iSp} / Q_{iF}) \quad (3)$$

Crab spider-prey interactions occur in conditions of high light intensity and a large proportion of spiders were found on bright 'white' and 'yellow' flowers. Internal receptor noise is thought to predominate at high light intensity (Vorobyev et al., 2001). The internal receptor noise, $e_{i,}$, is calculated as

$$e_i = \omega / \sqrt{\eta_i} \quad (4)$$

where ω is the Weber fraction assigned to each receptor class (0.13; Vorobyev & Osorio, 1998), and η_i is the relative density of the receptor class i of bees. Within a honeybee eye, ommatidia do not contain similar sets of photoreceptors. Wakakuwa et al. (2005) indeed found three types of ommatidia containing either one UV, one B and six G receptors (Type I), or two UV, one B and six G receptors (Type II), or one UV, two B, and six G receptors (Type III). They also revealed that the ratio of the Type I, II, III was 44:43:10 (Wakakuwa et al., 2005). Moreover, Spaethe and Briscoe showed that this heterogeneity also occurs in bumblebees (Spaethe and Briscoe, 2005). We thus used the ratio of 1:0.471:4.412 for all bees (for UV, B and G receptors respectively). This ratio takes into account both the ommatidia heterogeneity and the ratio of Types I, II, III.

Chromatic contrast is the dominant cue used by foraging bees for the identification of flowers at short distance, when a flower subtends a visual angle of at least 15 deg. (Giurfa et al., 1996). However, at long distance, when a flower subtends a visual angle between 5 deg. and 15 deg., honeybees and bumblebees use green contrast for flower detection, looking for a difference between background and target green receptor signals (Giurfa et al., 1996; Spaethe et al., 2001).

The green contrast between a spider and its flower can be calculated as

$$\Delta S_G = \Delta f_G / e_G = \ln (Q_{GSp}/Q_{GF}) / e_G \qquad (5)$$

in which S_G is the spectral sensitivity of the L-wavelength photoreceptor of bees. Δf_G is the natural log of the quantum catch (Q) for the Green ($_G$) receptor class between spider ($_{Sp}$) and flower ($_F$). Q_{GSp} and Q_{GF} are the quantum catch (Q) for a spider ($_{Sp}$) and a flower ($_F$) spectrum, respectively, in the Green ($_G$) receptor class of the bees. e_G is the internal receptor noise of the Green ($_G$) receptor class of bees.

For bird colour vision, we used the spectral sensitivities of the tetrachromatic insectivorous blue tit *Cyanistes caeruleus*, taking into account visual pigment, oil droplet and ocular media transmittances (Hart et al., 2000; Hart, 2001). Spectral sensitivities functions were taken directly from avian templates generously provided by Doris Gomez. The presence of blue tits has been reported in the meadows around Tours (Théry et al., 2005).

We measured the quantum catch (see equation 1) for a given spectrum in the ultraviolet sensitive (UVS), short-wavelength sensitive (SWS), medium-wavelength sensitive (MWS) and long-wavelength sensitive (LWS) photoreceptors of blue tits, as we did for bees.

The colour distance ΔS between each spider and flower for the tetrachromatic eyes of birds is given by

$$(\Delta S)^2 = ((e_{UVS}e_{SWS})^2(\Delta f_{LWS} - \Delta f_{MWS})^2 + (e_{UVS}e_{MWS})^2 (\Delta f_{LWS} - \Delta f_{SWS})^2 + (e_{UVS}e_L)^2 (\Delta f_{SWS} - \Delta f_{MWS})^2 + (e_{SWS}e_{MWS})^2 (\Delta f_{LWS} - \Delta f_{UVS})^2 + (e_{SWS}e_{LWS})^2 (\Delta f_{MWS} - \Delta f_{UVS})^2 + (e_{MWS}e_{LWS})^2 (\Delta f_{SWS} - \Delta f_{UVS})^2) / ((e_{UVS}e_{SWS}e_{MWS})^2 + (e_{UVS}e_{SWS}e_{LWS})^2 + (e_{UVS}e_{MWS}e_{LWS})^2 + (e_{SWS}e_{MWS}e_{LWS})^2) \qquad (6)$$

where e_i is the internal receptor noise for each receptor class *i* of birds (UVS, SWS, MWS and LWS) and Δf_i is the natural log of the quantum catches for receptor *i* (UVS, SWS, MWS and LWS) between spiders (Sp) and flowers (F) (See equation 3). The relative density of the receptor class *i* taken from *Pareus caeruleus* was 1, 1.92, 2.68 and 2.7 for UVS, SWS, MWS, LWS photoreceptors, respectively (Maier & Bowmaker, 1993). We also achieved the calculations with different photoreceptor ratios [1, 2, 2, 4 (Schaefer et al., 2007); 1, 1, 1, 2 (Lind and Kelber, 2009)] to assess how sensitive the results are to this choice.

For the receptor noise value in birds, we proceeded as Schaefer et al. (2007). Our reasoning was that not only (i) are the noise levels in avian photoreceptors still unclear (Lind & Kelber, 2009), but also that (ii) the absolute value of noise varies quite a lot, depending on the viewing conditions (Ghim & Hodos, 2006; Schaefer et al., 2007; Harmening et al., 2009). We thus performed calculations with several values of Weber fraction. Increase of the Weber fraction results in a corresponding increase of the threshold value in JND. The lowest Weber fraction was estimated as 0.1 from behavioural data (Maier & Bowmaker, 1993) and corresponds to a threshold of 1 JND. Because noise above 0.5 is physiologically implausible, we assumed that Weber fraction can increase up to 0.5, which corresponds to a threshold of 5 JNDs. We assumed that spiders with a contrast against their substrates higher than 5 JNDs can always be detected.

Birds use also achromatic contrast at long range (Osorio et al., 1999a, b), through double-cones. Thus, the achromatic contrast between a spider and its substrate is then measured as

$$\Delta S_{DC} = \Delta f_{DC} / e_{DC} = \ln (Q_{DC\text{-}Sp}/Q_{DC\text{-}F}) / e_{DC} \qquad (7)$$

in which S_{DC} is the spectral sensitivity of the double-cone photoreceptors of birds. Δf_{DC} is the natural log of the quantum catch for the double cone ($_{DC}$) receptor class between spider ($_{Sp}$) and flower ($_{F}$). $Q_{DC\text{-}Sp}$ and $Q_{DC\text{-}F}$ are the quantum catch (Q) for a spider ($_{Sp}$) and a flower ($_{F}$) spectrum, respectively, in the double cone ($_{DC}$) receptor class of the birds. e_{DC} is the internal receptor noise of the double cone ($_{DC}$) receptor class of birds. Chromatic and achromatic contrasts were calculated with Avicol© software (Paris, France; available upon request from D. Gomez at dodogomez@yahoo.fr) (Gomez and Théry, 2007).

We plotted the position of each flower and spider in the chromaticity diagram of both bees and birds, following the calculation given in Kelber et al. (2003). Trichromatic bees have a two-dimensional chromaticity diagram (**Figure 5a, b**) whereas it is three-dimensional for tetrachromatic birds (**Figure 5c, d**).

We also performed a more complex analysis using an assumption about bird vision which is natural but will need further testing. Studies have shown that the contrast threshold of birds is strongly affected by viewing conditions, especially the spatial frequency of the stimuli (Ghim and Hodos, 2006; Harmening et al., 2009). Indeed, contrast sensitivity functions display an inverted-U shape (Ghim & Hodos, 2006; Harmening et al., 2009). In the case of the motionless *M. vatia*, each spatial frequency corresponds to a specific distance at

which birds observe spiders. These studies thus provide contrast threshold according to a wide range of distances. However, contrast thresholds are given in 'Michelson contrast' values that cannot be used in the model developed by Vorobyev et al. (2001). Using a method described below, we thus transformed contrast threshold values into Weber fractions that can be integrated into the model developed by Vorobyev et al. (2001).

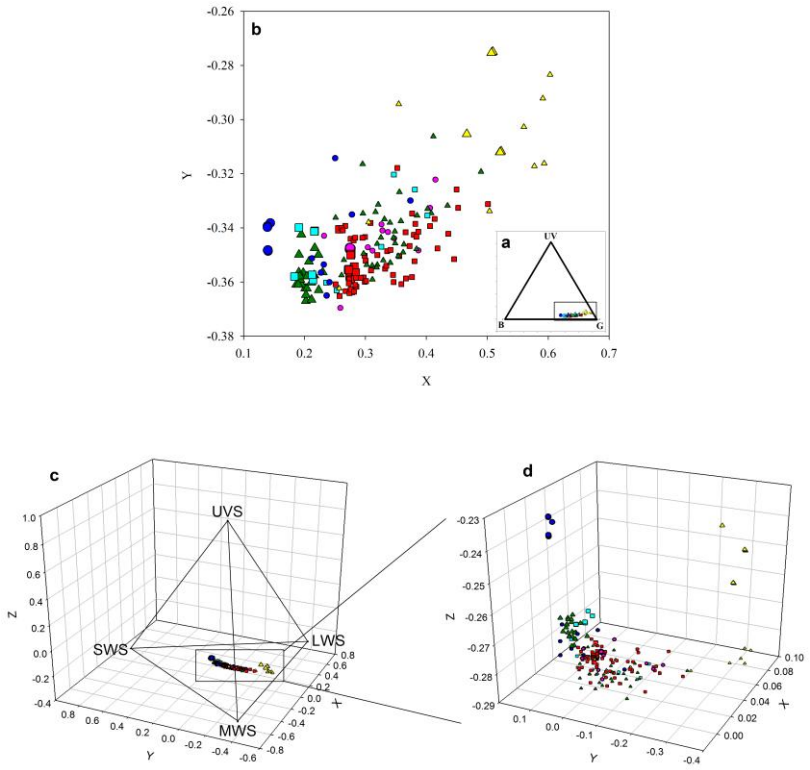

Figure 5: (a, c) Distribution of spider and flower colour loci on the chromaticity diagram of bees (a) and birds (c). (b, d) Selected enlarged area. Each small coloured symbol represents a spider found on a flower species (larger symbol). Pink circles indicate spiders found on *Heracleum sphondylium*, red squares indicate spiders found on *Filipendula ulmaria*, green triangles indicate spiders found on *Leucanthemum vulgare*, blue squares indicate spiders found on *Achillea millefolium*, blue circles indicate spiders found on *Cleome spinosa*, yellow triangles indicate spiders found on *Senecio* sp. UV= Ultraviolet, B= Blue, G= Green. UVS= Ultraviolet Sensitive, SWS= Short-Wavelength Sensitive, MWS= Medium-Wavelength sensitive and LWS= Long-Wavelength Sensitive.

We first determined the contrast discrimination threshold (the inverse of contrast sensitivity) for each distance from a bird to a spider. Generally, the contrast discrimination threshold for a given spatial frequency corresponds to the lowest Michelson contrast (luminance max – luminance min) / (luminance max + luminance min) at which maximum

contrast sensitivity occurs. In the starling, the maximum contrast sensitivity has a Michelson contrast value of 16% for 1.1 cycles deg.$^{-1}$ (Ghim & Hodos, 2006). We created two spectral reflectance curves that display not only a Michelson contrast of 16% but also a LWS receptor contrast equal to 16%, because Weber fraction are often calculated from LWS class cone (Vorobyev et al., 1998).

We assumed that these two spectra computed with the 'limiting Weber fraction' in Vorobyev and Osorio's model (1998) should have an achromatic contrast equal to 1 JND. Thus, by identifying the 'Weber fraction' that allows us to get an achromatic contrast between these two spectra equal to 1 JND, we also identify the 'limiting Weber fraction' at which the maximum contrast sensitivity occurs (16%). In this study, we used the maximum contrast sensitivity of the starling (16% at 1.1cycles deg.$^{-1}$), as no such data exist for *Cyanistes caeruleus*.

We estimated the most relevant range of 'Weber fraction' to use by referring to contrast threshold values computed in the starling *Sturnus vulgaris* (Passeriformes) (Ghim and Hodos, 2006). Following the same steps as above, we also calculated the weber fractions at the lowest (0.3 cycles deg.$^{-1}$) and highest (7cycles deg^{-1}) spatial frequencies at which the lowest contrast sensitivities occurs. We thus found a set of 'Weber fractions', ranging from 0.2 to 0.5, which is close to the range used by Schaefer et al. (2007). On the basis of an 8mm size for spiders, we finally assessed the distance of birds to spiders corresponding to each spatial frequency.

Assessing chromatic contrast in the fly visual system

Classical colour vision models used for bees or birds do not fit the vision of flies, despite good knowledge of spectral sensitivities of several flies species (Horridge et al., 1975; Hardie, 1979; Hardie & Kirschfeld, 1983; Bernard & Stavenga, 1979), and receptor noise value of fly photoreceptors involved in the colour vision process (Anderson and Laughlin 2000). Indeed, whereas bees and birds display a continuous colour vision, Troje (1993) showed that the flower-visiting blowflies *Lucilia* sp. possesses a categorical colour vision. For this species, the wavelength spectrum consists of four categories (UV, Blue, Yellow and Purple). *Lucilia sp.* discriminated monochromatic lights belonging to different categories. However, no discrimination occurs within a category. Troje (1993) proposed a colour opponent mechanism that matches its result well. Despite the fact that this model needs to be further tested and improved, we use it because (i) it is, to our knowledge, the single one available for any fly,

(ii) it is based on behavioural experiments and (iii) *Lucilia* sp. is a flower-visiting species that may suffer predation by crab spiders.

This model involves four types of central photoreceptors, named R7p, R7y, R8p and R8y, with a peak at 341, 362, 465 and 537nm respectively (Hardie & Kirschfeld, 1983). The model consists of two subsystems made of the pairs R7p/R8p and R7y/R8y, R7 and R8 being antagonistically connected in each one. The differences R7 – R8 gives input to a threshold mechanism such that each subsystem can have one of the two values (+, -). Each combination of values (+/+, +/-, -/+, -/-) corresponds to a specific category. For each stimulus, we thus calculated the differences 'R7p-R8p' and 'R7y-R8y'. Two stimuli eliciting the same combination of values are considered as similar for *Lucilia* sp.

The quantum catch for a given spectrum in the respective fly photoreceptors is calculated as in equation 1 (see above) and spectral sensitivities of *Lucilia* sp. are taken from Hardie & Kirschfeld (1983). We used templates fitted to *Lucilia*' spectral sensitivities (Stavenga et al., 1993). We did not compute the achromatic contrast for blowflies, as nothing is known about this aspect in flies.

Is perfect chromatic matching due to chance only?

We investigated whether perfect chromatic matching (JND<1) on the whitish *F. ulmaria* (harboring the largest number of spiders) was due to chance alone, by first calculating the chromatic discriminability, against *F. ulmaria,* of the spiders found on other flower species. We then compared the proportion of undetectable spiders in the simulated spider-*F. ulmaria* pairs with the proportion of undetectable spiders actually found on *F. ulmaria*. We assumed that if the observed matching was due to chance alone, the proportions of undetectable spiders would be similar in both sets of spiders. Thus, in this case, spiders hunting on flower species other than *F. ulmaria* would have matched *F. ulmaria* petals equally well as spiders hunting on *F. ulmaria*. A mean colour spectrum of *F. ulmaria* was used to measure chromatic contrast in the two sets of spiders. The same protocol was tested with the whitish *H. sphondylium*, the flower species harboring the second largest number of spiders.

Statistical analysis

We used various statistical tests to compare mean contrast values with chromatic and achromatic discrimination thresholds for bee and bird colour visions. We first tested the normality of distributions, using the Shapiro test, and then performed one-sample t-test for normally distributed variables and the non-parametric rank sign test for variables with non

normal distributions. We also assessed whether the proportions of perfect chromatic matching between two distributions were similar using a normal approximation of the chi-square test. All statistical analyses were performed with R and Statistica (Statsoft France, France).

Results

Chromatic and achromatic contrast values for bees

We observed no correlation between the stage of spider development and both the chromatic and achromatic contrast values (R^2=0.0221, p=0.14 and R^2=0.034, p=0.10, respectively; N=126). We analyzed the chromatic and achromatic discriminabilities using first the mean contrast values. The mean chromatic contrast values are above the discrimination threshold (1 JND) (t-test, p<0.01 for *H. sphondylium*; sign test, p<0.001 for *F. ulmaria*; sign test, p<0.001 for *L. vulgare*; t-test, p<0.01 for *A. millefolium*; t-test, p<0.001 for *C. spinosa*; sign test, p<0.01 for *Senecio* sp.) (**Figure 6a**). Mean achromatic discriminability values for the spiders did not significantly exceed the discriminability threshold value (1 JND) in honeybees (sign tests: p=0.86, p=0.17, p=0.11, p=0.74 for *H. sphondylium, F. ulmaria, L. vulgare* and *Senecio* sp., respectively; t tests: p=0.84, p=0.13 for *A. millefolium*, *C. spinosa*, respectively). Thus, *M. vatia* would not be detected by the green receptor of bees at long range (**Figure 6b**). To sum up the results for mean contrast values, we show that spiders always appear detectable at short range but undetectable at long distance for bees.

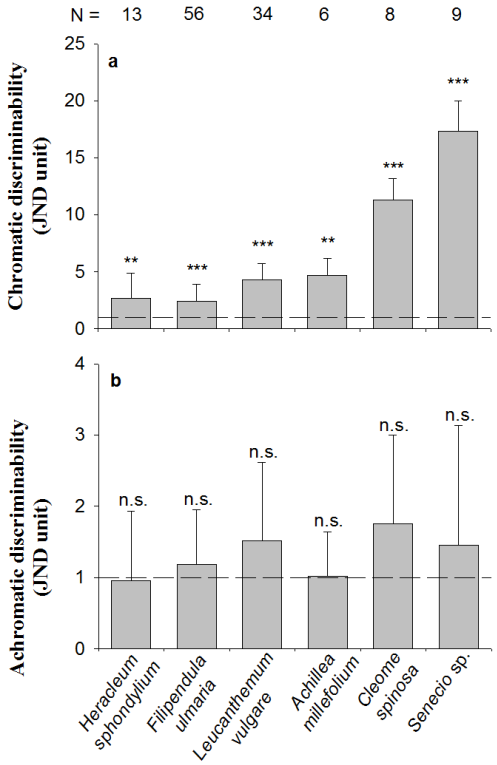

Figure 6: Mean (± SD) chromatic (a) and achromatic (b) discriminability, measured in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for the trichromatic prey, bees. Horizontal dashed lines indicate the threshold for crypticity in the bee's visual system. Note the difference in scale on the Y axis of the two graphs. n.s. = non significant. ** = p<0.01, *** = p<0.001.

If we consider individual chromatic contrast between pairs (**Figure 7**), the situation is more complex than that described above on the basis of mean values. Spiders may be either perfectly cryptic (undetectable spiders have values that are <1 JND) or poorly discriminable (pairs with values between 1 and 4 JNDs) on *H. sphondylium* (23% and 61% respectively) or *F. ulmaria* (19% and 71% respectively). On *L. vulgare*, *A. millefolium*, *C. spinosa* and *Senecio* sp., respectively 47 %, 33%, 0%, 0% of pairs produce values between 1 and 4 JNDs but no perfect chromatic matching was observed. All spiders hunting on *C. spinosa* and *Senecio* sp. appear quite visible (JND > 4) for bees.

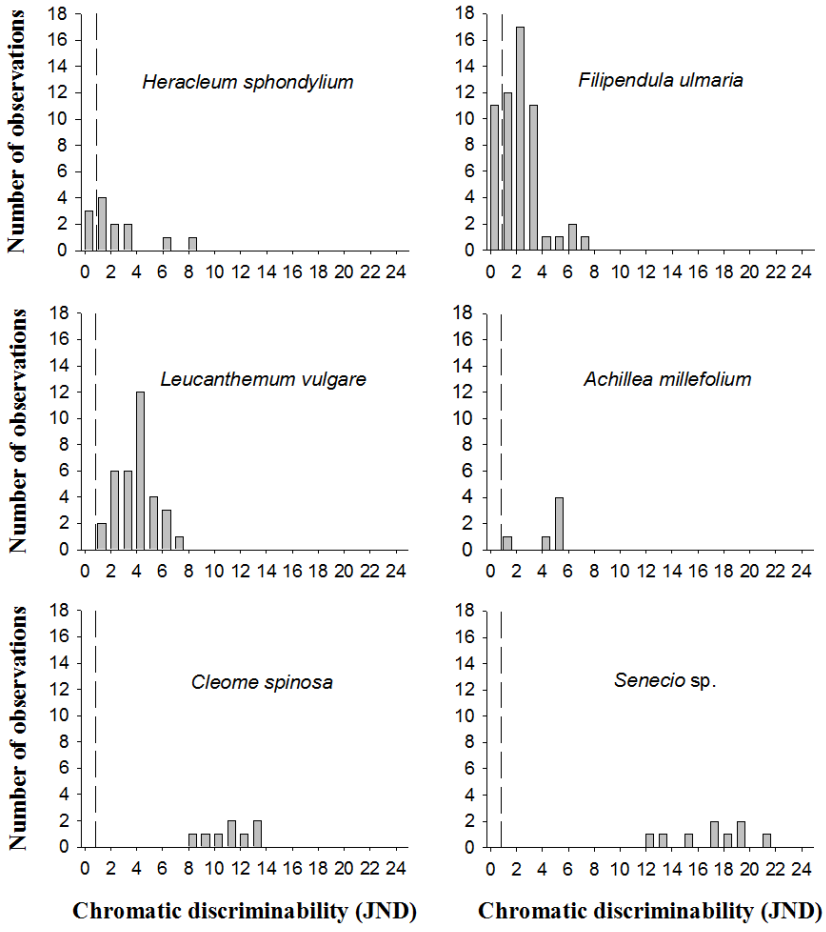

Figure 7: Individual chromatic discriminability distribution, in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for bee vision. Vertical dashed lines indicate the threshold for crypticity in the bee visual system.

A similar analysis with achromatic contrast distributions revealed low levels of variability in individual pairs (data not shown) and a larger proportion of spiders near the discrimination threshold of bees (0<JND<4) (100%, 100%, 97%, 100%, 87%, 88% for *H. sphondylium, F. ulmaria, L. vulgare, A. millefolium, C. spinosa* and *Senecio* sp., respectively), in contrary to what was found for chromatic contrast.

Finally we observed no difference in the degree of contrast between spiders hunting on a given species in either homogeneous or heterogeneous floral patches.

Chromatic and achromatic contrast values for birds

Our results revealed that, at short distance, *M. vatia* can be always chromatically detected on *L. vulgare, A. millefolium, C. spinosa* and *Senecio* sp. by birds, as their mean chromatic contrasts are significantly higher than 5 JNDs ($p<0.01$, t test, for *A. millefolium*; $p<0.001$ for *L. vulgare*, *C. spinosa*, t tests and for *Senecio* sp., sign test). Spiders hunting on *H. sphondylium* and *F. ulmaria* will be also detectable, except if receptor noise reaches values of 0.45 ($p=0.051$ for *H. sphondylium*, t test and $p=0.13$ for *F. ulmaria*, sign test) (**Figure 8a**). At long distance, we observed that *M. vatia* is achromatically undetectable whatever the flower species and the value of noise. Indeed, mean achromatic contrasts did not differ significantly from 1 JND (**Figure 8b**).

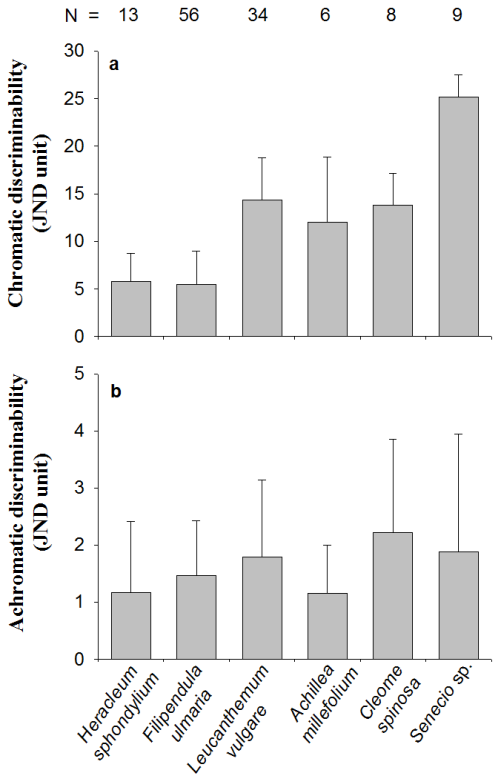

Figure 8: Mean (± SD) chromatic (a) and achromatic (b) discriminability, measured in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for a tetrachromatic passerine bird. JNDs of 1 to 5 represent the range of most likely threshold values obtained in the literature.

Individual chromatic contrast values allowed us to confirm that on each flower, a high proportion of spiders are always chromatically detectable (higher than 5 JNDs) (53%, 48%, 94%, 83%, 100% and 100% for *H. sphondylium*, *F. ulmaria*, *L. vulgare*, *A. millefolium*, *C. spinosa* and *Senecio* sp., respectively) (**Figure 9**). All of these conclusions remained valid when calculations are performed with different photoreceptor ratios (1, 2, 2, 4 and 1, 1, 1, 2 for UVS, SWS, MWS, LWS, respectively).

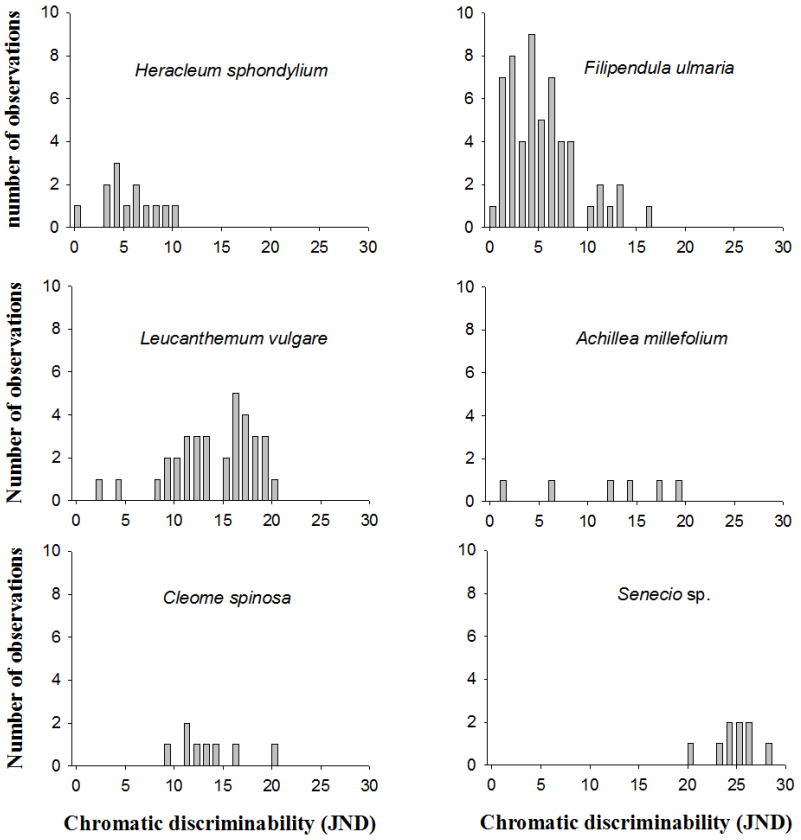

Figure 9: Individual chromatic discriminability distribution, in just noticeable differences (JNDs), for *Misumena vatia* against different flower species for bird vision.

We obtained similar results when taking into account the distance at which birds forage (**Figure 10**). Indeed, *M. vatia* is detectable at short distance through chromatic signal. However, we noticed that this chromatic contrast is quite dependent of the foraging distance. On all of the flower species, *M. vatia* is most conspicuous when birds are 50 cm away from spiders. At very short distance (16 cm) at which chromatic signal should be used, we

observed that *M. vatia* is always detectable. At the opposite, *M. vatia* is always achromatically undetectable whatever the distance at which it is observed by birds, especially at long distances when achromatic signals are most relevant.

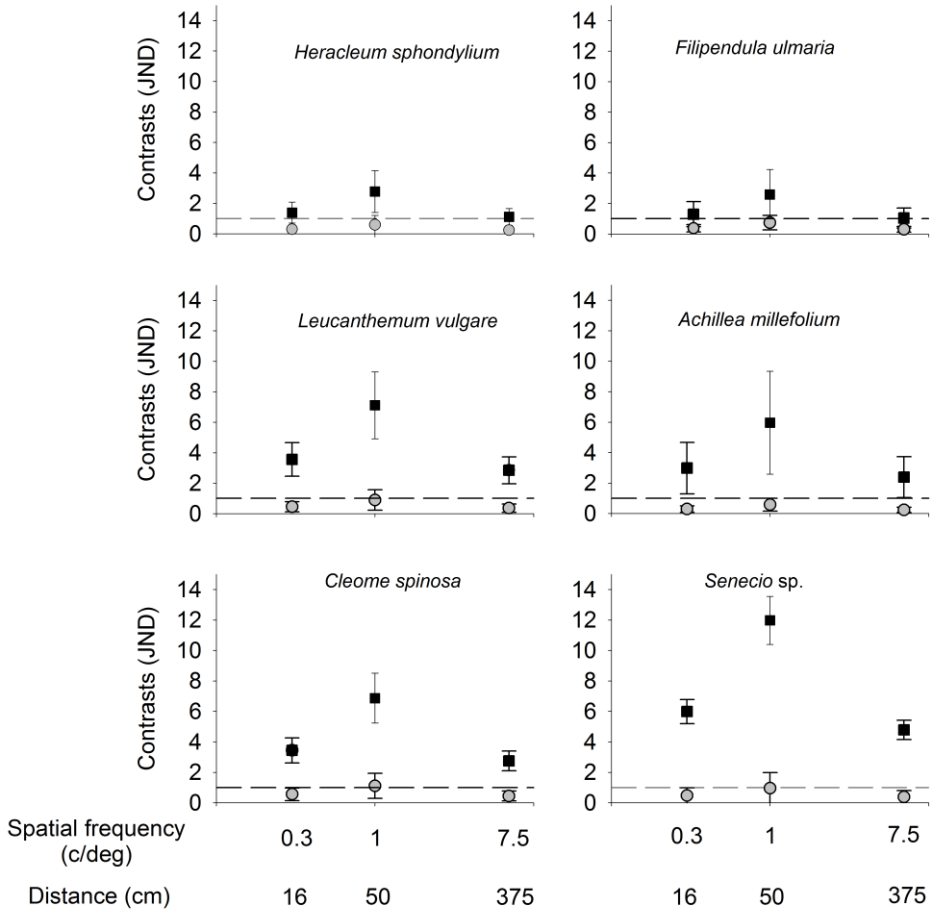

Figure 10: Mean (± s.d.) chromatic (black squares) and achromatic (grey circles) contrasts of spiders against different substrates in the perspective of birds, according to different spatial frequencies. On the basis of 8 mm long spiders, we also assessed the distance of birds to spiders corresponding to each spatial frequency. A logarithmic scale is used for the *x*-axis.

Chromatic contrast in the fly visual system

Using the colour opponent model developed by Troje (1993), we found that all spiders would appear cryptic for *Lucilia* sp., both spiders and substrates being ranked as (+/+) in the fly vision (N=126).

Proportions of perfect chromatic matching for simulated spider-flower pairs in bee visual system

We showed that perfect chromatic matching occurred in assessments of the chromatic contrast of spiders found on different flower species against petals of *F. ulmaria*. The proportion of matching did not differ significantly between spiders actually hunting on *F. ulmaria* and spiders initially found on the flowers of other species and then randomly assorted to *F. ulmaria* (11/56 and 12/70, respectively, d.f.=124, p=0.77). Similar proportion of undetectable spiders were also obtained between spiders initially hunting on *H. sphondylium* in assessments of the chromatic discriminability of spiders found on other flower species with respect to those on *H. sphondylium* (3 cryptic spiders out of 13 and 20/113, respectively, d.f.=124, p= 0.59).

Discussion

We observed that crypsis at long distance is systematically achieved, exclusively through achromatic contrast, in both bee and bird visions. At short distance, *M. vatia* is mostly chromatically detectable whatever the substrate for bees and birds. However, spiders can be either poorly discriminable or quite visible depending on the substrate for bee (**Tableau 1**).

	Short distance		Long distance	
	Chromatic contrast	Achromatic contrast	Chromatic contrast	Achromatic contrast
Bees	Mostly detectable	⊘	⊘	Undetectable
Blowfly	Undetectable	?	?	?
Blue tits	Mostly detectable	⊘	⊘	Undetectable

Tableau 1: Detectability of *Misumena vatia* according to the distance at which it is perceived for different visual observers. Cross circles indicate no neurophysiological relevant situations. Interrogation points indicate that there is a lack of study allowing to fill in the boxes. Distances are relative distances. However, for honeybees, calculations allow to determine that an 8 cm diameter flower would be identified with chromatic signal until a distance of around 30 cm. For foraging distances higher than 30 cm, honeybees will identify flower with achromatic (green) signal.

Indeed, *M. vatia* hunts sometimes on flowers on which it yields a high chromatic contrast for bee vision whereas other flowers provide substrate on which perfect chromatic crypsis can be achieved. The same trend was already suggested using Chittka's model but with two spider individuals only (Chittka, 2001). We show that these perfect matchings (JND<1) result from a purely random process, implying no particular local adaptation of the spiders to their flowers. This explains the small number of perfectly cryptic spiders observed in this study. A model proposed that colouration in a visually heterogeneous habitat can be optimized by either finding a compromise in the degree of crypsis between microhabitats or by increasing the degree of crypsis in one of the microhabitats at the expense of another (Merilaita et al., 2001). Here, we noticed that it is unlikely that the resulting colouration of *M. vatia* is a form of crypsis optimized for visually heterogeneous environments. Unlike for bees and passerine birds, chromatic crypsis seems to be always achieved for the blowfly *Lucilia* sp. In the following, we focus on both the chromatic and achromatic contrasts elicited by *M. vatia* and discuss their biological relevance in defensive and aggressive mimicry contexts.

Is crypsis at long distance sufficient to avoid bird attacks?

Our results suggest that the detectability of *M. vatia* through chromatic signal varies according to the distance at which passerine birds forage. *Misumena vatia* appears chromatically visible at short distance for insectivorous passerines on the substrate on which it sits. Despite this chromatic conspicuousness, the predation pressure from birds on *M. vatia* is very low. Indeed, Morse (2007) has not recorded any case of bird predation in 30 years of intensive field research on crab spiders. Moreover, Bristowe's (1971) records of over 10 000 spiders eaten by birds from sampling their stomach contents contain only four *M. vatia*, a very low number. Thus, these observations indicate that the lack of predation cannot be explained by vision at short distance. This raises the question whether bird attacks are low because birds are actually avoiding visible *M. vatia* or because protection is efficiently achieved through achromatic crypsis at long distance? Answering this question will require us not only to quantify the range of visual angles at which chromatic signals are used but also to relate the foraging paths taken by birds in the vegetation to the positions of their prey.

Are M. vatia *under selection by prey for crypsis?*

Bees, when reaching a new patch, detect flowers first through the achromatic signal (Spaethe et al., 2001), according to the visual angle at which chromatic vision may occur [>15 deg. in

honeybees (Giurfa et al., 1996)] and their spatial resolution (2.8 deg. x 5.4 deg. in honeybees: 5 deg. in bumblebees) (Autrum & Wiedemann, 1962; Eheim & Wehner, 1972; Meyer-Rochow, 1981). However, within a patch, bumblebees forage with a flight height ranging from 23 mm to 50 mm, depending on the flower diameter (Spaethe et al., 2001). From these data, it is likely that both chromatic and achromatic contrasts elicited by spiders are noticed by prey.

Other crab spider species have been reported to be either chromatically cryptic on a substrate in the perspective of bees, as for *Thomisus onustus* (Théry & Casas, 2002; Théry et al., 2005), or achromatically cryptic, as for the Australian crab spider *Thomisus spectabilis* (Heiling et al., 2005). However, there is a lack of knowledge about the role of the chromatic and achromatic crypsis in the prey capture rate and survival rate against birds. Indeed, despite the growing number of studies using crab spider-prey interactions, there is not yet any evidence, for any prey, that decreasing chromatic and/or achromatic contrasts provides the spider with a benefit in terms of predation efficiency (Gonçalves-Souza et al., 2008; Yokoi & Fujisaki, 2009; Brechbühl et al., 2010a; Brechbühl et al., 2010b). These studies however revealed that the way prey behave in response to a crab spider is not only species specific but also individual specific. We discuss these aspects in turn.

Some species of solitary bees and syrphid flies have been reported to be deterred by the presence of *M. vatia* (Brechbühl et al., 2010b), *Thomisus labefactus* (Yokoi and Fujisaki, 2009), *Xysticus* species (Brechbühl et al., 2010a) and an artificial *Misumenops argenteus* (Gonçalves-Souza et al., 2008). Syrphid flies *Sphaerophoria* spp., for instance, show a 100% flower rejection rate when flowers on which a spider sits are presented to them (Yokoi and Fujisaki, 2009). However, the lack of information about levels of contrasts and the relative importance of chromatic cues in these anti-predatory behaviours precludes us to conclude about any gain in being chromatically and achromatically cryptic.

The evidence for selection for crypsis is also lacking when discussed from the honeybee and bumblebee point of view, for which it is relatively easy to assess the degree of contrasts, and for which it has been shown that flower chromatic cues affect visitation rates (Lunau et al., 1996). In these species, predator-avoidance learning has been shown to modulate the level of predator detection. While naive bumblebees *Bombus terrestris* visit white flowers harboring a ‘white’ or ‘yellow’ artificial *M. vatia* at the same rate, those having suffered several unsuccessful spider attack can increase inspection times and display false alarms (erroneous rejection of flowers without predators), both decreasing their foraging efficiency (Ings & Chittka, 2008). Increased level of detection in bees suggests that crypsis

could be beneficial. However, not only false alarms but also the fact that some bumblebees and honeybees decide to leave the patch of flowers after several spider attacks (Dukas & Morse, 2003; Dukas & Morse, 2005), induce a loss of available prey, even for poorly discriminable spiders. Moreover, recent field experiments which do not take into account the 'learning state' of visiting bees suggested that the selective pressure of learning on crypsis may be less important than expected. Indeed, the number of honeybees and bumblebees visiting flowers with a highly chromatically contrasting *M. vatia* is similar to flowers without spiders (Dukas & Morse, 2003; Brechbühl et al., 2010b). Thus, the proportion of experienced bees efficiently avoiding crab spider may be too low to significantly impact the encounter rate and to drive the spider colouration towards crypsis.

Why then do spiders choose flowers on which they yield a high chromatic contrast? *Misumena vatia* will systematically produce high chromatic contrast on several floral reflectance types due to its inability to cover the entire flower colour spectrum, particularly the UV range (Herberstein et al., 2009). However, *M. vatia* can be found hunting on UV-reflecting flowers, such as *Cleome spinosa* and *Senecio* sp. Nothing is known about *M. vatia'* spectral sensitivities and whether a UV contrast may also act as an attractive stimulus for honeybees, in a similar fashion as the UV reflecting Australian crab spider *Thomisus spectabilis* hunting on UV absorbing flowers (Heiling et al., 2005; Bhaskara et al., 2009). Lunau et al. (1996) showed that bees innately prefer flowers with strongly contrasting markings. So, whether conspicuous colouration may be an alternative to crypsis on some substrate for an efficient predation is still unknown.

Conclusions

This spider has been assumed to be chromatically cryptic for more than a century. We show here, through a quantitative study carried out in the field, that the degree of chromatic contrast is quite dependent of the receiver and the substrate on which *M. vatia* sits. These results raise concerns about drawing conclusions based on human visual assessments. They also highlight the importance of studying background matching, in the field, from the sensory ecology of all main receivers. For generalist predators, a visual ecology community perspective seems mandatory before statements on adaptation of crypsis can be issued. This endeavour also leads to the identification of major gaps in our knowledge, such as the neuroethology of colour vision in flower-visiting flies, in particular the abundant syrphid flies (Brechbühl et al., 2010b), and of the crab spiders themselves.

Acknowledgments

We thank Doris Gomez for providing Avicol© software. We would also like to thank Teresita Insausti and Sylvain Pincebourde for their constructive reviews and reviewers who provided valuable comments on the manuscript. This study was performed as part of the PhD work of Jérémy Defrize at the University of Tours, under the supervision of Jérôme Casas.

Appendix: Chapter 1

Table S1: Composition of flower-visiting insect community according to different flower species. All values in table indicate percentages. Bold values indicate the highest percentage value for each flower species.

Insects / Flowers	**Bees**	**Flies**	**Lepidoptera**	**Wasps**	**Others**	References
Rosa carolina	**92**	8	0	0	0	Morse 1979
Bidens sp.	41	**56**	2	1	0	Schmalhofer 2001
Solidago sp.	26	**66**	5	3	0	Schmalhofer 2001
Centaurea scabiosa	**93**	4	0	0	3	Brechbühl et al. 2009a
Anthemis tinctoria	**79**	12	0	0	9	Brechbühl et al. 2009a
Erigenia bulbosa	**58**	42	0	0	0	Dailey and Scott 2006
Claytonia virginica	**78**	22	0	0	0	Dailey and Scott 2006
Dentaria laciniata	**74**	14	0	0	12	Dailey and Scott 2006
Stellaria media	**81**	17	0	0	2	Dailey and Scott 2006
Barbarea vulgaris	**84**	14	0	0	2	Dailey and Scott 2006
Chrysanthemum frutescens/Anthemis tinctoria/Knautia arvensis	**78**	5	0	5	12	Brechbühl et al. 2009b

Table S2: Composition of *Misumena vatia* prey according to different flower substrates. All values in table indicate percentages. Bold values indicate the highest percentage value for each flower species.

Prey / Flowers	**Bees**	**Flies**	**Lepidoptera**	**Wasps**	**Others**	References
Rosa carolina	43	**57**	0	0	0	Morse 1979
Rosa carolina	34	**66**	0	0	0	Morse 1981
Asclepias syriaca	**77**	16	7	0	0	Morse 1981
Solidago sp.	**61**	35	0	0	4	Morse 1981
Solidago sp.	19	44	1	12	24	Morse 1995
Lepidium papilliferum	**61**	34	5	0	0	Robertson and Maguire 2005
Chrysanthemum frutescens/Anthemis tinctoria/Knautia arvensis	**85**	2	0	0	13	Brechbühl et al. 2009b

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- CHAPITRE 2 -

Sensibilités spectrales et préférence colorée chez une araignée crabe cryptique

Article 2

Spectral sensitivities and colour preference in a cryptic crab spider

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In prep.

Abstract

The predation of species relying on background matching to fool prey is dependent on the colour contrast they yield on their substrates. One challenging task in a visually heterogeneous environment is to select substrates allowing the cryptic species to be poorly discriminable. In the present study, we tackled this question by focusing on a common cryptic crab spider *Misumena vatia*. We first investigated its spectral sensitivities using intra- and extracellular recordings. We then used choice experiments with artificial flowers of varying chromatic and achromatic components to study colour preference. Finally, we assessed the consequences of colour preference in term of spider chromatic and achromatic contrasts against the substrate in a relevant prey vision system. Our results show that *M. vatia* possesses two types of photoreceptors, a physiological requirement for the use of chromatic discrimination. We also disclosed a colour preference based on chromatic discrimination that leads to a low discriminability of spiders in the perspective of one of their main prey.

Introduction

Background colour matching is a form of visual crypsis defined as the ability to match the pattern and colour of one or several substrates (Stevens & Merilaita, 2009), allowing to make them difficult to detect by a receiver. The predation efficiency of species relying on background matching to fool prey is thus dependent on the colour contrast they yield on their substrates (Cooper & Allen, 1994; Johannesson & Ekendahl, 2002). One challenging task in a visually heterogeneous environment is to select substrates allowing the cryptic species to be poorly discriminable. Tropical butterfly, moths or reef fishes can actively select substrates that match their appearance (Papageorgis, 1975; Endler, 1984; Marshall, 2000). However, in these species the resulting colour contrast of this active choice has been assessed from a human perspective, with its unavoidable bias. The only species for which colour preference and the resulting colour contrast is available is the Australian crab spider *Thomisus spectabilis*. It was indeed showed that yellow *T. spectabilis* exhibits a preference for yellow flowers that make them poorly discriminable for prey, although it is not clear if this choice is based on chromatic or achromatic cues (Heiling et al., 2005). Moreover, in this spider, it was also observed that the white UV reflecting Australian crab spider *Thomisus spectabilis* prefers to sit on UV absorbing flowers to attract prey (Bahskara et al., 2009; Heiling et al., 2003).

One of the most common cryptic crab spiders, in terms of geographical distribution and devoted literature, is *Misumena vatia*. As numerous crab spider species, *M. vatia* is a

common sit-and-wait predators hunting on flowers and ambushing pollinator prey, such as honeybees and hoverflies (Morse, 2007). It has been shown that if *M. vatia* was undetectable at long distance through achromatic vision for Hymenoptera prey, the chromatic contrast value is quite dependent of both substrates and receiver identity (Defrize et al., 2010). The question of whether it uses chromatic or achromatic floral cues for foraging decisions is still unclear. Moreover, in this species, like for the other crab spider species, nothing is known about the number and the sensitivity of the different classes of photoreceptors. The aim of this study was (i) to investigate whether *M. vatia* possesses one or several classes of photoreceptors, (ii) to test whether this species displays colour preference, (iii) if the preference does exist, whether this preference is based on chromatic or achromatic cues, and (iv) what are the consequences of this colour preference in terms of spider chromatic and achromatic contrasts against the substrate in the Hymenopteran vision.

Materials and methods

Animals

Adult females of *M. vatia* (Clerck 1757) (Araneae: Thomisidae) were collected during spring and summer 2007 on several flower species in the surroundings of Tours, France (47°20’18’’N, 00°42’52’’E) and maintained individually in clear plastic vials containing pieces of damp cotton. Spiders were fed with flies (*Lucilia* sp) weekly. Vials were cleaned and discarded prey were removed weekly. For the ERG experiments, spiders were anesthetized with CO_2 for five minutes and placed on double-coated adhesive tape. We fixed the tergum and the four pairs of legs. Using a microscope, lateral parts of the prosoma as well as the chelicerae and palps were glued to the support with wax to prevent movements (Barth et al., 1993). All spiders survived the experiments.

In behavioural experiment, one clutch of approximately 50 eggs was recovered from a *M. vatia* female caught previously in the field. When juvenile crab spiders emerged, they were carefully transferred individually into transparent boxes positioned in an arena with black walls. Spiders were kept under a 12 hour light/dark cycle. Dark brown pieces of paper were used to provide water. Spiders were fed only once with *Drosophila* sp., one week before the experiments. Before and throughout the experiments, illumination was provided by fluorescent lighting (Osram, Lumilux Daylight 36W/954) mimicking natural daylight.

I - Electrophysiological experiments

Stimulation

A monochromator (Polychrome IV, Till-photonics), containing a Xenon lamp (150W) as a light source, was used to provide monochromatic light flashes. In the monochromator, the white light of the xenon lamp is deflected onto a grating fixed to a galvanometric scanner. By turning the scanner, a specific spectral fraction of the light is projected onto the exit slit. A quartz light guide led the light to the preparation. The end of the light guide (diameter 5 mm) was positioned 40 mm away from the eye surface. The spider and the light guide were positioned so that light reached the eye in the middle of its visual field. The intensity of each monochromatic light was calibrated with neutral density filters (Melles-Griot fused silica filters; 03 FNQ 089: 39.8% transmittance; 03 FNQ 057: 10% transmittance; 03 FNQ 049: 19.9% transmittance; Schott, Mainz, Germany: NG 4) to create flashes containing equal numbers of photons. For each monochromatic light, the light intensity reaching an eye was measured with a radiometer equipped with a flat response detector (IL 1400A radiometer International Light, Newburyport, USA). Intensities were converted into photon flux according to wavelength. In our experiments, the photons flux was $4.7x10^{14}$ photons/cm^2/s^1 for each wavelength. We transformed the amplitude signal to equivalent intensities (LogI) through a V-logI (response-intensity) curve established for each run. We then used the following equation to convert each recorded bioelectrical signal into sensitivity value (Sn):

$$\text{Sensitivity (Sn)} = 100*10^{-[\log Imax - \log In]}\ \%$$

where *log Imax* represents the equivalent intensity of the largest voltage response and *log In* the equivalent intensity of each voltage response. Finally, each individual record was normalized, using its maximal value, before pooling over spiders.

The flash duration was 200ms and the interval between flashes was 20 s. Recordings were made from 340 nm to 680 nm or from 680 nm to 340 nm, in steps of 10 nm. Individuals were randomly allocated to either stimulation direction, and any dependence on the direction of stimulation was noted.

Recording

Electroretinograms

To register ERG responses, the tip of a glass microelectrode filled with a Ringer solution was placed close to the eye's surface so that the electrolyte bridged the small gap between the electrode and the lens and provided electrical contact (Barth et al., 1993). A silver wire was used as an indifferent electrode. It was slightly inserted into the posterior dorsal part of the prosoma. Recordings were made from all eyes of the four pairs (AM: Anterior Median, PM: Posterior Median, AL: Anterior Lateral, PL: Posterior Lateral). A Syntech ID AC-02 signal interface box was used to amplify and digitize signals. All recordings took place at 20°C.

Intracellular recordings

In posterior median and both anterior and posterior lateral eyes, intracellular recordings were performed. Spiders were anesthetized with CO_2 before gluing them ventrally with wax, immersing them in spider Ringer solution (Rathmeyer, 1965), and finally cutting off the pedicel to avoid the possible influence of heart movement (Yamashita & Tateda, 1978). We removed a specific part of the prosoma and inserted a microelectrode (40-60 MΩ) filled with 3M KCl into the retina under microscope control. Intracellular recordings were done on dark-adapted eyes, i.e. spiders were maintained 30 min in darkness before beginning a recording. Due to the movements of the AM retina, intracellular recordings were not possible as it was difficult to position an electrode in a single cell in a stable fashion.

Selective adaptation

ERG recordings were conducted on eyes having undergone these following treatments:

1) dark-adapted eyes; 2) adaptation to monochromatic lights: eyes were adapted to a specific wavelength for 30 min before recording. The rationale behind this procedure is that selective adaptation to a wavelength decreases the sensitivity of a photoreceptor whose peak is near the chosen adapting wavelength (Jacobs, 1993; Kirchner, 2005). This decrease may reveal other peaks that reflect the presence of other visual pigments. After 30 min of adaptation, the monochromatic adaptation light continued to be applied, except during each 200 ms flash, for the duration of the experiment.

II – Behavioural experiment

Innate colour preference

We gave naive, third instar *M. vatia* a choice between four vertically oriented artificial flowers of different colour ('UV+/white', 'UV-/white', 'UV-/blue', 'UV-/yellow') in front of a green background. UV+ indicates UV reflecting flowers whereas UV- indicates UV absorbing flowers. Each flower consisted of a circular corolla (12 mm diameter). 'UV+/white', 'UV-/blue', 'UV-/yellow' colours were produced using acrylic paint (Liquitex, USA). The UV-/white colour was produced by cutting a 12mm diameter piece in petals of Oxy daisy (*Chrysanthemum rubellum*), as no artificial paint was able to produce the desired effect. These pieces were then carefully positioned on a circular corolla, similar to the other artificial flowers. As it has been shown that crab spiders can use flower olfactory signals in foraging decisions (Morse, 2007), all the corolla were embedded in a translucent sealing film to avoid any olfactory cues (Heiling et al., 2005). This polyethylene film has the propriety to be impervious to odours (Diversified Biotech, Boston, USA). In the choice arena, the 'natural' flowers were removed and replaced every 45 min to avoid any natural decay affecting the flower color.

Spiders were first anaesthetized with carbon dioxide and then placed 40 mm away from the flowers. We considered that *M. vatia* made a choice when an individual made contact with one of the corolla, after climbing on the stem. After 40 min without any choice, the spider was removed from the arena and discarded. Between tests, the arena was carefully cleaned, to exclude any influence of silk and olfactory cues, and the relative position of each colour were changed randomly. Each spider was used only once.

Modeling chromatic and achromatic contrasts in the bee's visual system

Small bees, such as solitary bees, are one of the main prey of *M. vatia* (Brechbhül et al., 2010b). Chromatic contrast is the dominant cue used by foraging bees for the identification of flowers at short distance, when a flower subtends a visual angle of at least 15° (Giurfa et al., 1996). However, at long distances, when a flower subtends a visual angle between 5° and 15°, bees may use green contrast for flower detection, looking for a difference between background and target green receptor signals (Giurfa et al., 1996; Spaethe et al., 2001).

To calcultate the chromatic and achromatic contrasts that naïve juvenile would induce on the different flowers as seen by bees, we used the model of Vorobyev & Osorio (1998). The chromatic and achromatic contrasts between two spectra are measured in units of just

noticeable difference (JND). A value of 1 JND between two spectra corresponds to the discrimination threshold under ideal conditions and under which two spectra are considered to be indistinguishable (Wyszecki & Stiles, 1982). Ten spiders were chosen randomly and their spectral reflectance was measured (**Figure 11**).

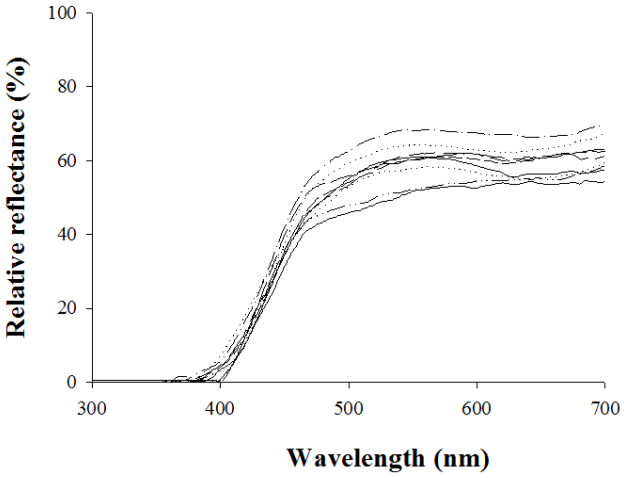

Figure 11: Relative spectral reflectance of ten juveniles *Misumena vatia*.

We proceeded as detailed in Defrize et al. (2010) for substrate and spider spectroradiometric measurements, as well as for the modeling of bee vision. We assumed a ratio of 1:0.471:4.412 for UV, B and G receptors respectively for all trichromatic bees. This ratio takes into account the ommatidia heterogeneity within a bee eye (Wakakuwa et al., 2005; Spaethe & Briscoe, 2005). We used the photoreceptor noise value of 0.13 for all bee photoreceptor classes (Vorobyev & Brandt, 1997; Vorobyev & Osorio, 1998).

Results

I - Electrophysiological experiments

The crab spider *Misumena vatia* possesses eight simple eyes arranged in two rows (**Figure 12**). The anterior lateral (AL) and posterior lateral (PL) eyes are larger (75 and 65 µm diameter, respectively) than the anterior (AM) and posterior median (PM) eyes (59 and 55µm diameter, respectively). The AM eyes constitute the *principal eyes* of spiders and the rest, the so called *secondary eyes*.

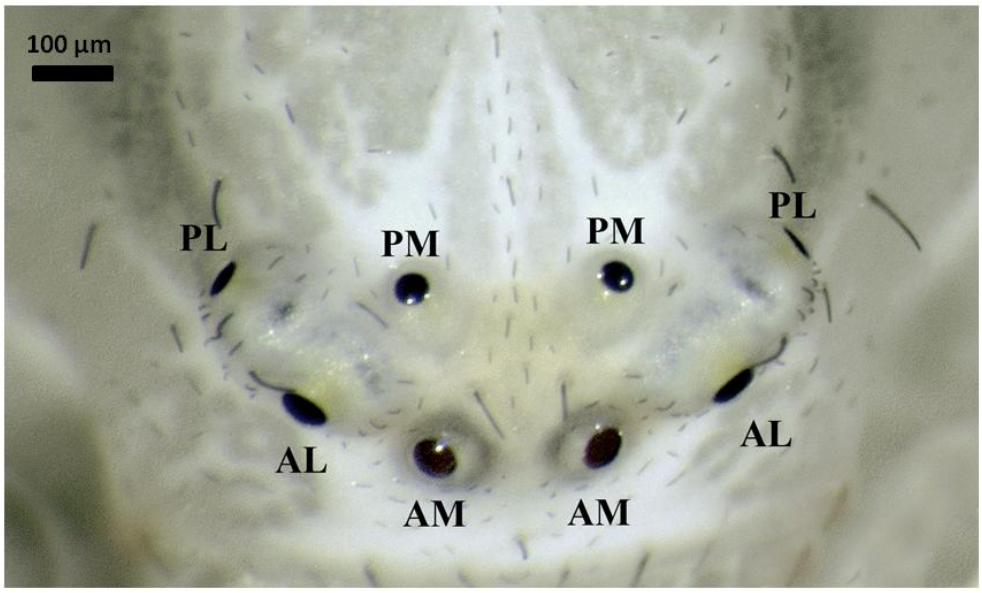

Figure 12: Organization of the four pairs of eyes of *M. vatia*. AM = Anterior Median, PM = Posterior Median, AL = Anterior Lateral and PL = Posterior Lateral.

Spectral sensitivities

The ERG electrical responses obtained in the different eyes were negative-going waves similar to those found for *Cupiennius salei* and many other arthropods (Autrum 1958; Barth and al. 1993). The highest ERG amplitude attained was 15mV.

- *Principal eyes*

ERGs of the dark-adapted AM eyes (**Figure 13A**) revealed a maximal peak around 340 nm (1.0 ±0.0) in the ultraviolet A region of the spectrum. Moreover, a second peak around 530 nm reached a relative sensitivity of 0.89±0.06. Selective adaptation to monochromatic light of 340 nm (**Figure 13B**) modified the shape of the dark-adapted spectral sensitivity curve, leaving a peak around 520 nm (0.91 ±0.07). A visual pigment template with peak absorption at 525 nm (Stavenga et al. 1993) fitted the spectral sensitivity curve for wavelengths between 450 nm and 680 nm well, suggesting the presence in this region of a single green visual pigment type (**Figure 13B**). Next, selective adaptation to monochromatic light of 480 nm was tested to answer the question whether the spectral sensitivity curve between 400 and 680 nm reflects the presence of a single class of visual pigment or results from the presence of two different classes. Indeed, if two visual pigments have their sensitivity peaks between 490 nm

and 530 nm, this adaptation will favour a putative receptor around 500 nm quite strongly but will leave a receptor around 530 nm unaffected. Thus, in the 480 nm-adapted AM eyes, we observed no change in the overall shape of the spectral sensitivity curve in the green region (**Figure 13C**) especially in the 500/540 nm ratio, compared to dark-adapted eyes (0.85 and 0.91 for dark-adapted eyes and 480 nm-adapted eyes respectively). This confirmed the presence of a single type of visual pigment in the green region, in addition to the UV one in the AM eyes.

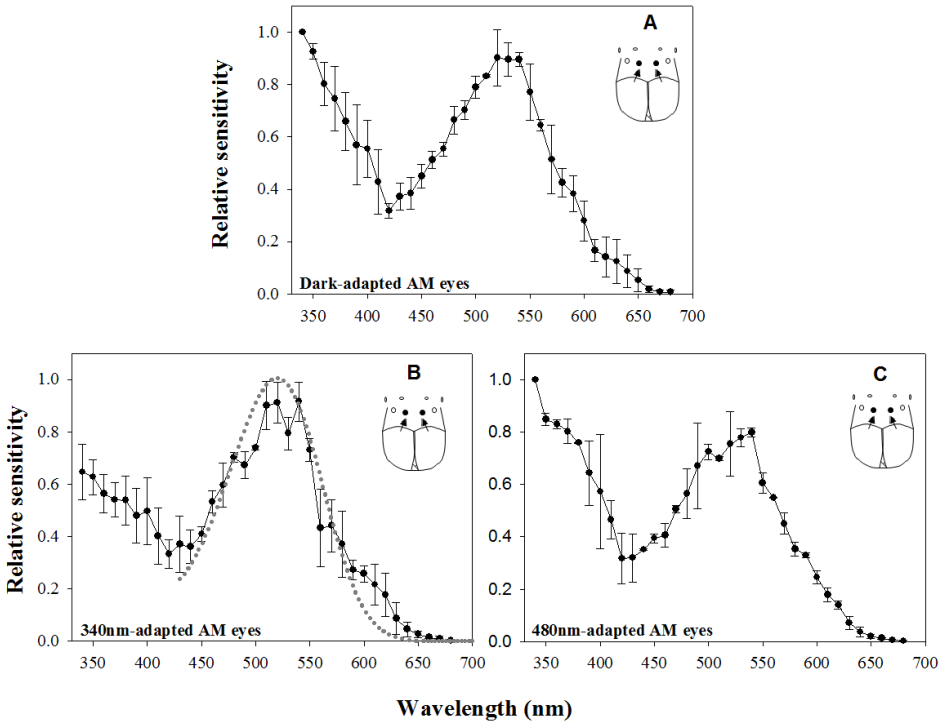

Figure 13: ERG recordings. Spectral sensitivity curves for the anterior median eyes (AM eyes) in the dark-adapted state (A), after adaptation for 30 min to 340 nm monochromatic light (B) and after adaptation for 30 min to 480 nm monochromatic light (C). The dashed line represents the predicted absorption curve of a visual pigment with a sensitivity peak at 525 nm (C). Values are means ±S.D. N=3 for each graph.

- *Secondary eyes*

A common feature of the spectral sensitivity curves of dark-adapted secondary eyes was a high sensitivity in the green region between 500 and 540 nm (0.97±0.03, 0.89±0.14, 0.95± 0.04 at 510 nm for the PM, PL and AL eyes respectively) (**Figure 14A, 14C, 14E**). A visual pigment template with a sensitivity peak at 525 nm fits our data at wavelengths between 450 nm and 680 nm well, indicating that a green visual pigment with this peak absorption might be present (dotted line; **Figure 14A, 14C, 14E**). To make sure that no further visual pigment

was present in this region of the spectrum, we adapted the secondary eyes with 480 nm monochromatic light. This did not alter the shape of the green region of the spectral sensitivity curves and so did not reveal other peaks (**Figure 14B, 14D, 14F**). Selective adaptation to 560 nm also yielded similar results (data not shown).

Nevertheless, selective adaptation at 480 nm and 560 nm revealed a UVA peak around 340 nm in AL and PM eyes, whereas the UVA sensitivity level for the PL eyes remained unaltered. Indeed, in the AL and PM eyes, the change in the 340/540 ratio between dark-adapted and 480 or 560 nm-adapted eyes strongly suggests the presence of a UVA visual pigment with an absorption peak around 340 nm. A visual pigment template (Stavenga et al. 1993) with a sensitivity peak at 335 nm fits our data well between 335 nm and 380 nm in AL eyes (**Figure 14D**), suggesting the presence of a UV visual pigment. Thus, we can conclude that the AL and PM eyes, like the AM eyes, possess two types of visual pigments, one sensitive in the UVA region around 340 nm and the other in the green region around 525 nm. In contrast, the PL eyes may only possess a single green-sensitive visual pigment.

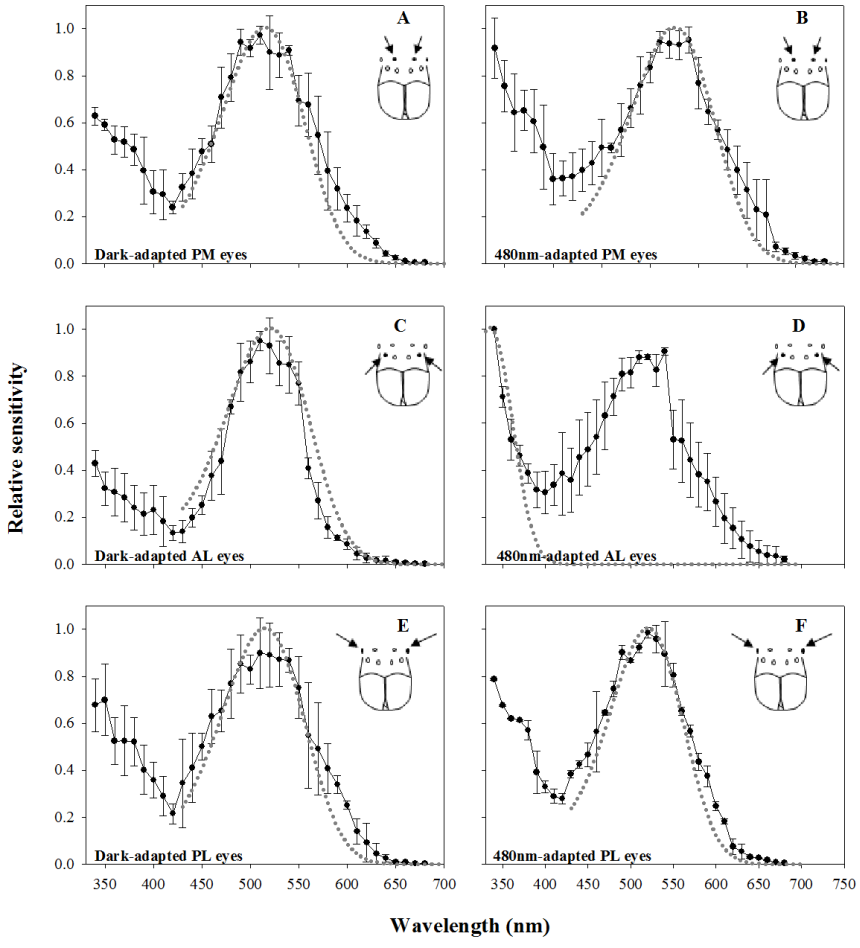

Figure 14: ERG recordings. Spectral sensitivity curves for the posterior median eyes (A,B), the anterior lateral (C, D) and the posterior lateral (E, F) eyes in the dark-adapted state and after adaptation for 30 min to 480 nm monochromatic light. The dotted lines represent the predicted absorption curve of a visual pigment with a sensitivity peak at 525 nm or at 340 nm. Values are means ±S.D. N=3 for each graph.

Intracellular recordings were stable enough to carry out a complete spectral scan in 6 dark-adapted preparations in PL and AL eyes. Despite numerous intracellular attempts, we did not find any UV or Green cells in PM eyes. In both anterior and posterior lateral eyes, we recorded cells which responded maximally in the green region of the spectrum, at around 520-530 nm (**Figure 15A, B**). Visual pigment templates, with a sensitivity peak at 525 nm for the anterior lateral eyes and 530 nm for the posterior lateral eyes, match the physiological data between 430 and 680 nm quite well. This is consistent with the green-sensitive photoreceptor class detected using ERGs. The intracellular results also show that the UV pigment class must be real in PL eyes. We indeed noted that the β-peak of the spectral sensitivity curve is much smaller than the UV peak in the ERG curves.

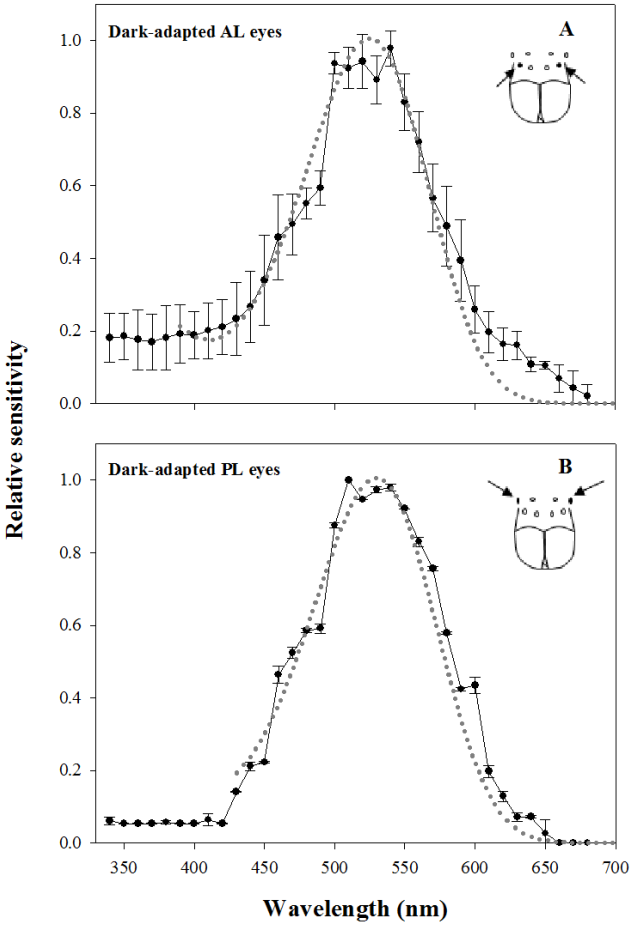

Figure 15: Intracellular recordings. Mean (± s.d.) dark-adapted spectral sensitivities of single photoreceptors in (A) anterior lateral and (B) posterior lateral eyes (solid lines). Dotted lines are theoretical absorption curves with a sensitivity peak at 525 (A) and 530 nm (B) (Dartnall nomogram). N=4 and 2 for anterior lateral and posterior lateral eyes respectively.

II – Behavioural experiments

Among the different flower (**Figure 16A**), we observed that *M. vatia* chooses preferentially the flower colour UV-/white (N=25, χ^2=8.44, d.f.=3, p=0.03) (**Figure 16B**). Moreover, we also noted a low number of visits for the yellow flower.

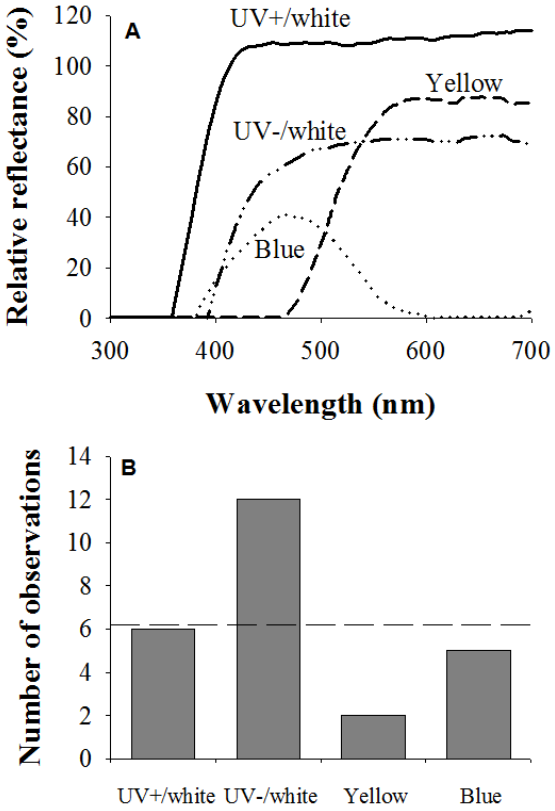

Figure 16: (A) Reflectance spectra used in our experiment. Colour names are based on human perception. UV+ indicates a UV reflecting substrate whereas UV- indicates a UV-absorbing substrate. (B) Innate colour choice of *Misumena vatia* (N=25). The dashed line represents a uniform distribution.

To manipulatively disentangle whether spiderlings select the flower UV-/white according to its achromatic component, we gave spiders a choice between three corollas of UV-/white type differing only in their achromatic component (**Figure 17A**). If the UV-/white flower I s chosen according to its achromatic component, spiders should prefer flower number 1, as this flower is achromatically similar to the UV-/white flower in the first experiment. Furthermore, spiders should not display any preference between the three corollas if they are indifferent to the achromatic component. Naïve *M. vatia* did not make a specific choice

between the three flowers (N=15, χ^2=0.56, d.f.=2, p=0.75) (**Figure 17B**), suggesting that the preference is not generated by the achromatic component of UV-/white flower. Thus, the combination from both experiments indicates that the chromatic component is determining the choice of the flower colour by the spider.

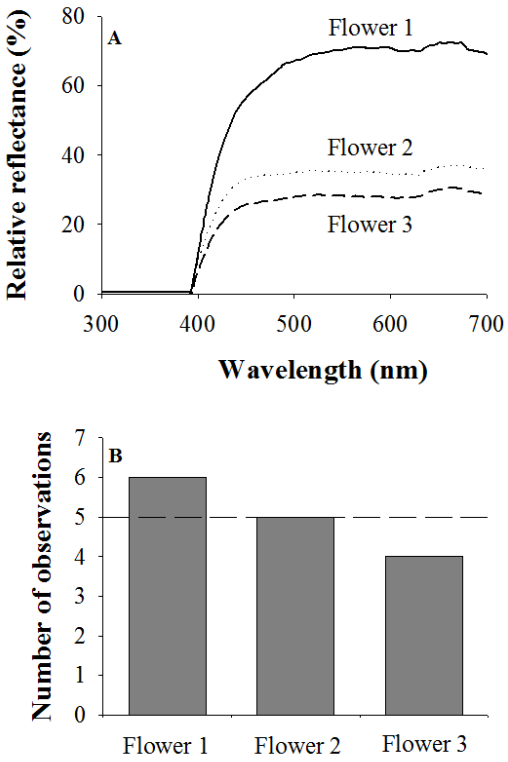

Figure 17: (A) Different intensities (achromatic component) of the flowers of UV-/white type. (B) Innate colour choice of *Misumena vatia* (N=15). The dashed line represents a uniform distribution.

This chromatic preference induces low chromatic detectability from the perspective of a bee in the first experiment (**Figure 18A**). By contrast, it generated a wide range of achromatic contrasts according to the substrate intensity in the second experiment (**Figure 18B**). Indeed, on flower 1, spider produce both low chromatic and achromatic contrasts (2.40±0.73 JNDs and 1.65±0.51 JNDs, respectively), whereas they produce only a low chromatic contrast on flower 2 and 3 (Flower 2: chromatic contrast = 2.62±0.54 JNDs and achromatic contrast = 3.50±0.62 JNDs; Flower 3: chromatic contrast = 2.56±0.86 JNDs and achromatic contrast = 5.25±0.67 JNDs).

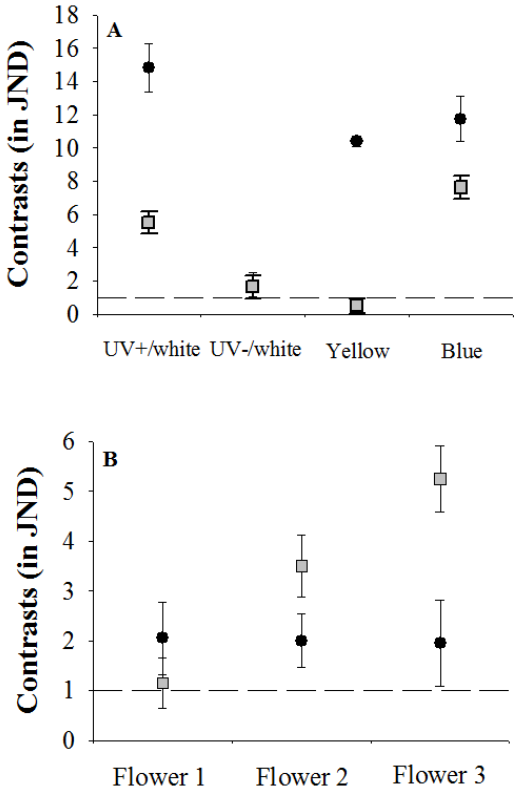

Figure 18: A-B: Chromatic (black circles) and achromatic (grey squares) contrasts between spiders and flowers from the perspective of bees on the different reflectance types. Dashed lines indicate the discrimination thresholds.

Discussion

Electroretinograms combined with chromatic adaptation revealed a green-sensitive visual pigment which, once fitted with a known template, peaked at about 525 nm in each of the four pairs of eyes. Furthermore, we identified an UV visual pigment in the anterior median, the anterior lateral and the posterior median eyes. Moreover, in the anterior lateral eyes, between 340 nm and 380 nm, the spectral sensitivity of this pigment is well fitted by a template with a peak at 335 nm. The enhanced relative ultraviolet sensitivity revealed for the anterior median eyes of *M. vatia* is similar to the one observed for the anterior median eyes of wolf spiders and jumping spiders (DeVoe et al., 1969; DeVoe, 1975). The behavioural significance of this high UV sensitivity is however not clear.

The presence of a UV visual pigment in the posterior lateral eyes cannot be ascertained with the same degree of confidence. One hypothesis to explain why the UV peak cannot be revealed in this eye is that the number of UV-sensitive cells might not be great enough to be detected by chromatic adaptation. Alternatively, the UV peak might lie outside the measured region, as our device did not enable us to stimulate eyes with wavelengths shorter than 340 nm. Indeed, the shortest UV peak found so far in spiders lies at 335 nm, in the anterior lateral eyes of *Cupiennius salei* (Walla et al., 1996). Recently, Li et al. (2008) even found that females of the jumping spider *Phintella vittata* are sensitive to UVB light between 280 nm and 315 nm (which is reflected from the dorsal scales of males).

Number of photoreceptor' classes

Visual pigments in single or mixed composition have already been found in spiders. Anterior lateral eyes with UV and green photoreceptor classes have been observed in the ctenid spider *C. salei* (Walla et al., 1996). In contrast, the presence of multiple visual pigments in a single visual cell has been suggested in wolf spiders. Indeed, DeVoe (1972) recorded a UV and a green peak from single cells of the anterior median eyes of the wolf spiders *Lycosa baltimoriana, L. miami* and *L. carolinensis*. In *M. vatia*, the few intracellular recordings of green photoreceptors in anterior median and anterior lateral eyes suggest that their retinae are composed of photoreceptors containing only one type of visual pigment. Thus, we conclude that *M. vatia* has at least two classes of photoreceptors, one UV and one green. The presence of UV and green photoreceptors is also observed in the principal eyes of Salticidae and Argiopidae (DeVoe, 1975; Yamashita & Tateda, 1976; Blest et al., 1981), and in secondary eyes of the Salticidae and Ctenidae (Yamashita, 1985; Walla & al., 1996). Apart from spectral sensitivities, the ERGs also gave clues about the retinal organisation of the principal eyes. Our results indeed suggest that the two types of photoreceptors in the AM eyes are arranged in layers, as shown by the suppression of sensitivity to UV and not to green when we adapted the eye to 340 nm. Because only the UV part of spectrum revealed adaptation, this means that a UV receptor probably absorbed most of the UV light before it reached the green receptor, i.e. the UV receptor was distal to the green. The tiered organization suspected with electrophysiological recordings is consistent the organization disclosed by ultrastructural study (Insausti and Casas, unpublished data; See Annex 1). Such an organisation of photoreceptors in layers has been reported in the AM eyes of the thomisid *Hedana sp.* and of salticids (Land, 1969; Blest et al., 1981; Blest & O'Carroll, 1990). Moreover, as it is highly suggested in *M. vatia*, the UV receptor class in the AM retina of the Salticids is the most

distal. In salticids, the function of this peculiar retina organization is especially to reduce chromatic aberration. In Thomisids, further structural and optic studies are needed to evaluate the role of the tiered retina in colour vision.

The adaptive significance of colour preference

Our results also show that third instar *M. vatia* display colour preference. As *M. vatia* does not choose this colour according to its intensity, it is likely that achromatic vision is not used in this context. Moreover, the presence of wavelength selective behaviour is unlikely, as this visual process is intensity dependent (Kelber & Pfaff, 1999). Further experiments are needed (1) to confirm that colour vision, i.e. the ability discriminate stimuli only by differences in chromaticness, irrespective of their intensity, is used in this context, and (2) which pairs of eyes are involved for this task. In spiders, the different pairs of eyes are known to have different functions (Schmid, 1998; Dacke et al., 1999; Dacke et al., 2001; Strausfeld et al., 1993a, b). In several species, colour vision is assumed to be mediated by anterior median eyes only (Kastner, 1950; Land, 1969); (3) to determine whether this preference is innate like in some flower-visiting insects (Lunau & Maier, 1995), or if *M. vatia* might take into account its own colouration when taking foraging decisions. *M. vatia* has the possibility to see different parts of their own body (See appendix). Such visual feedback mechanisms in substrate selection have already been shown in cryptic species, such as for the Australian crab spider *Thomisus spectabilis* and for the grasshopper *Circotettix rabula rabula* (Gillis, 1982; Heiling et al., 2005). We showed that this preference allows spiders to be poorly chromatically discriminable in the perspective of bees. In the field, several common 'white' flower species, such as *Chrysanthemum vulgare, Stellaria media or Stellaria palustris* have reflectance spectra close to that chosen by *M. vatia* (Arnold et al., 2008). On all these flowers, juveniles *M. vatia* would produce a low chromatic contrast. These species attract a lot of different prey species, especially small hymenoptera (Daily & Scott, 2006; Arnold et al., 2008; Brechbühl et al., 2010). Whereas last instars and adults can change colours from white to yellow and back within a few days, according to the colour of the substrate (Weigel 1941; Théry 2007), early whitish instars of *M. vatia* do not change colour (Weigel, 1941; Defrize, personal observation). Moreover, unlike last instars and adults that feed on small and large prey (Erickson & Morse, 1997), the early instar can only catch small prey. Brechbühl et al. (2010) recently showed that prey that avoid flowers harboring a visible crab spider were small dipterans and hymenopterans. It may be important for spiderlings to match the colour of their substrate in order to not deter relevant prey.

Conclusion

Our study provides the first detailed investigation of the visual system of a colour-changing crab spider. Recordings revealed two types of photoreceptors, but there is also the possibility of additional classes of photoreceptors, especially in the AM eyes. In addition to the results that *M. vatia* possesses the physiological basis for colour vision, we provided behavioural evidence for chromatic discrimination in the relevant context of flower colour choice. The numerous chromatic mismatches seen in the field, for later instar (Defrize et al., 2010), are most likely not due to the unability of spiders to see colours. Rather, the selection forces for crypsis in ambush predators have to be thought in term of prey availability and metabolic needs (Charnov, 1976a, b; Caraco & Gillespie, 1986). This is true not only for this species, but also for the vast majority of cryptic species. Unfortunately, only a fraction of the knowledge regarding substrate colour variability and selection of foraging sites gained with *M. vatia* is available for them (Théry et al., 2010).

Appendix: Chapter 2

Visual fields of *M. vatia*

Defrize, J., Insausti, T., Lazzari, C. and Casas, J. Unpublished data

Materials and methods

We used the reflectance properties of the grate-shaped tapetum of Thomisidae to map out the visual fields of the anterior lateral (AL), posterior median (PM) and posterior lateral (PL) eyes using an apparatus first described by Homann (1928). Indeed, the reflecting crystal layers of this type of tapetum reflect out light almost exactly along its original direction of incidence (Land, 1985). Each eye was rotated around a telescope and a coaxial light source, allowing us to measure the angular extent of the retina. Thus, by using the Homann'method, the co-ordinates of the field of view of each eye were obtained at various latitudes and longitudes and plotted onto a sphere. The lack of tapetum in the AM eyes of *M. vatia* did not allow us assessing their visual fields by this technique. The visual field of the AM eyes was measured by means of serial histological sections in the three planes (horizontal, transverse and sagittal). The histological procedure was the same as for the morphological analysis. Briefly, the prosoma region containing the eyes was dissected rapidly under fixative (2.5% glutaraldehyde and 2.0% paraformaldehyde in phosphate buffer, at pH 7.3, with glucose and CaCl2 added) and stored in the same solution for about 3 hs. Subsequently, the pieces were postfixed with buffered 1% osmium tetroxide for 1-2 h. After dehydration, they were embedded via propylene oxide in Durcupan ACM (Electron Microscopy Sciences no. 14040). Blocks were serially sectioned at 1.5-5 µm using glass knives mounted in a microtome. The sections were stained on a hot plate with Toluidine Blue-Basic Fuchsin and mounted on a slide with DPX (Electron Microscopy Sciences no. 13510).

Results

The AL and PL visual fields displayed a similar shape, with a frontal and lateral field of view respectively, extending to the rear for PL eyes whereas the PM eyes look upwards. We observed a slight overlap of fields of view between AL and PL eyes and between PL and PM eyes, whereas PM and AL eyes have contiguous fields of view. A region of binocularity was observed for AL eyes. The AM eyes exhibit a wide field of view, superposed with that of the other eyes. A medial binocular area could also be determined. Thus, the horizontally

elongated visual fields of AL, PM and PL eyes covered almost all the upper hemisphere of the globe, indicating that the spider eye organisation might provide visual information about almost all of its upper environment, whereas the inferior hemisphere will be only covered in the frontal region by the AL and AM eyes.

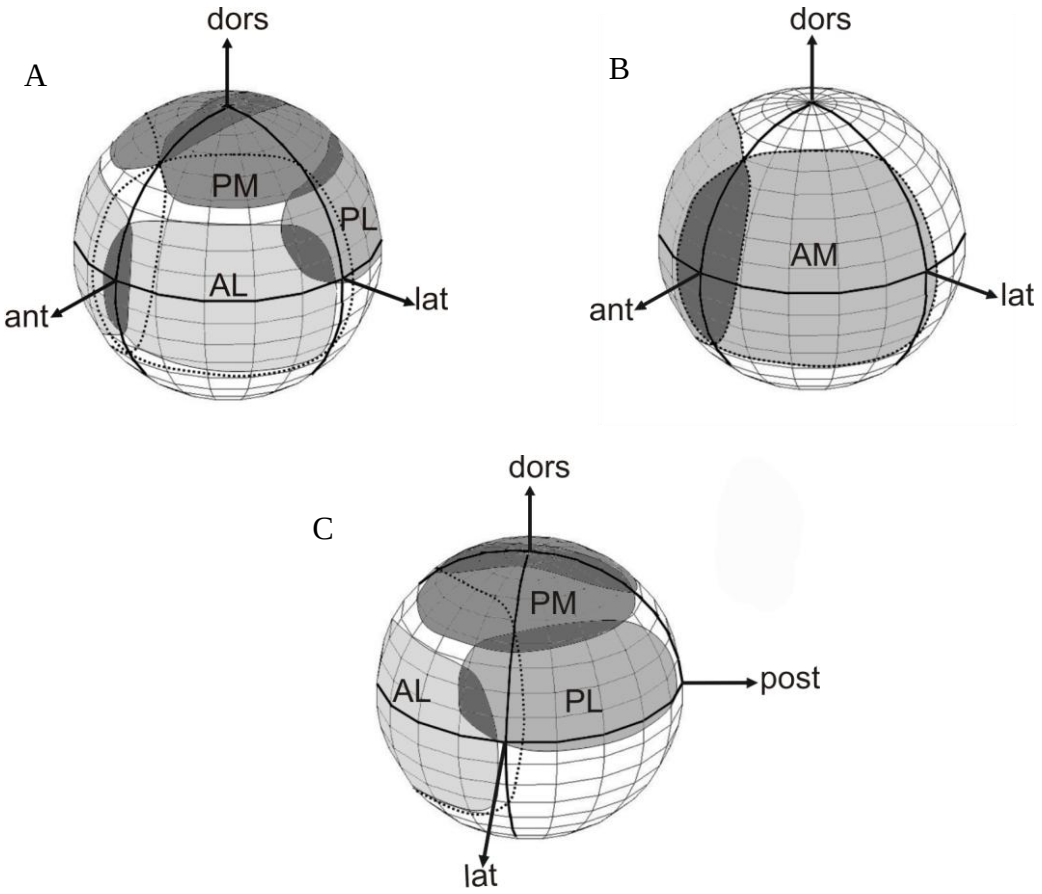

Figure: Frontal (A, B) and Lateral (C) views of the visual fields of the AL, PL, and PM eyes (n=4 for the secondary eyes and n= 4 for the principal eyes). The spider's head is assumed to be at the center of the sphere. The anterior-posterior axis (ant, post) represents the body axis of the spider.

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Homann, H. 1928. Beitrage zur Physiologic der Spinnenaugen. I and II. *Zeitschrift für vergleichende Physiologie*, **7**, 201-268.

- TROISIEME PARTIE -

Absence d'évidence pour l'utilisation de la couleur du substrat comme indicateur de la qualité du site de fourragement chez une araignée chassant immobile sur les fleurs

Article 3

No evidence for the use of substrate colour as indicator of profitable foraging site in a sit-and-wait spider on flowers

Defrize, J. & Casas, J.

In prep.

Abstract

Colour vision has been strongly suspected in several spider species, but never clearly proved in an ecological relevant context, such as foraging. Testing colour vision in a foraging context would be of special interest for ambushing spiders of the Thomisidae family, which hunt on colourful flowers. In the present study, we tested whether the crab spider *Misumena vatia* may associate a specific colour substrate with the presence of prey in an ecological relevant context, using two experimental designs taking into account the behavioural and ecological characteristics of this spider. One classic design associated a specific background color with secured prey capture. One original design relies on a training phase consisting in observing unreachable bumblebees visiting artificial flowers of a specific colour, followed by a test phase consisting in a choice of colored flowers as foraging site. We did not demonstrate colour vision. We discuss experimental and ecological hypotheses that may explain the absence of the use of colour vision in this foraging context.

Introduction

True colour vision, i.e. the ability to discriminate two lights of different spectral composition, regardless of their relative intensity (Menzel, 1979; Kelber et al., 2003), plays an important role in intraspecific communication and foraging decisions (Menzel & Backhaus, 1989; Marshall et al., 1996; Briscoe & Chittka, 2003). This ability has been behaviourally disclosed in a large array of both vertebrates and invertebrates species (See review in Kelber et al., 2003). Among the numerous examples of species possessing true colour vision, spiders are however under-represented. Colour vision has been strongly suspected in several jumping spider species (Crane, 1949; Kastner, 1950), but never clearly proved in an ecological relevant context. It has been however demonstrated by heat avoidance learning, a rather unnatural setting, in the jumping spider *Hasarius adansoni* (Nakamura & Yamashita, 2000). This lack of data for spiders is mainly due to the fact that they are difficult to test with classical conditioning methods. As colour vision is context-dependent, one of the key aspects to disclose colour vision is to design a relevant context in which colour vision in spiders could be expressed. This is the overall aim of this study.

In many animals, colour vision has been revealed by associating colour with rewards. In spiders, testing colour vision in a foraging context would be of special interest for some spiders of the Thomisidae family, which hunt on colourful flowers, waiting motionless for visiting insects (Rabaud, 1929; Morse, 1981; Morse, 2007). Several studies have already

shown that visual floral cues, in addition to shape cues, are used by these spiders to take foraging decisions, without however showing the use of colour vision. In particular, Baskhara et al. (2009) showed that the colour changing crab spider *Thomisus spectabilis* is UV-sensitive, as white spiders prefers UV-absorbing flowers over UV-reflecting ones. Moreover, yellow *Thomisus spectabilis* prefer to visit yellow flowers (Heiling et al. 2005). It was not known in this case whether chromatic or achromatic cues were taken into account. Finally, it has been recently shown that early instar *Misumena vatia* select flower according to its chromatic cues (Chapter 2). *M. vatia* is a crab spider hunting on a wide diversity of flower species, waiting for pollinator prey. Chapter 2 shows also that *M. vatia* possess both a UV and Green photoreceptor classes in the four pairs of eyes, indicating that it possess the physiological basis to see colour. In addition to behavioural and physiological clues, structural studies of the eyes also beget the question of the ability of colour vision in Thomisidae. *M. vatia* possesses a tiered retina in their anterior median eyes three layers of morphologically distinct photoreceptors (Insausti and Casas, unpublished data; See annex 1). This tiered organization was also reported in another Thomisid *Hedana* sp. (Blest & O'Carroll, 1990). The adaptive significance of such an organization and whether each layer has a specific spectral sensitivity is however unknown. A tiered retina with four distinct layers, each having a specific spectral sensitivity, has been observed in Salticidae (Blest et al., 1981). This peculiar organization has been shown to be beneficial for colour vision, as it reduces chromatic aberration, and also to compensate for its inability to accommodate (Land 1969; Blest et al., 1981; Richman and Jackson, 1992). In the present study, we examined the presence of colour vision in *M. vatia* in two relevant foraging contexts, in which *M. vatia* could associate the presence of prey with a specific colour substrate. One classic design associated a specific background color with secured prey capture. One original design relies on a training phase consisting in observing unreachable bumblebees visiting artificial flowers of a specific colour, followed by a test phase consisting in a choice of colored flowers as foraging site.

Materials and methods

Animals

Last instar and female adult crab spiders *M. vatia* were collected in the surrounding of Tours, France, and maintained individually in clear plastic boxes with a piece of wet cotton. Spiders

were fed with flies (*Lucilia sp*. or *Drosophila melanogaster*) weekly. Discarded prey were also removed weekly. Before each experiment, spiders were deprived of food for one week. Each crab spider used in each experiment was tested only once.

Spectral reflectance of flowers and spiders

For each experiment, we measured the spectral reflectance of the artificial flowers and the green background, using a spectroradiometer (Avantes Avaspec 256) and a deuterium-halogen lamp (Avantes Avalight D/H-S) emitting at wavelengths of 215 to 1100 nm. Reflectance was expressed relative to a 99% (300-700 nm) reflectance standard. A reference reading was taken and dark current calibration was carried out before taking the measurements of green background and artificial flowers (See reflectance **Figure 19**). An optic fiber sensor 1.5 mm in diameter, equipped with a quartz window cut at a 45° angle, was used. Three measurements were taken for each recordings and mean values were used.

We chose two flower colours corresponding to floral spectral reflectance on which *M. vatia* can be found in the field. We did not offer to the spiders the preferred floral reflectance type (UV-absorbing 'white', see Chapter 2) to ensure that spiders are equally motivated by both types of flowers at the beginning of the experiments.

We designed experiments so that the disturbance of spiders was as reduced as possible. We indeed observed in preliminary experiments that manipulation of spider or attempts to offer them prey as a reward lead to odd behaviours (tonic immobility, running escape) not compatible with learning experiments.

First experiment

In this first experiment, spiders were trained to associate a colour with the offering of prey. Spiders have thus the possibility to capture and eat prey during the training phase. Illumination was provided by artificial daylight lamp, mimicking natural daylight (Lumilux Daylight, Osram 36W).

*Training phas*e

The training phase is done in two steps, a feeding step and a starvation step, repeated four times. Each step is associated with a specific colour. Two series of colours were tested: Yellow-White and White-Yellow, the first name indicating the colour of the 'feeding' step. Yellow' and 'White' flowers are known to be the most common colours of substrates used by

M. vatia as hunting sites (Weigel, 1941; Morse, 2007; Defrize et al., 2010). Acrylic white and yellow paint were used (reflectance spectra are given in **Figure 19**).

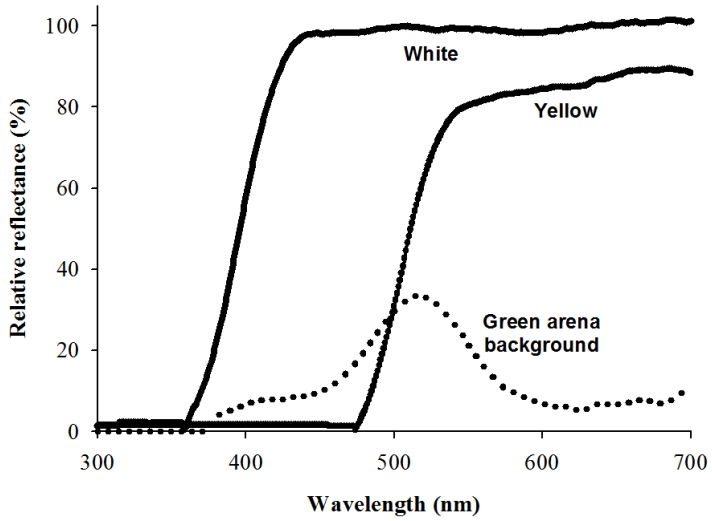

Figure 19: Reflectance of the different flower colours and of the green substrate used in the experiments. Colour names are based on human perception.

A first group is trained to learn food availability with the yellow colour, a second group with the white colour. A group of 15 spiders was tested in each series. The feeding step consisted in placing the spider into a coloured circular box with *Drosophila sp.* for 90 min, i.e. for the period needed to capture and eat one *Drosophila* (Defrize, personal observation). In the second starvation step, we transferred each spider in a second coloured box, free of prey, for 24 hours. (**Figure 20A**)

Colour choice of M. vatia

After the training phase, spiders were placed inside an experimental device described in the following (**Figure 20B**). We made artificial flowers composed of a green stem and a circular corolla. Two artificial corollas with a diameter of 40 mm and a 2 mm hole in the center were positioned at a distance of 60 mm of each other, 50 mm above the ground into device of dimension 200x300 mm. These artificial flowers had an angle of 60° to a vertical plane. A background consisting of a green paper was placed all around the device and on the ground. Spiders were positioned 100 mm away from the flower centres, heading towards the flowers.

The device is bordered by water, constraining spiders to stay within the device. We considered that *M. vatia* made a choice when a contact was made with one of the corolla, after climbing on the stem. We compared the spiders' distribution on both types of flower colours with a random distribution. Between each experiment, the devices were cleaned to remove silk and to avoid any effects of olfactory cues.

Experiment 2

In this experiment, we wanted to assess whether *M. vatia* associates the colour cues of a flower with the likelihood to catch a prey on it. To carry out this experiment, we used the well-known colour learning abilities of bees. Experiments took place under natural daylight conditions with a temperature range from 20 to 27°C.

Bees learning

Bumblebee hives (Standard Hive, Biobest, Westerlo, Belgium) containing flower-naive workers, *Bombus terrestris*, were kept in a flight cage and positioned one meter away from the experimental device, which is similar to the 'test' device previously detailed in the first experiment. Bumblebees are one of the main prey of last instar and adult *M. vatia* (Morse, 1979; Morse, 1981; Brechbühl et al., 2010c). Not only the colour vision, but also their strong ability to quickly associate a colour with a reward has been demonstrated in these bees (Menzel, 1967; Menzel, 1985). Bees were free to forage on artificial flowers. As for the first experiment, we used both 'white' and 'yellow' colour flowers. One of the two flowers was filled up with sugar solution (Sucrose 1.5M), according to the colours we wanted that bees visit, whereas the other flower was fill up with water. Bees were allowed to feed ad libitum to increase their foraging motivation (Gumbert, 2000). Bees were also fed daily with fresh pollen. They were with the device for around 10 hours, to ensure that all the worker bumblebees of the hive had associated the right colour with the reward before the experiments.

Crab-spider training and test

After one day used for bee learning, we placed a crab spider at the center of a small transparent plastic box (40 mm diameter and 5 mm height) inside the device (**Figure 20B, C**). It was positionned at 50 mm above the ground, and 50 mm of each flower. Movements of each spider were thus constrained by the plastic box. Spiders were left 20 min in the plastic box while bees visited one of the two flowers. We checked that the box does not act as a filter,

especially for UV light. The position of the body axis relative to both flowers was recorded using a camera (Herculex dualpix, Guillemot Corporation, France) during the 20 min of training. As soon as a spider stayed motionless for more than one minute, we measured the angle between the spider body axis and a reference axis, i.e. the axis passing through the spider prosoma and the center of the visited flower (**Figure 20B**). We also assessed the number of bee landing on the flowers for each spider.

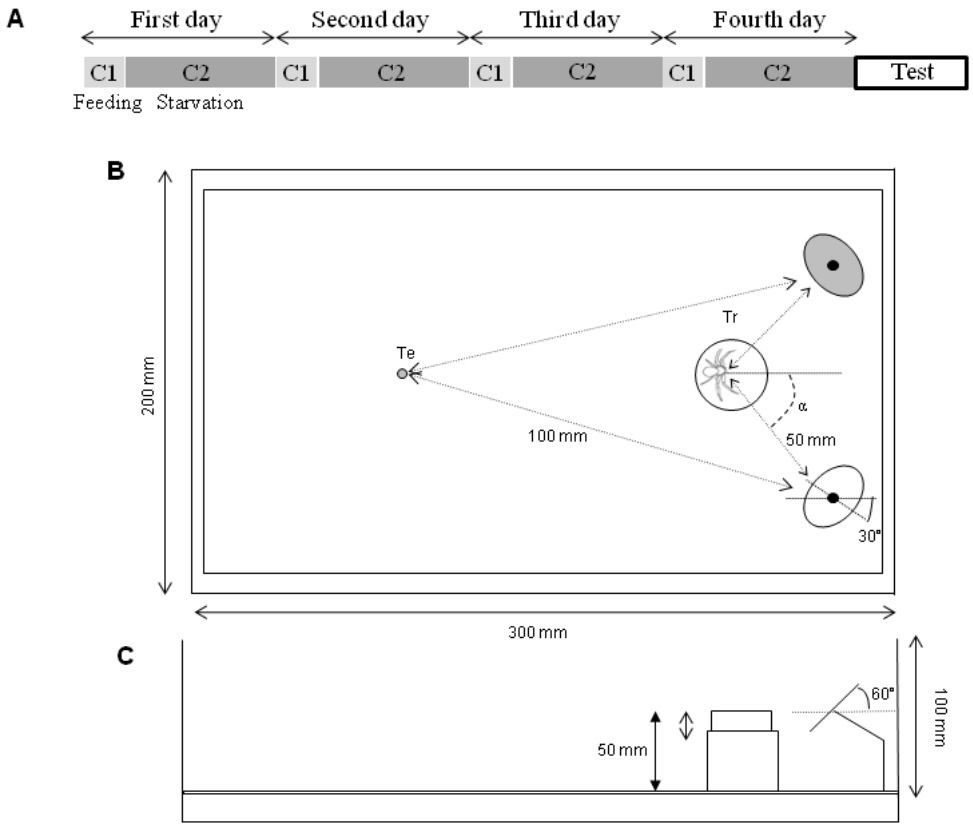

Figure 20: (A) Sequences of 'feeding' and 'starvation' steps used in the training phase of the first experiment. C1 (light grey) indicates the colour associated with the presence of prey (90min) whereas C2 (dark grey) indicates colour associated with starvation (22h30). Top (B) and lateral (C) views of the set up. Tr indicates the position of the spider during training whereas Te indicates the starting point where spiders are released for the test. The angle (α) is between the spider body axis and a referent axis, i.e. the axis passing through the spider prosoma and the center of the visited flower.

After this 20 minutes training phase, spiders were carefully transfered in a second device. This device is identical to the first one, except that the position of the coloured corollas has been inverted to avoid any spatial learning and that bees did not have access to it. In the 'test device', spiders were released 100 mm away of both flowers. They were free to move within

the device. As for the first experiment, the device was bordered with water to constrain spiders within the device. We considered that *M. vatia* made a choice when a contact was made with one of the corolla, after climbing on the stem. We recorded the choice of each spider. Between each experiment, the devices were cleaned to remove silk and to avoid effect of putative olfactory cues.

Control

The position of the body axis during training phase and the frequencies of correct choice were compared to control values. For each series of experiments, we carried out a control experiment consisting of placing spiders in the same 'training' and 'test' protocol, except that the spiders did not experience the presence of bees during the training phase. Spiders were in a plastic box 20min before being transferred and released in the second 'test' device. The control test also allowed us to ensure that *M. vatia* had no preference between white and yellow flowers.

Statistical analysis

We used the binomial exact test to compare a uniform distribution with the observed distribution during the test phase. The angles (α) displayed by spider were analysed by means of circular statistics (Zar, 1984). The V-test (Zar, 1984) was carried out to assess whether the mean angle calculated from the sample was statistically different from the stimulus direction (0°).

Results

First experiment

The control revealed that *Misumena vatia* does not display any preference between white and yellow (Exact binomial test, p=0.32, N=16). During the training phase, each spider caught and ate at least two prey out of the four proposed. In the subsequent test, in which we gave a choice between 'rewarded' and 'unrewarded' colours, spiders visited the two types of colours in a similar proportion, and this irrespective of the learning sequence (Exact binomial test, p=0.84 and p= 0.77 for serie 1 and 2 respectively) (**Figure 21**).

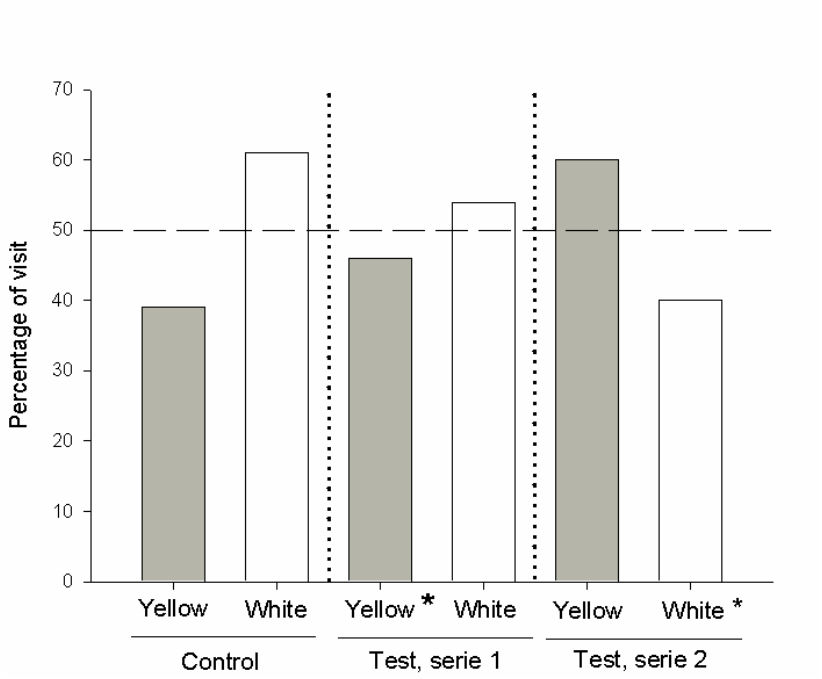

Figure 21: Percentage of visits to yellow and white flowers colour for control experiment (N=16), and for both series of experiment (N=15 for series 1 and 2). Asterisks indicate the rewarded colour during the training phase. The dashed line represents a uniform distribution.

Experiment 2

Naive bees learned quickly to forage on the 'rewarded' colour. The percentage of bees visiting increased indeed abruptly after few visits, up to 100%. After few hours, all bees correctly chose the 'rewarded' colour and did not make any mistakes. This learning was still displayed on the next day. During the training phase, no bees visited the 'unrewarded' flower. We observed an average number of bee visitations of 102±12 and 95±15 when yellow and white are the rewarded colour, respectively.

Whereas the spider orientation had a uniform angle distribution during the 'training' control in the absence bumblebees (V test, $p=0.519$), spiders oriented themselves towards the visited flower colour during the training phase (V test, $p=0.006$ and $p<0.001$ for yellow and white flowers respectively) (**Figure 22**). We found that they choose equally both flower colours when given the choice during the test phase (Exact test binomial, $p=0.88$ for both series) (**Figure 22**). This also applies to control tests in which we did not find any tendency for spiders to choose a specific colour (Exact test binomial, $p=0.85$).

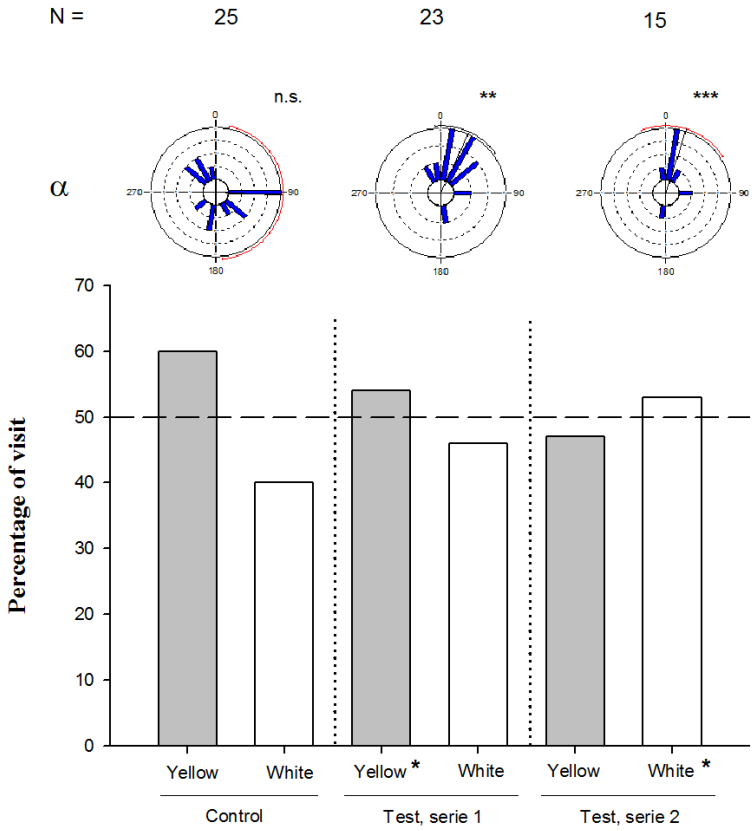

Figure 22: Spider orientation during training and control of the second experiment. Asteriks denote a statistically significant preferred direction around stimulus location. ** $p<0.01$ and *** $p<0.001$. n.s. = non significant. Percentage of visits according to the flower colour in both control (N=25) and test series (N=23 and 15). Asteriks indicate the visited colour during the training phase. The dashed line represents a uniform distribution.

Discussion

Our experiments did not demonstrate colour vision. As mentioned in the introduction, true colour vision through colour learning has been suspected until now in several spider species but behaviourally demonstrated in only one species. Nakamura & Yamashita (2000) showed indeed that the jumping spider *Hasarius adansoni* may learn to avoid a specific hue when associated with a heat shock. In *M. vatia*, we did not revealed colour learning processes, although we noticed that spiders detected and strongly reacted to the presence of prey in the second experiment. We indeed observed that spiders positioned themselves to capture bees in the training phase. This is consistent with the observation that this spider may change quickly from a stem to another in order to capture prey (Chittka, 2001).

Three hypotheses may explain the absence of colour learning in our experiments. The first one is that our experimental conditions may not be suited to test for the colour learning process, despite great care for ecological relevance. The second hypothesis is that *M. vatia* take foraging decision using information at a higher spatial scale than the floral scale. The third hypothesis is that *M. vatia* does not use colour as a reliable cue indicating foraging site quality in the field. These three hypotheses are discussed in turn.

It has been shown, for many species, that the number of trials, the intertrial intervals and the test interval are important variables in the initiation of memory formation and in the determination of the strength of retention (Tully et al., 1994; Kogan et al., 1997; Menzel, 2001). In the first experiment, we used an intertrial interval of 22 hours and 30 minutes, as long intervals between trials are indeed assumed to lead to better acquisition and retention (Menzel et al., 2001). Further experiments are clearly needed to test the effect, on the colour learning process, of intertrial intervals, and of the possibility to catch prey during the training. The second hypothesis is that spiders may also consider both flowers in our experiment as 'one' profitable area, and do not make a distinction between a low and high quality foraging site at a such small scale. Further experiments are needed to assess whether the distance between flowers within a patch could affect the foraging decisions. Finally the last hypothesis is that *M. vatia* does not use flower colour as a reliable cue to assess the prey visitation rate. It has been shown that two different flower species can attract different prey species composition and have different insect visitation rates (Schmalhofer, 2001), despite having the same reflectance spectra. It could be thus irrelevant for a spider to learn to associate a specific flower colour with a high visitation rate. Moreover, a recent study suggested that late instar and adult *M. vatia* do not need to occupy such 'hot spots'. Indeed, Brechbühl et al. (2010c) indicate that *M. vatia* might grow with only one 'big' prey per day, such as flies, honeybees or bumblebees. Earlier, Kareiva et al. (1989) also showed that the giving-up time function on a specific flower was quite flat for *M. vatia*, implying no sharp optimum and no strong selective force on the decisions to leave. Overall, the correlation between flower colour and visit rate might be too low to select for colour learning. It might be more efficient to identify profitable foraging sites using directly the visitation rate.

The two last hypotheses however beget the question of why spiderlings use floral chromatic cues when given the choice between different flower colours (See Article 2), whereas last instar and adults did not do so. The use of colour vision is context dependent (Kelber et al., 2003). Thus, when information about prey availability is lacking, spiders might rely on floral chromatic cues for foraging decisions. However, in presence of prey or after

recently experiencing the presence of prey within a patch, colour may be not relevant in foraging context.

- DISCUSSION GENERALE -

Le camouflage a fait l'objet de nombreuses études (Endler 1984; Endler 1991; McFall-Ngai 1990; Merilaita 1998; Cuthill et al. 2005). Dans cette thèse, nous avons pris le parti d'étudier l'écologie du camouflage chez *Misumena vatia*, partiellement sur le terrain, en utilisant des approches de physiologie sensorielle qui tiennent compte de la communauté des interactions. Cette étude a permis de mettre en évidence (i) les niveaux de contrastes des populations naturelles de *M. vatia*, en tenant compte de la diversité des receveurs et des substrats (chapitre 1); (ii) les sensibilités spectrales de cette araignée, données qui seront importantes dans la compréhension des mécanismes visuels qui affectent la coloration (chapitre 2); (iii) une préférence d'ordre chromatique chez les premiers stades juvéniles qui induit un camouflage chromatique dans le système visuel des proies (chapitre 3). Enfin dans le chapitre 4, (iv) des biotests comportementaux n'ont pas révélé chez les adultes l'utilisation de la vision des couleurs dans la recherche des sites les plus visités par les proies. D'autres travaux sur le camouflage (Théry 2007), le changement de couleur (Insausti & Casas 2008; Insausti & Casas 2009), et l'interaction proie/prédateur (Brechbühl et al. 2010b; Brechbühl et al. 2010c) ont été menés en parallèle à cette étude chez *M. vatia*. La diversité de ces approches et leurs complémentarités font de *M. vatia* une des espèces cryptiques, avec la seiche *Sepia officinalis* (Hanlon & Messenger 1988; Chiao & Hanlon 2001), pour laquelle la compréhension du changement de couleur et du camouflage est la plus avancée. Cependant, les résultats obtenus dans ma thèse posent deux questions fondamentales: quels sont les facteurs influant le changement de couleur et quelle est la valeur adaptative du changement de couleur. Dans une première partie, nous discuterons les mécanismes du changement de couleur. Dans une seconde partie, nous traiterons de l'interprétation fonctionnelle du changement de couleur. La troisième partie abordera la question de l'optimalité des décisions dans le contexte des stratégies de fourragement. Enfin, dans une quatrième partie, nous montrerons la nécessité d'une approche d'écologie sensorielle des communautés chez les espèces cryptiques.

I - Mécanismes du changement de couleur

1.1 Mécanismes d'interaction visuelle

Comme mentionné dans l'introduction générale, ainsi que dans le chapitre 1, il a été démontré que l'interaction visuelle avec la lumière réfléchie du substrat constitue une étape primordiale dans le processus de changement de couleur chez *M. vatia* (Weigel 1941; Théry 2007). L'aptitude à changer de couleur selon le substrat via l'entrée visuelle est supposée chez

de très nombreuses espèces de vertébrés et invertébrés (Needham 1974; Hinton 1976) mais réellement prouvée que chez un nombre restreint d'entre elles, essentiellement invertébrés. Par exemple, chez les orthoptères, *Oedipodia coerulescens* a la capacité d'adapter sa coloration à celle de son substrat (Levita 1970). En effet, des expériences en milieu contrôlé ont permis de montrer que les individus prennent la couleur du substrat sur lequel ils sont élevés. Ils deviennent jaunes sur du sable, rouges sur un sol ferrugineux ou encore noirs sur un substrat sombre. Cette variation de couleur entre individus disparait chez des individus élevés dans l'obscurité ou dont les yeux composés sont peints (Levita 1970).

Différents types de signaux visuels pourraient influer le changement de couleur. Ce processus pourrait être déclenché par des longueurs d'ondes particulières ou par des signaux d'ordre chromatique et/ou achromatique. Nous avons vu dans le chapitre 2 que *M. vatia* possédait, au niveau de toutes les paires d'yeux, un nombre de types de photorécepteurs suffisant pour discriminer le caractère chromatique d'un objet, indépendamment de la composante achromatique. Cette capacité cognitive est nommée 'true colour vision' dans la littérature (Kelber et al. 2003). En effet, chaque paire possède non seulement un type de photorécepteur ayant une sensibilité maximale dans les longueurs d'ondes du spectre correspondant aux ultraviolets (UV) mais aussi un second type ayant une sensibilité maximale dans la région du spectre correspondant au vert (environ 525nm). Ainsi, chez *M. vatia*, différents types de signaux (chromatiques, achromatiques ou longueur d'onde spécifique) sont candidats pour expliquer comment le substrat agit via la vision sur le changement de couleur.

Plus restreint encore est le nombre d'études qui ont permis de révéler quels types de signaux visuels étaient impliqués dans le changement de couleur (Fraser-Rowell 1970; Garcia & Sih 2003a, b). Chez *M. vatia*, comme chez la très grande majorité des espèces qui changent de couleur en réponse aux caractéristiques visuelles de leur substrat, la question concernant quel(s) signal(aux) visuel(s) sont impliqués dans le processus de changement de couleur reste ouverte. Seules des expériences de changement de couleur où chaque composante du substrat pourra être manipulée de façon spécifique permettront de répondre à cette question. Dans les sous-parties suivantes, nous discutons quelques exemples pour chaque type de signal, puis nous analysons la pertinence de ces différents signaux chez *M. vatia* en fonction des caractéristiques de réflectance spectrale des différents substrats observés en milieu naturel.

1.1.1 Les longueurs d'ondes spécifiques

Est-ce qu'une gamme de longueurs d'ondes spécifiques émises par le substrat pourrait influer le changement de couleur ? L'incidence d'une longueur d'onde spécifique ou d'une gamme

restreinte de longueurs d'ondes provenant du substrat sur le changement de couleur n'a jamais été démontrée chez les animaux. Elle a néanmoins été suggérée chez quelques espèces comme *Pieris rapae* and *P. brassicae*. Chez ces deux espèces, les pupes peuvent avoir différents aspects chromatiques (dont vert et marron) et achromatiques pour diminuer leurs contrastes avec le substrat aux yeux des éventuels prédateurs (Hazel, 1995). Plusieurs types de pigments épidermiques comme les caroténoides et les ptérobilines sont responsables de ces différences de chromaticité observées alors que les variations achromatiques proviennent de la quantité de mélanine présente. Le mécanisme responsable de ces variations a été mis à jour par Oltmer (1968). Peu avant la phase de pupe, la perception visuelle de longueurs d'onde réfléchies supérieures à 500nm induirait un changement de couleur adapté au substrat. Cependant, si l'effet d'une longueur d'onde réfléchie par le substrat reste encore à démontrer, l'action d'une longueur d'onde incidente sur la production de pigment au niveau du corps a déjà été montrée chez deux espèces de salamandre, *Ambystoma barbouri* et *A. texanum*, qui, sous l'effet d'une exposition aux ultraviolets, deviennent plus sombres (Garcia et al. 2003b).

Dans le cas de *M. vatia*, les fleurs blanches se distinguent des fleurs jaunes non seulement parce qu'elles reflètent les longueurs d'ondes comprises entre 380 et 450 nm mais aussi parce qu'elles absorbent les UV dans de nombreux cas. Environ 5% des fleurs blanches reflètent les UV et environ 40% des fleurs jaunes (Kevan et al. 1996). La perception de longueurs d'onde spécifiques situées dans l'ultraviolet pourraient-elles déclencher la synthèse d'ommochromes ? Probablement pas, car les observations sur le terrain révèlent que *M. vatia* est jaune sur des fleurs jaunes absorbant l'UV. De plus, nous n'avons pas observé de changement de couleur suite à des expériences visant à exposer *M. vatia* à de fortes quantités de lumière UV réfléchie et incidente (**Figure 23**). On peut donc conclure que les UV, seuls, ne peuvent pas induire la synthèse d'ommochromes.

Des expériences supplémentaires sur l'effet de la présence ou l'absence de certaines longueurs d'ondes réfléchies par le substrat seront à mener pour conclure sur l'influence de ce type de mécanisme visuel.

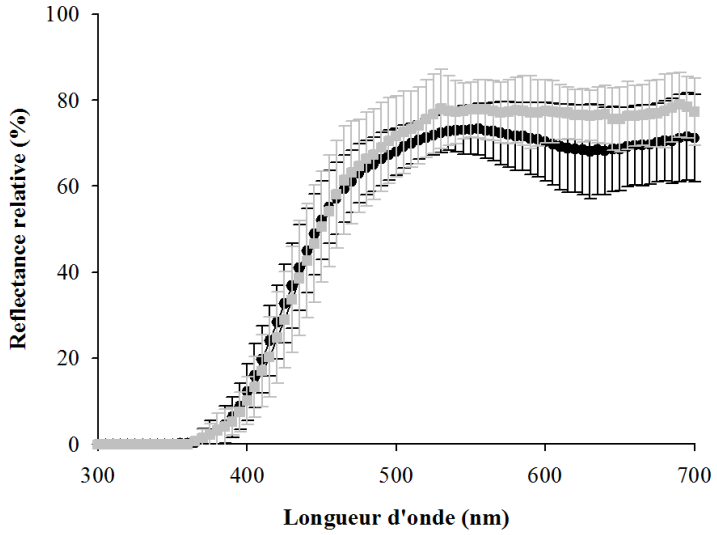

Figure 23: Spectres de reflectance moyen (± s.d.) de *Misumena vatia* blanches (N=10) avant (courbe noire) et après (courbe grise) avoir subi une exposition aux ultraviolets (courbe d'irradiance en annexe) de 15 jours successifs. L'intensité de la lumière UV illuminant les araignées était de 141, 3 µW/cm².

1.1.2 Les signaux chromatiques

Il existe un seul cas avéré de changement de couleur adaptatif dépendant de la perception chromatique du substrat. En 1970, Fraser-Rowell montra que la gamme de couleurs, du jaune à l'orange, que peut arborer l'orthoptère *Gastrimargus africanus* varie en fonction de la réflectance spectrale des substrats. De ces observations, qui s'ajoutent à celle qu'aucune lumière monochromatique ne pouvait à elle seule déclencher le changement de couleur, il a été fortement suggéré que ce processus soit réalisé *via* une discrimination chromatique des substrats. Un signal chromatique spécifique pourrait-il donc influer sur la synthèse d'ommochromes chez *M. vatia*? Des araignées qui apparaissent 'jaunes' pour le système visuel humain sont aussi bien observées chassant sur des fleurs 'jaunes' qui réfléchissent les ultraviolets (comme environ 70% des espèces de fleurs jaunes; Kevan et al., 1996) que sur des fleurs jaunes les absorbant. *M. vatia* étant sensible aux ultraviolets, ces deux groupes de fleurs, qui apparaissent similaires pour nous par l'absence de sensibilité visuelle aux UV, devraient être perçues de manière très différente par l'araignée. En effet, si le codage des informations chromatiques résulte d'une comparaison ou opposition des niveaux d'excitations entre photorécepteurs comme pour la majorité des espèces (voir introduction), les fleurs jaunes réfléchissant ou absorbant les UV vont produire deux types de signaux chromatiques

distincts (UV-/G+ ; UV+/G+). Ainsi, si l'interaction visuelle avec le substrat est d'ordre chromatique, plusieurs types de signaux pourraient être responsables de la synthèse d'ommochromes (coloration jaune). Des expériences qui manipulent les composantes chromatiques du substrat et contrôlent les signaux chromatiques générés chez l'araignée devront être réalisés.

1.1.3 Les signaux achromatiques

Comme pour le signal chromatique, un signal visuel achromatique provenant du substrat et plus particulièrement la composante achromatique de la fleur pourrait moduler le changement de couleur. La larve de la salamandre, par exemple, change sa composante achromatique en réponse à l'albedo, c'est-à-dire en fonction du ratio entre lumière réfléchie par le substrat et lumière incidente (Garcia & Sih, 2003a, b). Un signal achromatique peut-il donc influer sur le changement chromatique de *M. vatia* ? Pour cela il faudrait que les substrats 'jaunes' qui induisent la synthèse d'ommochromes fournissent un ou des signal(aux) achromatique(s) spécifique(s) par rapport aux substrats 'blancs' qui n'entraînent pas de variations chromatiques.

Certains hyménoptères et oiseaux utilisent un type de photorécepteur spécifique pour évaluer la composante achromatique des fleurs (Kelber et al., 2003). Par exemple, l'abeille *Apis mellifera* utilise les signaux générés par ses récepteurs sensibles au vert (Pic d'absorption à 540nm) pour identifier les fleurs à longue distance (Giurfa et al., 1996). Nous nous sommes demandés si les fleurs où sont observées des araignées de couleur 'jaune' pourraient générer un signal achromatique spécifique capté par le récepteur vert des araignées. Nous avons pour cela calculé le flux photonique absorbé par le récepteur vert pour différentes espèces de fleurs 'blanches' et 'jaunes' (**Figure 24**).

On observe que les fleurs 'blanches' et 'jaunes' stimulent le récepteur vert à peu près dans les mêmes proportions. Il est ainsi peu probable que le niveau d'excitation de ce récepteur spécifique intervienne dans le déclenchement du changement de couleur. D'autres mécanismes neuraux basés sur la composante achromatique pourraient néanmoins être impliqués. En effet, chez certaines espèces, dont l'espèce humaine, les signaux achromatiques résultent de la sommation de plusieurs types de photorécepteurs (Krauskopf et al., 1982).

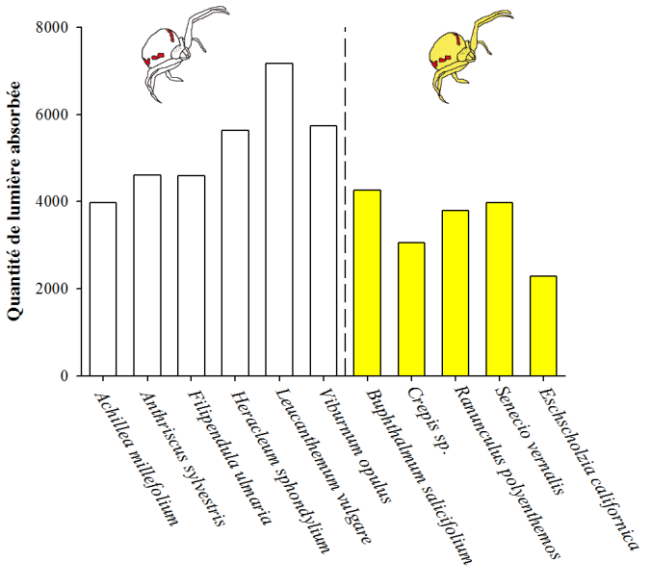

Figure 24: Signal achromatique. Quantité de lumière absorbée par le photorécepteur vert de *Misumena vatia* (maximum d'absorption à 525nm) pour différentes fleurs 'blanches' et 'jaunes'. La couleur de l'araignée représente la couleur prédominante des araignées trouvées sur ces fleurs.

Cependant, chez *M. vatia*, la forte probabilité qu'un troisième type de photorécepteurs, encore non identifié, soit présent au niveau des rétines des yeux antérieurs médians empêche pour le moment de tester ce type de mécanisme achromatique (Insausti & Casas, communication personnelle; Annexe 1). Même si l'effet d'un signal achromatique du substrat sur le déclenchement du changement de couleur est encore à déterminer, on peut néanmoins fortement suspecter que l'intensité du rayonnement réfléchi ou incident influe sur la vitesse de synthèse des ommochromes. En effet, le changement de coloration en laboratoire se déroule dans un laps de temps compris entre 15 et 20 jours (Weigel, 1941; Théry, 2007). Weigel (1941) a montré que ce même changement prenait 10 jours sous serre et seulement 3 à 4 jours dans le milieu naturel. Il a été aussi montré que *M. vatia* manifeste des variations d'intensité avec un rythme circadien sans en connaître la signification biologique (Boutry & Casas ; données non publiées).

1.2 Autres facteurs intervenant dans le changement de couleur chez M. vatia

Il est très probable que quelque soit la nature du signal visuel pertinent pour le changement de couleur, il n'est pas le seul facteur déterminant. S'il a été montré que la lumière réfléchie module la synthèse et le catabolisme des ommochromes comme démontré ci-dessus, plusieurs expériences suggèrent fortement qu'ils ne sont pas les seuls. En effet, Théry (2007) observa

qu'un grand nombre d'araignées blanches placées sur un substrat jaune n'entamait jamais le processus de synthèse d'ommochromes. De plus, des expériences répétées en laboratoire, similaires à celles de Théry (2007) et en milieu naturel révélèrent qu'environ seulement 25% des araignées blanches placées sur un substrat jaune devenaient jaunes, alors que le passage du jaune au blanc semble lui systématique (observation personnelle) et peut être assimilé à une décoloration. Ainsi, des araignées soumises à des conditions environnementales identiques et à une même source de nourriture présentent une plasticité de réponse importante au niveau de la synthèse d'ommochromes. D'autres facteurs comme la nourriture ou la reproduction pourraient agir de façon combinée avec la réflectance du substrat. Théry (2007) montra notamment que le type d'alimentation influe le changement de couleur chez *M. vatia*.

1.3 Une dépendance hormonale du changement de couleur ?

L'influence hormonale dans le processus de changement de couleur morphologique a été mise en évidence chez de nombreuses espèces. Bien que cette relation soit peu étudiée chez les araignées, il a déjà été montré chez les invertébrés que des hormones stéroïdes et juvéniles peuvent moduler la synthèse de pigment comme la mélanine, la biline, les caroténoïdes et les ommochromes (Bagnara, 1961; Kreiner et al., 1973). Comme la couleur jaune de *M. vatia* résulte de la synthèse d'ommochromes, nous allons nous intéresser plus particulièrement à des exemples d'hormones qui ont été directement identifiées comme étant associées à la synthèse d'ommochromes.

Chez les insectes, il existe plusieurs exemples où la synthèse d'ommochromes est régulée par l'hormone juvénile (JH). Chez l'orthoptère *Locusta migratoria*, des adultes traités par injection de JH pendant le dernier stade larvaire peuvent contenir une quantité d'ommochromes 2 à 3 fois supérieures par rapport à des adultes non traités (Bouthier, 1976). La larve du vers à soie *Bombyx mori* possède des zones colorées composées de différents types de pigments comme la mélanine, des ptéridines et des ommochromes qui sont sous l'influence de la concentration en hormone juvénile dans l'hémolymphe (Kiguchi, 1974). Une autre hormone, l'ecdysone, qui agit souvent en interaction avec l'hormone juvénile, est connue pour influer aussi sur la synthèse d'ommochromes chez les arthropodes (Karlson & Sekeris, 1966). La synthèse d'ommochromes chez *Cerula vinula* par exemple, ne se réalise qu'à des moments précis du développement qui correspondent à des niveaux spécifiques d'ecdysone dans l'hémolymphe. Ainsi chez cette espèce, la mue et le changement de couleur sont régulés par des niveaux de concentrations différents de la même hormone (Fuzeau-Braesch, 1972).

Chez *M. vatia*, une des hypothèses pour expliquer l'absence de synthèse d'ommochromes chez des araignées blanches placées sur un substrat 'jaune' est que le changement de couleur du blanc au jaune dépend de la concentration d'une hormone spécifique. Il se pourrait donc que la synthèse d'ommochromes ne puisse être déclenchée qu'à des concentrations spécifiques d'une certaine hormone. Chez les araignées, la caractérisation et le rôle des hormones sont très peu étudiés, comparé aux connaissances disponibles chez les insectes et les crustacés. Une seule étude sur *Pisaura mirabilis* a permis pour l'instant de montrer l'effet de l'hormone juvénile ou de leurs analogues sur le développement post-embryonnaire (Bonaric, 1988). Quant à l'ecdysone, des études ont révélé que la 20-hydroxyecdysone influait sur le comportement sexuel et le cannibalisme chez la femelle *Tegenaria atrica* (Trabalon et al., 2005), ainsi que sur la vitellogénèse (Pourié & Trabalon, 2003). Enfin, le rôle de l'ecdysone dans le phénomène de mue a été fortement suggéré chez *Pisaura mirabilis*. Chez cette araignée, il a été mesuré comme chez les autres arthropodes une forte augmentation de la concentration d'ecdysone les jours précédant l'exuviation (Bonaric & De Reggi, 1977). Chez *M. vatia*, des dosages des taux d'hormone juvénile et d'ecdysone ou de leurs analogues et leurs injections pourraient être réalisés pour connaître l'influence de ces hormones sur la synthèse d'ommochromes.

II - Interprétation fonctionnelle de la coloration chez *M. vatia*

Une des grandes questions, inattendue, qui émerge des résultats obtenus dans cette thèse (Chapitre 1 et 3) et ceux de l'équipe Suisse (Brechbuhl et al., 2010b, c) est s'il existe bel et bien un lien entre la coloration de *Misumena vatia* et son succès de fourragement. Cette question renvoie inévitablement à la fonction du changement de couleur chez cette espèce. Notre étude et celles des suisses apportent à la fois des éléments qui vont dans le sens de l'hypothèse de la coloration comme moyen de camouflage, et d'autres qui l'invalident. De façon intéressante, Rabaud, dès 1923, rapportait qu'il n'est pas rare d'observer des *M. vatia* d'une couleur bien différente de celle de leurs substrats avec malgré tout un certain succès en terme de capture de proie. Nous allons ainsi consacrer une partie de ce chapitre à synthétiser les connaissances indispensables à posséder pour estimer le niveau de pression de sélection sur la coloration dans l'interaction araignée crabe-proies. Nous détaillerons ensuite les expériences à effectuer afin de pouvoir clairement se prononcer. Enfin, nous discuterons des fonctions alternatives possibles au changement de couleur chez *M. vatia*.

2.1 Ecologie évolutive des interactions araignées crabe-proies

Pour identifier de manière précise la pression de sélection sur la coloration par les proies, on se doit de prendre en compte la réaction des proies face à des contrastes colorés, leurs capacités cognitives et l'écologie de la prédation de l'araignée. On se doit de s'interroger aussi sur les bases évolutives des comportements d'évitements innés chez les proies. Ces différents aspects sont discutés dans les paragraphes suivants.

2.1.1 L'impact du contraste chromatique et achromatique sur l'interaction comportementale avec les proies

De nombreuses études se sont intéressées aux réponses comportementales des proies face à la présence d'une araignée crabe visible. Cependant, aucune d'entre elles n'a pris en compte le système visuel des receveurs, impliquant que la distinction 'araignée camouflée/visible' est basée sur une appréciation et une vision humaine. Ces expériences ont néanmoins pu démontrer que les proies ne réagissent pas toutes de façon similaire à la présence d'une araignée crabe.

Plusieurs études expérimentales ont montré que certains diptères comme *Eristalix tenax* ou hyménoptères comme *Apis mellifera*, *Bombus terrestris*, *Colletes sp.* visitaient les fleurs malgré la présence d'une araignée crabe chromatiquement visible (Ings & Chittka, 2008; Brechbühl et al., 2010a, 2010b). Brechbuhl et al. (2010b) ont notamment montré que le nombre de visites des proies était similaire entre une fleur où était placée une araignée de la même teinte, et la même fleur où était placée une araignée de teinte différente. Cependant, ces deux situations, qui pour l'œil humain semblent refléter un cas de camouflage et un de non-camouflage, traduisent en réalité une seule et même situation de non-camouflage pour un certain nombre de proies comme les hyménoptères (**Figure 25**).

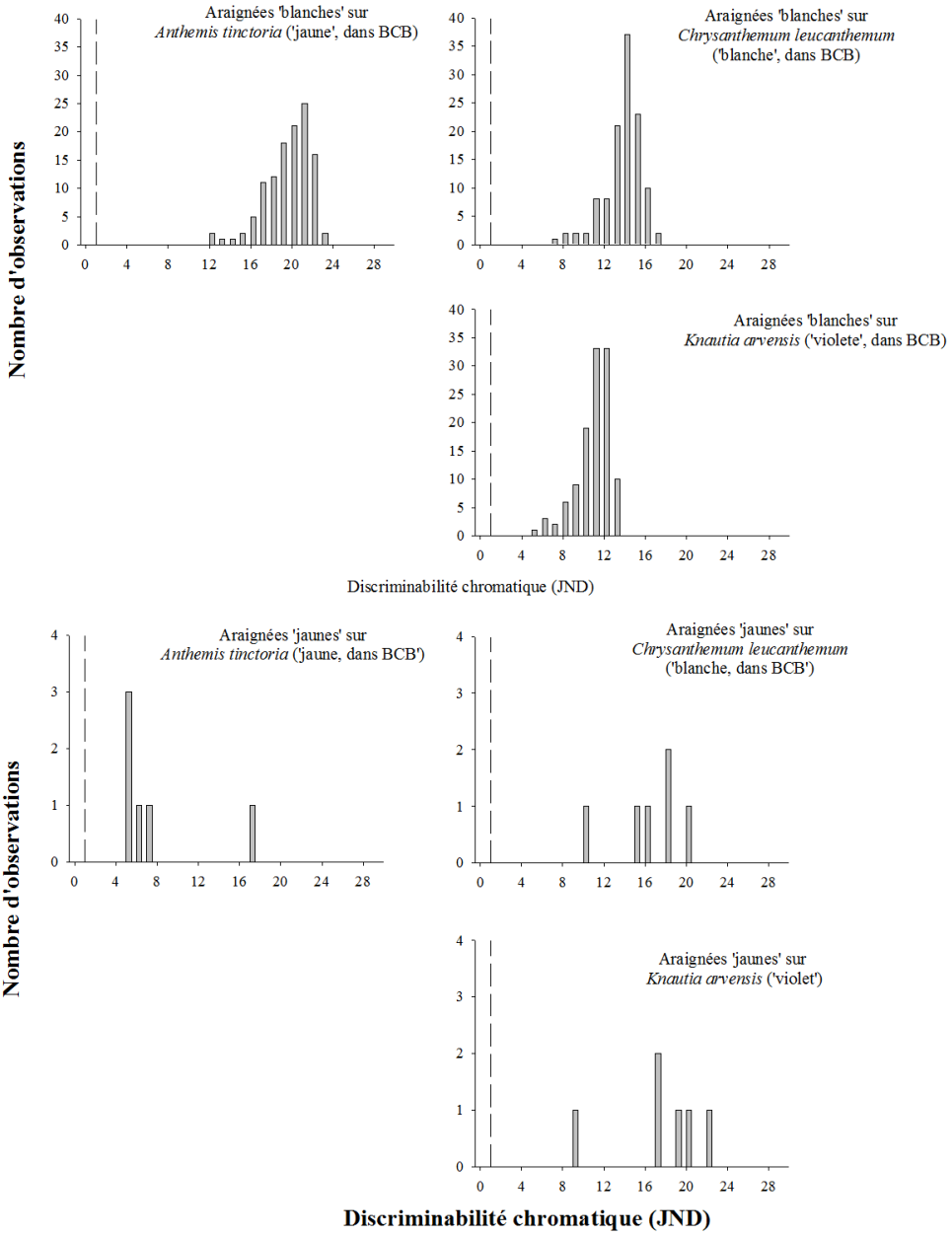

Figure 25: Distribution des valeurs individuelles de discriminabilité chromatique en JNDs ('Just noticeable difference') pour des *Misumena vatia* blanches (N=120) et jaunes (N=6) sur les fleurs utilisées dans l'étude de Brechbühl et al. (2010) (*C. leucanthemum, A tinctoria* et *K. arvensis*) dans le système visuel des abeilles. Pour les détails de calcul, se référer au chapitre 1. Les lignes verticales indiquent le seuil de discrimination chromatique pour le système visuel des abeilles. Toutes les araignées proviennent de la région de Tours.

L'idéal serait de comparer le nombre de visite des proies entre une araignée cryptique et visible du point de vue de la proie. Ces mêmes études ont aussi révélé que des espèces particulières de syrphes et d'hyménoptères évitent les fleurs qui sont occupées par une araignée. Cependant, on ne sait pas si ces comportements anti-prédateurs sont basés sur la perception des contrastes chromatiques. En effet, la comparaison entre l'absence et la présence d'araignée laisse la possibilité que de tels comportements soient expliqués par la présence même de l'araignée, indépendamment de son contraste chromatique. Comme pour l'aspect chromatique, l'impact du contraste achromatique sur les proies reste inconnu. On ne sait pas quel est le rôle du contraste achromatique dans les comportements anti-prédateurs précédemment évoqués et dans l'absence de réactions face à une araignée. Pourtant, *M. vatia* semble indétectable dans l'achromatique pour les hyménoptères quelque soit la fleur sur laquelle elle se trouve (Chapitre 1). La question est donc de savoir si ce camouflage parfait est le fruit du hasard ou lié à la sélection naturelle. Les prochaines études se devront d'étudier de façon indépendante le rôle de la composante chromatique et achromatique et d'analyser la crypticité en fonction du système visuel des proies.

2.1.2 L'importance de prendre en compte les capacités cognitives des receveurs

Pour quantifier les pressions évolutives, on se doit aussi de considérer les comportements des receveurs. Un exemple concret est donné par les études d'Ings & Chittka (2008) sur les bourdons *Bombus terrestris*. Un bourdon 'naïf' visite une fleur occupée par une araignée même si le contraste chromatique engendré est élevé. La pression de sélection sur ce contraste par ce type d'individu est donc très faible voire nulle. Cependant, après avoir subi plusieurs attaques ratées par l'araignée (le taux de capture d'un bourdon est de 3% ; Brechbühl et al., 2010b), un bourdon développe des capacités cognitives qui lui permettent de diminuer le risque de prédation. Certains bourdons par exemple peuvent augmenter le temps d'inspection des fleurs au détriment de la rapidité du fourragement ('Speed-accuracy trade offs') (Ings & Chittka, 2008). Ce type de comportement va favoriser les araignées cryptiques. Ainsi, selon son état (naïf ou expérimenté), un individu ne va donc pas agir de la même façon sur la coloration de l'araignée. La proportion de bourdons naïfs va donc déterminer le niveau de pression exercée par ce type de proie sur la coloration. Le niveau de pression 'moyen' (à une échelle populationnelle) pourra être mesuré sur le terrain, car une comparaison du nombre de visites entre une fleur occupée par une araignée cryptique et une araignée visible tiendra compte des habilités cognitives des proies, et de la proportion relative de proies naïves.

2.1.3 Un système multi-proies

Outre la grande diversité des substrats floraux sur laquelle *M. vatia* peut être observée, cette espèce de prédateur généraliste chasse de nombreuses espèces de proies appartenant à différentes familles. Il est commun qu'un prédateur cryptique immobile soit généraliste et qu'il ait donc à interagir visuellement avec un grand nombre d'espèces, chacune ayant des capacités visuelles qui lui sont propres.

2.1.4 Bases évolutives des comportements d'évitements innés chez les proies

Même si il reste, comme énoncé dans les paragraphes précédents, à déterminer quels signaux visuels sont utilisés pour déclencher ou non une réaction chez une proie, on peut se demander finalement ce qui explique que certaines espèces de proies possèdent des stratégies innées de défense alors que d'autres non (Brechbuhl et al., 2010b; Yokoi & Fujisaki, 2009). La première raison serait liée aux risques en terme de succès reproducteur qu'implique de visiter des fleurs occupées par une araignée. Brechbhul et al. (2010b) supposent en effet que les espèces solitaires seraient plus à même de développer de tels comportements que les espèces sociales. Chez les espèces sociales, où la fitness des ouvriers est liée à celle des reproducteurs au sein de la colonie, la perte d'un individu, et plus particulièrement celle d'une ouvrière, est en effet négligeable à l'échelle de la colonie. Une seconde raison tiendrait à la taille de la proie. On peut imaginer que la taille pourrait constituer à elle seule un moyen de défense efficace. Les grosses proies devraient subir un nombre d'attaques plus faibles que les proies de tailles moyennes, puisque seules les araignées adultes les chassent. Une fois l'attaque lancée, on ne note toutefois aucune corrélation entre la taille de la proie et le taux de succès (Brechbuhl et al., 2010b).

2.2 *De la théorie à la pratique: La nécessité d'une approche sensorielle et comportementale intégrée*

Comme décrit dans les paragraphes précédents, malgré la diversité des études portant sur les effets de la coloration chez les araignées crabe, il n'y a pas, à ce jour, de démonstration empirique d'un bénéfice, notamment en terme de prédation. Seule une étude impliquant (i) une approche communautaire ; (ii) des modèles physiologiques spécifiques pour évaluer les contrastes, et (iii) les réactions comportementales des proies permettra de définir l'importance de la coloration dans la prédation.

La première étape consistera à mesurer sur le terrain la relation entre le degré de contraste de *M. vatia* et le taux de visites sur différents substrats pour un maximum d'espèces de proie. La

gamme de contraste chromatique devra recouvrir aussi bien des cas de camouflage que des situations de visibilité des araignées, ceci impliquant de maitriser le degré de contraste des araignées dans le système visuel des différentes proies. De plus, la réponse des proies face à des araignées cryptiques donnera de précieuses indications sur la présence de signaux, autres que chromatiques, émis par l'araignée, et impliqués dans les comportements anti-prédateurs. Enfin, il est à noter que de telles études sur le terrain ne permettront pas d'évaluer l'impact de l'apprentissage sur le type de relation obtenue. Seul des travaux similaires à ceux effectués par Ings and Chittka (2008), où 'l'historique' des individus approchant les fleurs est connu et contrôlé, pourront contribuer à mesurer l'effet de l'apprentissage sur le taux de visite.

La deuxième étape consiste à déterminer comment l'ensemble des relations obtenues pour chaque espèce interagit pour façonner la coloration de *M. vatia*, en d'autres termes de passer d'une relation propre à chaque espèce à une relation globale (à une échelle communautaire) qui tiendrait compte de l'ensemble de ces relations et de leur poids relatif. Dans cette hypothèse, des paramètres spécifiques comme la masse des proies capturées, le taux de capture et la fréquence de visite peuvent se révéler primordiaux dans la compréhension du type de relation 'globale' entre coloration et prédation. Il faudra aussi clairement déterminer si *M. vatia* est sous pression de sélection par des prédateurs, tels que les oiseaux.

2.3 La coloration chez les Thomisidae

La question du rôle de la coloration et du changement de couleur peut être abordée aussi en observant les couleurs et l'écologie des araignées crabe. Un grand nombre d'espèces d'araignées crabe chassant dans les fleurs manifeste des variations chromatiques et/ou achromatiques sur l'ensemble ou sur des zones restreintes du corps. Que ce soit les zones où la coloration est fixée ou les zones qui changent de couleurs, il semble cependant que la concordance entre coloration de l'araignée et du substrat ne soit pas toujours la règle. *Synaema sp.* par exemple a (i) le céphalothorax et une partie de l'abdomen qui ont coloration noire et qui contrastent fortement avec les couleurs des substrats fréquemment utilisées; (ii) les zones latérales inférieures de l'abdomen où l'on observe des variations de couleurs (rouge, orange, jaune) qui ne semblent pas s'harmoniser avec celles des substrats (Théry & Casas, 2009). Comme chez *M. vatia*, le rôle de la coloration et du changement de couleur reste ouverte chez ces espèces, et notamment celle sur le lien entre coloration et prédation. On peut se demander cependant si les changements de couleurs ont une origine commune chez ces espèces écologiquement très proches. Le seul exemple concret où une prédation facilitée, liée à la coloration, a été révélé concerne l'araignée crabe Australienne *Thomisus spectabilis*

(Heiling et al., 2005). Cette araignée crabe choisit des substrats sur lesquels elle produit un contraste UV important, ce qui aurait pour conséquence d'attirer certaines proies et donc d'augmenter le taux de visite. On ne se trouve donc pas alors dans un cas de camouflage.

2.4 Fonctions alternatives du changement de couleur

Comme énoncé dans l'introduction, la coloration d'un individu à un moment donné peut avoir diverses fonctions autres que le camouflage, ou complémentaires à ce dernier. Ainsi, chez *M. vatia*, les changements de coloration pourraient apporter un autre type de bénéfice que celui d'augmenter son efficacité de prédation. Théry et Casas (2009) suggèrent que le camouflage pourrait ne pas être la force de sélection sous-jacente au changement de couleur. Chez cette espèce, la cuticule est transparente et l'exposition continue aux radiations solaires. Ils se demandèrent si les granules d'ommochromes ne pourraient pas servir à se protéger des effets délétères des UV, comme dans les yeux d'insectes (Langer, 1975). Cependant, des tests en conditions contrôlées ont révélé qu'une exposition continue aux UV-A ne déclenchait jamais la synthèse d'ommochromes chez des araignées blanches (**Figure 23**). Théry (2007) émis l'hypothèse que les variations de coloration pourraient jouer un rôle dans la communication intraspécifique (Heiling et al., 2005). Malheureusement, à ce jour, aucune étude n'a traitée la coloration dans un tel contexte. Enfin d'autres fonctions liées au métabolisme énergétique suggéré par la forte quantité de glycogène observée dans les cellules pendant le cycle de pigmentogenèse (Insausti & Casas, 2009), ou encore liées à la maturation ovarienne devront être testées. En conclusion de cette seconde partie, la fonction cryptique de la couleur chez *M. vatia* reste pertinente de par certains éléments de cette thèse, mais elle est mise à mal par d'autres arguments tout aussi persuasifs (**Tableau 2**). La future étude à mener, décrite précédemment, basée sur les travaux de Brechbühl et al. (2010a, b) permettra d'apporter un certain nombre de réponses à la question de l'interprétation fonctionnelle de la coloration chez *M. vatia*.

		Arguments **pour** l'utilisation de la couleur dans la prédation		Arguments **contre** l'utilisation de la couleur dans la prédation	
		Premiers stades juvéniles	Derniers stades Juvéniles et adulte femelle	Premiers stades juvéniles	Derniers stades Juvéniles et adulte femelle
Critères	Degré de contrastes dans le système visuel des hyménoptères.	⊘	Indétectable dans l'achromatique (Chapitre 1)	⊘	Visible chromatiquement (Chapitre 1)
	Préférence colorée	Préférence pour une couleur de substrat qui permet d'être peu visible chromatiquement (Chapitre 2)	⊘	⊘	Absence d' apprentissage (Chapitre 3)
	Réponses comportementales des proies face à une araignée crabe	Certaines petites proies semblent éviter les fleurs occupées par araignées chromatiquement visibles (Brechbuhl et al., 2010a)	⊘	⊘	Les grosses proies visitent des fleurs occupées par araignées chromatiquement visibles (Brechbuhl et al., 2010a)
	Ecologie des araignées crabes autres que *M. vatia*	Présence d'espèces ayant un changement de couleur leur permettant d'être indétectable pour les proies et les prédateurs		Présence d'araignées à forts contrastes sur les fleurs et attrapant des proies similaires à celles de *M. vatia*.	

Tableau 2: Eléments allant dans le sens et à l'encontre de l'hypothèse de l'utilisation du camouflage dans la prédation chez *Misumena vatia*. Le pictogramme indique l'absence de donnée.

III - Optimal foraging ou Satisficing ?

L'optimisation est à l'origine un concept économique qui repose sur la maximisation des gains par **unité de temps**. Les biologistes évolutifs ont rapidement intégré cette notion dans l'étude des stratégies de recherche de nourriture, considérant que la sélection naturelle devrait avoir favorisé les stratégies les plus optimales (Pyke et al., 1977; Pyke, 1984). La notion d'optimisation, quelque soit son champ d'application, est indissociable de la notion de contraintes. Ce sont en effet les contraintes, qu'elles soient temporelles, environnementales ou physiologiques, qui vont façonner les caractéristiques optimales à adopter pour une espèce (MacArthur & Pianka, 1966). La théorie de l'Optimal Foraging' est donc apparue *via* l'idée que dans un cadre de contraintes données, les individus les plus efficaces dans leur recherche de nourriture auraient une meilleure valeur adaptative ('Fitness'). Des modèles d'Optimal Foraging' permettant de vérifier si les prédictions étaient cohérentes avec des données empiriques, et donc de déterminer si les espèces possèdent des stratégies de fourragement

optimal ou du moins qui se rapprochent de l'optimalité ont été proposés dans les années 70 (Schoener, 1969; Rapport, 1971; Charnov, 1976a, b; Best & Bierzzychudek, 1982). L'utilisation complémentaire des prédictions des modèles et des données empiriques ont permis de révéler des cas où les espèces utilisent les ressources de manière optimale (Cowie, 1977; Pyke, 1978; Howell & Hartl, 1980; Tome, 1988). Cependant, en parallèle, un grand nombre d'études ont aussi montré que pour d'autres espèces, les observations de laboratoire ou de terrain ne correspondaient pas avec les prédictions (Nonacs, 2001). Pour expliquer ces divergences, certains auteurs ont lancé l'idée que l'Optimal Foraging' pouvait ne pas être l'unique stratégie de fourragement utilisé par les animaux. Ward (1992) proposa le concept de 'satisficing' développé par l'économiste Herbert Simon (1955) comme possible alternative à l'Optimal Foraging'. Le 'satisficing' est défini par deux notions complémentaires : (i) satisfaire des besoins minimum et (ii) choisir parmi un ensemble de comportements quand l'intégration des informations ou les contraintes de temps limitent l'habilité d'un décideur de prendre une décision optimale. Même si ce concept a fait l'objet de débats intenses sur sa validité, cette théorie alternative semble se vérifier chez un certain nombre d'espèces (Carmel & Ben-Haim, 2005). Chez les araignées crabe, au vue de certaines caractéristiques écologiques que nous discuterons dans les paragraphes suivants, on peut se poser la question si les araignées crabe optimisent leur activité de fourragement ou se contentent du minimum ?
Pour des espèces prédatrices d'insectes pollinisateurs, l'optimisation du fourragement passe par l'occupation des fleurs les plus visitées. Pour les araignées crabe, une telle stratégie peut se réaliser en adaptant le temps d'occupation en fonction du nombre de visites, ce qui en d'autres termes, signifie abandonner rapidement les fleurs peu ou pas visitées pour augmenter la probabilité de trouver une fleur très visitée (Morse, 2007). Kareiva & Morse (1989) décidèrent de tester cette hypothèse par l'utilisation de différents modèles. Les simulations du temps que devrait rester une araignée sur une fleur en fonction du nombre de visites et les observations sur le terrain furent assez divergentes. Ils notèrent en effet que les araignées peuvent rester plusieurs jours sur une fleur pas visitée alors que l'optimisation aurait nécessité de les quitter rapidement. Ils en conclurent que les araignées quittent les fleurs de façon aléatoire. Mais pourquoi rester sur des fleurs peu visitées ? Brechbuhl et al., (2010c) ont récemment émis l'hypothèse que les *Misumena vatia* adultes pouvaient probablement se contenter d'une seule grosse proie par jour. La question est de savoir si chasser sur une fleur qui permet d'attraper une grosse proie par jour peut être considéré comme de l'optimal foraging ?

Comme mentionné précédemment, une des caractéristiques du 'satisficing' est la présence de contraintes temporelles ou d'informations lors des décisions. L'activité de fourragement des araignées crabe se déroule dans un cadre environnemental soumis à des variations non prédictibles à différentes échelles spatiales et temporelles. La qualité d'un substrat va fortement varier selon l'espèce de fleurs, mais aussi selon le patch de fleurs. De plus, pour une même fleur, le taux de visite va varier fortement à la fois au cours d'une journée et entre plusieurs journées successives selon les conditions météorologiques qui vont affecter l'activité de fourragement des proies. Enfin, la période d'activité des araignées et des proies peut varier fortement d'une année à l'autre. On peut penser que des animaux comme les araignées crabe qui subissent un niveau de variabilité environnementale spatiale et temporelle élevée à court et moyen termes pourraient favoriser des stratégies alternatives comme le 'satisficing'. Le concept d'optimal foraging' pourrait ne plus être pertinent dans les cas où la notion de prédictibilité est absente. De plus, le fait de changer de fleur pourrait induire des coûts surpassant ceux de rester sur une fleur peu visitée.

IV – L'importance de l'approche écologie sensorielle des 'communautés' dans l'étude du camouflage

Un point fondamental qui ressort de cette étude sur le camouflage est l'importance de prendre en compte la diversité des interactions écologiques propre à l'organisme étudié. Dans le contexte du camouflage, on se doit ainsi de considérer tous les différents principaux protagonistes.

Peu nombreux sont cependant les travaux qui ont abordés l'étude du camouflage chez une espèce à changement de couleur morphologique en relation avec les différents partenaires potentiels. Le niveau de contraste chromatique et achromatique des caméléons sur leur substrat a été mesuré par exemple dans le système visuel de deux types de prédateurs, les oiseaux et les serpents (Stuart-Fox et al. 2006). La plupart des études étudient cependant le camouflage d'une espèce en se focalisant sur un seul receveur. Pourtant, le mimétisme, agressif ou défensif, se déroule rarement uniquement entre deux protagonistes. Les phasmes doivent faire face par exemple à différentes espèces de prédateurs qui utilisent les contrastes pour les repérer comme les oiseaux, les araignées ou certains mammifères (Reitze & Nentwig, 1991). Les prédateurs immobiles cryptiques ont eux aussi souvent à interagir avec de multiples proies. Outre l'exemple des araignées crabe, la grenouille cryptique *Ceratophrys*

cornuta attend immobile pour attraper des proies aussi diverses que des insectes ou des petits vertébrés (Duellman & Lizana, 1994). Or, chaque receveur a des capacités visuelles, des stratégies comportementales innées ou apprises qui peuvent lui être propre. Chez l'araignée crabe, on retrouve une forte variabilité du niveau de contraste chromatique émis par une araignée selon qu'elle est observée par un passereau, une abeille ou une mouche (Chapitre 1), et aussi une variabilité dans les réponses des proies face à la présence d'une araignée visible (Brechbühl et al., 2009; Brechbühl et al., 2010). Cette spécificité à l'échelle de chaque partenaire limite la portée des conclusions des études où un seul receveur est considéré. De plus, une perspective communautaire est presque obligatoire si on s'intéresse à la manière dont les forces de sélections façonnent la coloration de l'animal. En effet, si plusieurs proies et/ou prédateurs interagissent avec un organisme, la coloration va résulter d'un compromis entre toutes ces pressions de sélection, chacune avec son poids propre.

Conclusion

L'apport principal de cette thèse est de montrer qu'une approche d'écologie sensorielle à l'échelle de la communauté est nécessaire dans l'étude du camouflage. Cependant, la pertinence de cette approche reste fortement dépendante du niveau de connaissances sur la vision des principaux protagonistes. En effet, l'écologie sensorielle nécessite un savoir sur la physiologie sensorielle et les traits d'histoire de vie des protagonistes disponible que pour très peu d'espèces. Je montre dans cette thèse que *M. vatia* constitue une des espèces les plus adaptées pour ce type d'approche, et propose des pistes pour continuer son étude.

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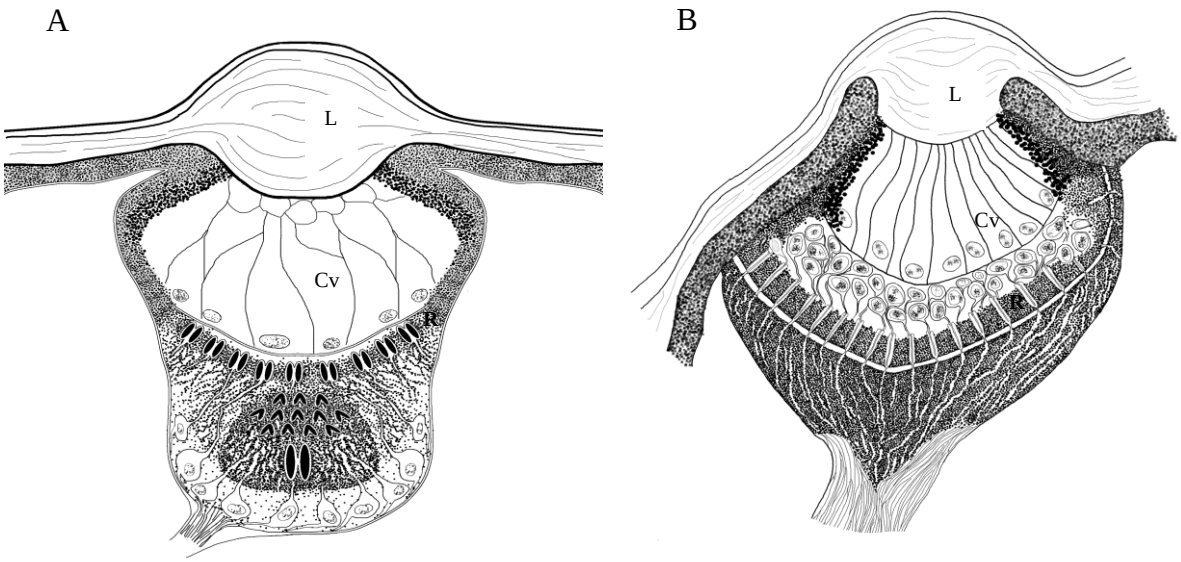
- ANNEXES –

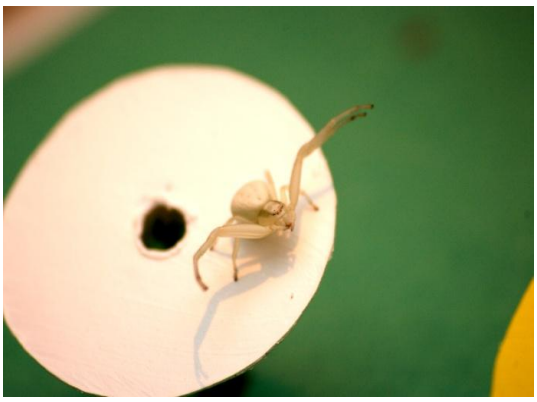
Annexe 1: Structure de la rétine des yeux principaux (**A**) et secondaires (**B**) chez *Misumena vatia*. La rétine des yeux principaux diffèrent fortement des yeux secondaires. En effet, alors que les yeux secondaires possèdent une rétine contenant une couche unique de photorécepteurs formant des rhabdomes de morphologie identique, les yeux principaux abritent une rétine composée de trois couches de rhabdomes morphologiquement distincts. Figures adaptées de Insausti, T., Lazzari, C. and Casas, J. (Unpublished data). R = Rhabdome, L = Lentille et Cv = Corps vitreux.



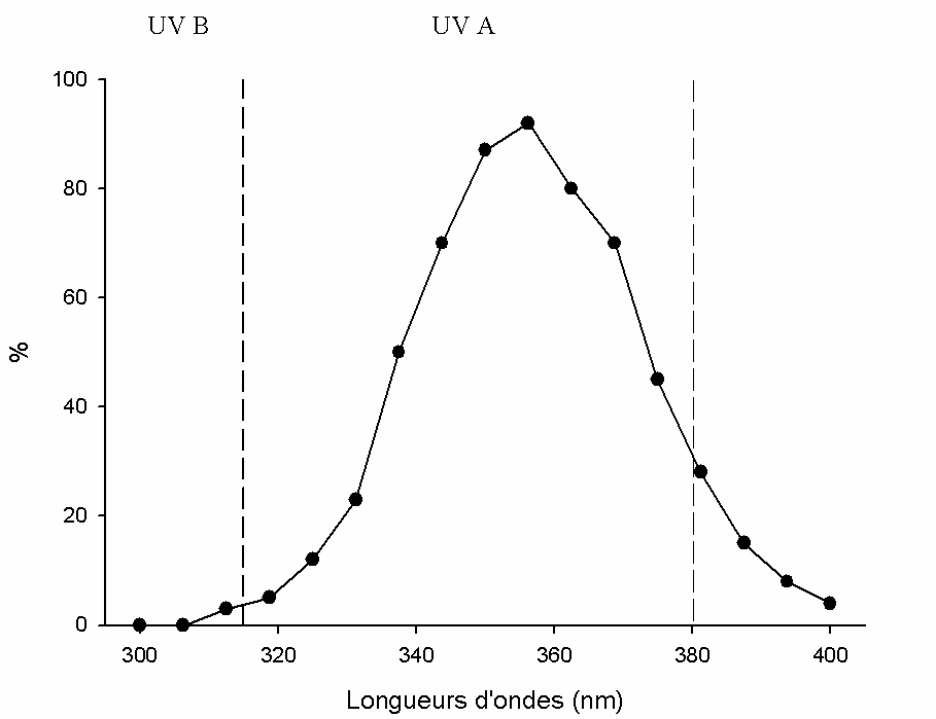
Annexe 2:

A: Araignée crabe observant des proies potentielles (*Bombus terrestris*) visitant la fleur flaune lors de la phase d'entrainement de l'expérience 2 du chapitre 3. Le but de cette expérience est de tester si l'araignée est capable d'associer une couleur de fleur avec la présence de proies. Sur la photo, l'axe du corps de l'araignée est dirigé vers la fleur visitée par les bourdons.

B: Positionnements de *Misumena vatia* observés à la fois sur les fleurs en milieu naturel et sur les fleurs artificielles utilisées dans les expériences du chapitre 2 et 3.



Annexe 3: Composition spectrale du Néon UV Eversun Osram L100W79. UV A = Ultraviolet A. UV B = Ultraviolet B.



Annexe 4:

The multiple disguises of spiders

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Short title: Spider and web disguise

Summary

Diverse functions have been assigned to the visual appearance of webs, spiders and web decorations, including prey attraction, predator deterrence and camouflage. Here, we review the pertinent literature, focusing on potential camouflage and mimicry. Webs are often difficult to detect in a heterogeneous visual environment. Static and dynamic web distortions are used to escape visual detection by prey, although particular silk may also attract prey. Recent work using physiological models of vision taking into account visual environments rarely support the hypothesis of spider camouflage by decorations, but most often the prey attraction and predator confusion hypotheses. Similarly, visual modelling shows that spider coloration is effective in attracting prey but not in conveying camouflage. Camouflage through colour change might be used by particular crab spiders to hide from predator or prey on flowers of different coloration. However, results obtained on a non-cryptic crab spider suggest that an alternative function of pigmentation may be to avoid UV photodamage

through the transparent cuticle. Numerous species are clearly efficient locomotory mimics of ants, particularly in the eyes of their predators. We close our paper by highlighting gaps in our knowledge.

1. Introduction

This paper aims at a broad exploration of the literature pertinent to the subject of spider camouflage, from web colour and decorations, body colour to movement. It is an extended and updated version of a previous paper (Théry & Casas, 2009). Several functions have been assigned to spider web decorations, the most extensively studied being visually related, like camouflage from predator and/or prey, prey attraction and signalling to animals that are likely to damage the web (Herberstein *et al*., 2000; Bruce, 2006). The function of these structures is highly controversial, as well as other visual aspects of spider ecology, like the appearance of spiders themselves. Moreover, few spider species have the ability to change their body coloration, a peculiarity that has been suggested to improve camouflage or to constitute a form of aggressive mimicry (Oxford & Gillespie, 1998). Are such visual appearances used to lure prey, deter predators or hide from predators or prey?

In this study, we carry out a critical review of the abundant literature on spider and web appearance, predominantly focusing on the potentiality of camouflage and mimicry. For this reason, we will not explore non-visual aspects like spider olfactory and tactile mimicry or several other hypothetic functions of web decorations. When possible, we will highlight studies considering the visual sensitivities of prey and predators, and the transmission properties of visual signals through the environment. In addition to reviewing possible cases of camouflage, we will report on the nature of pigments used for colour change, and evoke physiological and ecological hypotheses for colour change. We will also discuss one neglected hypothesis, the protection against UV photodamage, by making a comparison of the pigmentation of two crab spider species, one being cryptic and the other non-cryptic.

2. Web design, colour and visual environment

Spiders specializing on small prey which are characterized by highly evolved visual systems and flight behaviour face the problem of avoiding detection, and studies of insect vision and flight show that it is surprising that webs capture any prey at all (Craig, 1986). However, the sophisticated design of webs enhances prey capture by making the web difficult to detect. Low-frequency oscillations of webs with low fibre density designed to resist only

low impact, like those of *Theridiosoma globosum*, are specialized to capture small slow-flying prey by fluctuating with the low airflow the web surface in and out of an approaching prey's range of visual resolution (Craig, 1986). In contrast, high impact webs such as those of *Mangora pia* are built with denser and more visible silk and do not oscillate because changes in light intensity across the web surface would cause the web to appear as a visual flag (Craig, 1986). As an alternative to dynamic distortion, some spiders in the genera *Theridiosoma* and *Epeirotypus* use static distortion by pulling the web centre approximately 3-5 cm with a fibre attached to surrounding vegetation. They build a cone web that escapes the range of visual resolution of potential prey, because when prey are flying at the base of the cone web they are not able to see the web centre or area of highest fibre density (Craig, 1986). The centre thread is released and the web projected towards a prey when it comes within the reach of the distorted web.

Web visibility is also greatly affected by the light environment. Background pattern has little influence on web visibility in dim-light environments, whereas small background patterns close to the web disrupt the web outline in bright-light environments (Craig, 1990). The changing pattern of shade and sunflecks on the web also make the orb difficult to detect (Craig & Freeman, 1991). In laboratory experiments, *Drosophila melanogaster* has difficulty in seeing webs suspended close to backgrounds of high spatial frequency in bright light, and are unable to see and avoid webs characterized by low reflectivity (Craig, 1990).

Particular silks affect attraction of prey. Webs of Araneidae and Tetragnathidae, which include viscid droplets of glycoprotein, have a sparkling appearance that functions to attract prey to the web area although at short range they make webs more visible (Craig & Freeman, 1991). Viscid silk increases the probability of prey interception of both diurnal and nocturnal species, although this is only true in the brightest habitats for nocturnal species (Craig & Freeman, 1991). However, using more sticky viscid silk also make webs more visible to prey. Consequently, nocturnal spiders or those living in dim habitats are able to enhance web stickiness by using highly visible viscid silk, whereas species foraging in bright habitats are constrained to build less visible and consequently less sticky orbs that are less efficient at retaining large prey (Craig, 1988). *Nephila clavipes*¸ the golden orb weaver, is unique among spiders studied to date for its ability to adjust web reflectance to local light and to produce pigments that enhance web visibility by increasing light reflected by their silk (Craig *et al*., 1996). It produces yellow silk that exploits the visual and behavioural systems of insects in the different light environments where it forages. In environments with high light intensity or in forest gaps, *N. clavipes* produces yellow silk that attracts bees. In contrast, they do not

produce pigments in dim sites where silk colours are difficult to see, probably to achieve energetic savings. Similarly, *Argiope aetherea* and *A. keyserlingi* build more and longer decorations under dim light than bright light, probably to increase the attractive signal for approaching prey or to advertise the web to oncoming birds (Elgar *et al*., 1996; Herberstein & Fleisch, 2003).

3. Web decorations

Web decorations are conspicuous silk structures spun in webs by females of some species of orb-web spiders. While the most-studied decorations are entirely made of silk, some spider species combine silk with organic items such as egg sacs and debris. Because empirical studies showed that decorations made of different materials functioned quite differently, we will consider them separately.

3.1. Silk decorations

Silk decorations were originally called stabilimenta because they were thought to help the web to stabilize. Several other functions have been advanced, including camouflage, prey attraction, increase in apparent female size, signalling to species likely to damage webs, thermoregulation, stress, regulation of excess silk, balance of water metabolism and male attraction (Eisner & Nowicki, 1983; Herberstein *et al*., 2000; Starks, 2002; Bruce, 2006; Walter *et al.*, 2008*a*, 2009). To solve this controversy, one suggestion of Herberstein *et al*. (2000) was to identify phylogenetic clusters of web decorations, because within these clusters decorations may have similar functions as a result of common ancestry. This hypothesis is not supported in the most studied cluster, the 'argiopine'. If we consider the most extensively studied hypothetic functions, the foraging and the anti-predatory functions, opposite results have been found in the genus *Argiope*. Most studies have found support for improved foraging success of decorated webs (Craig & Bernard, 1990; Craig, 1991; Elgar *et al*., 1996; Tso, 1996, 1998; Herberstein, 2000; Bruce *et al*., 2001; Craig *et al*., 2001; Li *et al*., 2004; Li, 2005; Cheng & Tso, 2007; Gálvez, 2009; Rao *et al*., 2009), but other studies found opposite results (Blackledge, 1998a; Blackledge & Wenzel, 1999, 2000; Bush *et al*., 2008). Even more surprisingly, contradictory results have been found in the same species, *Argiope aurantia* (Tso, 1998 supporting the improved foraging function, Blackledge & Wenzel, 1999 not). Similarly, testing the anti-predatory hypothesis in *Argiope* led to diverging conclusions: some studies support this hypothesis (Schoener & Spiller, 1992; Blackledge, 1998*a*; Blackledge & Wenzel, 1999, 2001) but others do not (Herberstein, 2000; Bruce *et al*., 2001; Craig *et al*.,

2001; Seah & Li, 2001; Li & Lee, 2004; Li & Lim, 2005; Cheng & Tso, 2007). Therefore, the hypothesis that similar decoration patterns, like the bright white silk bands of decorations frequently spun by spiders of the 'argiopine' cluster, may be convergent in form and function (Herberstein *et al*., 2000), cannot be supported.

The general absence of decorations in nocturnal spiders supports a visually mediated function. One common trend is that, when the prey attraction function is supported, the anti-predatory function is not (Herberstein, 2000; Bruce *et al*., 2001; Craig *et al*., 2001; Cheng & Tso, 2007; Tan & Li, 2009) or the reverse (Blackledge, 1998*a*, *b*; Blackledge & Wenzel, 1999; Eberhard, 2006; Jaffé *et al*., 2006). The only studies simultaneously validating both functions are very speculative and provide no direct evidence for support of both hypotheses (Herberstein & Fleisch, 2003; Rao *et al*., 2009). A recent study of silk tuft decorations in *Gasteracantha cranciformis* supports neither the prey attraction nor the web advertisement hypothesis, and suggests an aposematic function (Gawryszewski & Motta, 2008). Using silk decorations may constitute a conditional strategy which performs multiple functions both within and across populations (and species) depending on (i) spider developmental stages, (ii) their energetic state or (iii) environmental factors as the relative proportions of predator types, the population-specific prey differences in decoration susceptibility, the presence of bird species likely to damage webs or differences in temperature or ambient light (e.g. Watanabe, 1999; Craig *et al*., 2001; Seah & Li, 2002; Starks, 2002; Li *et al*., 2003; Bruce, 2006; Uhl, 2008; Walter *et al.*, 2008*b*).

Evidence for camouflage has been found when decorations conceal the spider from predators or change its apparent shape, although earlier studies did not perform field or laboratory experiment and were more descriptive and speculative (Ewer, 1972; Eberhard, 1973; Edmunds, 1986; Li *et al*., 2003). Blackledge & Wenzel (2000) argued that decorations are cryptic to insects because their reflectance spectra are flat, but they do not provide any data to test this assumption. On the contrary, Craig & Bernard (1990) showed in a closely related *Argiope* species that both decorations and spiders reflect UV wavelengths that act as a visual signal to attract prey. Li *et al.* (2004) also showed that the discoid decoration spun by juvenile *Argiope versicolor* is a prey attractant under white light containing UV. Spiders which decorate their webs at higher frequency not only grow faster, but also take higher predation risks (Li, 2005). Numerous recent studies indeed showed that silk decorations induce significant cost to spiders by attracting specialized spider-eating predators (e.g. Bruce *et al.*, 2001; Seah & Li, 2001; Cheng & Tso, 2007). Evidence for prey deception has been suggested when decorations attract pollinating insects by reflecting UV light in patterns

similar to UV markers on flowers. Similarly, UV patches created by web decorations may resemble gaps in vegetation that elicit flight behaviour in many insects (Craig & Bernard, 1990). By reconstructing a molecular phylogeny of Asian *Argiope* spiders and by conducting field experiments on the luring effectiveness of decorations forms, Cheng *et al.* (2010) showed that linear decorations are ancestral and cruciate decorations derived, the later being more attractive to insect prey. Their results suggest that the innate preference of pollinating insects for particular bilateral or radial symmetrical patterns might be driving the arrangement pattern of web decorations. However, until recently, the visually mediated functions of web decorations could not be properly tested with regard to the visual sensitivities of prey or predators, as well as the spectral characteristics of the visual background and ambient light.

Bruce *et al.* (2005) were the first to evaluate the visibility of silk decorations to both prey and predators by considering visual systems, background colour and the ambient light spectrum. Both achromatic and chromatic contrasts were calculated to estimate conspicuousness of the spiders against green vegetation background or against their decorations, at long and short distances, respectively. It was found that decorations were highly conspicuous to both predators and prey at long and short distance. However, the discoid decoration of *Argiope mascordi* could provide some camouflage for spiders seen by hymenoptera, either prey or predator.

A second study has used visual system modelling to evaluate the conspicuousness of silk decorations to potential prey and predators (Rao *et al*., 2009). In the orb-web spider *Argiope radon,* it was found that spider abdomens generate pronounced chromatic and achromatic contrasts on web decorations when seen by hymenoptera, and even stronger contrasts when seen by birds. Although the authors used values of detection threshold (the minimal distance in the colour space allowing separating a target from the background) computed for chromatic contrast (0.01 for honeybees by Dyer & Chittka, 2004; 0.06 for birds by Théry & Casas, 2002) to estimate discrimination of achromatic contrast, spiders clearly appear conspicuous to both prey and predators. Because in both visual systems decorations are more conspicuous than spiders, the function of decorations could be to confuse the attack of avian or insect predators. Recently, Blamires *et al.* (2008) have shown that spiders attract insects with decorations by exploiting visual sensory biases of prey sensitivities in the blue and UV light. However, it is still unknown whether UV, blue light or both are the most important cue.

Another approach to test the anti-predator function of silk decorations has been used by Nakata (2008) who simulated the approach of a flying insect predator with a vibrating

tuning fork, and examined if *Eriophora sagana* spiders modified the total thread length and the area of decorations of their subsequent web. It was found that spiders exposed to the simulated predator did not increase their thread length but attached more decorations to their new web, contrary to control spiders. These experiments support the anti-predator function of silk decorations. Nakata (2009) used the same approach with *Cyclosa argenteoalba*, but this time also experimentally tested the influence of prey availability on web design. His results confirmed the anti-predator function of decorations, and also showed that spiders increase their thread length but not the area of decorations when more prey is available. Overall, this shows that web decoration does not necessarily involve a trade-off between deterring predators and being avoided by prey.

3.2. Detritus decorations

Detritus decorations are generally viewed to function as camouflage for the spider (Eberhard, 2003; Chou *et al.*, 2005; Gonzaga & Vasconcellos-Neto, 2005). Detritus decorations added to the webs of two *Cyclosa* species could reduce the intensity of predation, possibly by disrupting the spider's outline (Gonzaga & Vasconcellos-Neto, 2005). Egg sac and silk decorations were also suspected to be used for camouflage by *Allocyclosa bifurca* spiders at the hub, although no rigorous behavioural test was conducted to support this interpretation (Eberhard, 2003). However, the odour of yeast growing on prey remains or decaying plant material incorporated above the orb web may also be used to attract insect prey (Tietjen *et al.*, 1987; Bjorkman-Chiswell *et al.*, 2004).

Physiological models of vision were used to calculate chromatic and achromatic contrasts of *Cyclosa confusa* spiders and their prey carcass decorations as they are viewed by their hymenopteran predator (Chou *et al.*, 2005). However, the authors compare both chromatic and achromatic contrasts with a discrimination threshold value of 0.05 computed by Théry & Casas (2002) for hymenopteran insects, a value which was estimated for chromatic contrast discrimination, but is not known for achromatic contrast (Théry & Casas, 2002; Bruce *et al.*, 2005; Théry *et al.*, 2005). Filming prey interception and predation events showed that carcass decorations do not attract insects and even generate a foraging cost, but that predators redirect their attacks towards decorations, which allows spiders to escape predation (Chou *et al.*, 2005). The function of *Cyclosa confusa* decorations is neither related to camouflage from predator or to prey attraction, but is apparently to confuse the attacking predator.

Tan & Li (2009) also used physiological models of vision to evaluate the camouflage efficiency of *Cyclosa mulmeinensis* spiders on their egg-sac and prey-remain decorations as they are seen by an insectivorous avian predator and hymenopteran prey or predator. Direct tests performed in the field showed that decorated webs intercept more insects, probably because spiders could not be discriminated from their decorations by prey using chromatic contrast at short distance. An alternative explanation is that, even if spiders are conspicuous to prey viewing them on their decorations using achromatic contrast at long distance, yeast may be growing on decorations an attract prey by olfaction, as shown by Tietjen *et al.* (1987). On the other hand, decorations seem to camouflage spiders against bird predators but not against wasps. Contrasting with the results obtained in other *Cyclosa* species (Baba, 2003; Chou *et al.*, 2005; Gonzaga & Vasconcellos-Neto, 2005), detritus decorations of *C. mulmeinensis* thus appear to constitute a trade-off between improving foraging success and reducing predation risk. Tseng & Tso (2009) also studied the camouflage efficiency of *C. mulmeinensis* on their egg-sac and prey-remain decorations as they are seen by their wasp predators. Predators' responses to spiders on webs were recorded on the field. As in the study of Tan & Li (2009), it was found that spiders and decorations were conspicuous to wasp predators, and that webs with more decorations suffered higher predation. However, because decorations resemble spiders in size and colour, they distracted predators and were frequently attacked, enhancing spider survival. The trade-off between improved foraging success and reduced predation may explain the variable incidence and polymorphism of web decorations in this species.

Tan *et al.* (2010) tested the prey-attraction and the anti-predatory hypotheses in *Cyclosa ginnaga*, a species which decorates its web with plant material and/or silk. They found that silk decorations were used as luring signals that attract prey visually, and that plant detritus and the silvery body coloration may also be attractive to insect prey. However, they could not conclude on the effectiveness of decorations to provide protection from predators because no instance of predation was observed for any web.

4. Spider coloration: generalities

Spider coloration has been reviewed in Oxford & Gillespie (1998) and their excellent overview is still up to date a decade later. Coloration serves multiple purposes, from crypsis and aposematism to sexual selection, and its underlying physiological processes are as numerous. Since then, the biochemical foundation of coloration in spiders has seen little progress compared with the sensory physiology of colour perception. The genetical and

evolutionary work on the colour polymorphism is reviewed in Oxford & Gillespie (2001) for the happy-face spider (*Theridion grallator*) and in Oxford (2005) for the candy-stripe spider (*Enoplognatha ovata*). The evolutionary forces for the persistence of colour polymorphism in spiders remain generally elusive. In contrast, two areas have attracted most of the attention, the colour changing properties of crab spiders and the striped and bright body coloration in web spiders. The studies conducted on those two aspects are similar in spirit to the work on the web decorations, often produced by the same species. In a recent study, Bush *et al.* (2008) carried out ingenious experiments on the wasp spider *Argiope bruennichi* by masking the spiders behind a leaf or painting their otherwise brightly coloured body, as did Tso *et al.* (2006) and Chuang *et al.* (2007, 2008). The marked decrease in prey capture in all cases is strong proof of the attractive nature of the brightly coloured body, and is consistent with the work of Chuang *et al.* (2007, 2008) and Tso *et al*. (2007) on brightly coloured nocturnal spiders. Quite different results were obtained in *Micrathena gracilis* by Vanderhoff *et al.* (2008), who found that that the presence of spiders on webs did not increase prey capture rates. In addition, spider colour did not seem to attract prey since they found a non-significant trend that blackened spiders captured more prey than unpainted spiders. By using dummies for controlling the size of conspicuous colours of the giant wood spider *Nephila pilipes*, Fan *et al.* (2009) showed that female coloration reflects a trade-off between opposite pressures of prey and predator attraction. With studies using physiological models of colour vision or using the animal eye specific imaging system (Chiao *et al.*, 2009), we seem to come to an end of an enduring discussion regarding attraction and crypsis of the bright coloration in web spiders (Craig & Ebert, 1994; Hauber, 2002; Tso *et al*., 2002, 2004, 2006; Hoese *et al*., 2006; Vaclav & Prokop, 2006). The next heading deals with the coloration of crab spiders in more detail, as its relationship to camouflage is clear-cut.

5. Spider coloration: pigments responsible for colour change

The colour changing crab spiders of the family Thomisidae, in particular *Misumena vatia* and *Thomisus onustus*, have been studied since 1891 (Heckel, 1891) with respect to pigmentation. *Misumena vatia* represents one of most studied spiders, with a monograph devoted exclusively to its life history (Morse, 2007). This spider is unusual as it is able to change reversibly, in the time delay of a few days, from white to yellow and back. Colour change is induced by background colour and colour of prey (Théry, 2007 and references therein). The background matching ability of these spiders is at times astonishing, below the

discrimination ability of bees for example (see **Fig. 1**; Chittka, 2001; Théry & Casas, 2002; Théry *et al*., 2005). Both food and light quality have been found to increase the range of colour change, but the variability in the response level was very high, with many individuals remaining white despite strong yellow stimuli (Théry, 2007). This form of crypsis has been interpreted as being potentially both a defensive (hiding from predators) and aggressive (hiding from prey) one. Bees and other flower-visiting insects are indeed common prey. Predation events by vertebrate predators, however, have never been observed (Morse, 2007), whereas predation by mud-dauber and spider wasps has often been observed. The impact of these invertebrate predators on spider populations is nonetheless unknown. Aggressive crypsis might therefore be the only type of crypsis present. Such impressive camouflage begets many questions about its proximate and ultimate mechanisms. In the following, we first report on the nature of pigments. We then move on to the physiological and ecological hypotheses for colour change, and close our discussion with one neglected hypothesis, the protection against UV photodamage, by making a comparison with another, non-cryptic, crab spider.

Figure 1: Importance of translucent teguments and white reflectance from guanine in background matching by the crab spider *Misumena vatia*. The same pale yellow female is represented in the four pictures, taken at an interval of a few minutes. Depending on the exact location of the spider on a plant, (*a*, *b*) the different hues between the cephalothorax and legs, and the opisthosoma, may make the animal more difficult to detect, (*c*) the green coloration of leaves may shine through the translucent legs and (*d*) the strong yellow hue within the corolla can be reflected by the guanine, leading to a high degree of camouflage. Scale bar, 6 mm.

Older studies assumed that the yellow colour of *M. vatia* was due to carotenoids (Millot, 1926), but ommochromes were later found to be the pigments responsible for this colour (Seligy, 1972). Ommochrome pigments are a class of pigments, widespread in insects and other arthropods, which constitute the main chromogenic class in the pathway from tryptophan and range from gold through red, purple and violet, up to brown and black. The reduced form is usually red and the oxidized form usually yellow. The characteristic properties of ommochromes (redox behaviour, absorption of UV and visible light, and low solubility) enable them not only to act as authentic functional pigments (eyes, integument), but also as an electron-accepting or -donating system and as metabolic end products (Needham, 1974). Ommochromes, principally xanthommatin, are widely distributed in arthropods as screening pigments in the accessory cells of the eyes and are also present in the retinula cells (Linzen, 1974). Ommochrome pigments are little known in general and their catabolism is very poorly understood, except for the latest work by Insausti & Casas (2009). The biochemical basis for the reversible colour change is not understood. One remains simply dismayed at the disappearance of solid biochemical work on a complete class of pigment after the 1970s and 1980s, just before the advent and rise of molecular biology (Linzen, 1974; Needham, 1974; Fuzeau-Braesch, 1985; Kayser, 1985). Luckily, the situation is somewhat better in terms of the ultimate reasons for the colour change.

The functions of ommochromes are diverse and several complementary and non-exclusive hypotheses have been suggested for their common occurrence (reviewed in Insausti & Casas, 2008). The first hypothesis states that the ommochrome pathway is the main pathway for avoiding excess accumulation of the highly toxic tryptophan. Supporting this hypothesis is the observation that ommochrome formation is strongly correlated with the massive breakdown of proteins at the onset of metamorphosis. This is the oldest and most popular view for the function of ommochromes. This conclusion is however invalidated for *M. vatia* by Insausti & Casas (2008) on the basis of the red stripes in white spiders. The absence of a change of colour from white to yellow cannot be due to a lack of precursors or enzymes (as found in the white eyes clone of *D. melanogaster*, Mackenzie *et al*., 2000), as these spiders have both. Tryptophan might already be neutralized as ommochrome precursor in those granules containing most likely kynurenine.

The second hypothesis states that main *raison d'être* of ommochromes is signalling, mimicry and crypsis. This is the hypothesis supported by most of the community working on colour changing insects such as stick insects and mantids (Fuzeau-Braesch, 1985), including

Mantis religiosa, *Sphodromantis viridis* and *Locusta migratoria* (Vuillaume, 1968), and spiders (Rabaud, 1918, 1919; Gabritschevsky, 1927; Schmalhofer, 2000; Chittka, 2001; Théry & Casas, 2002; Heiling *et al*., 2003, 2005*a, b*; Théry *et al*., 2005; Théry, 2007). In order to test this hypothesis, we need to assess the fitness value of the camouflage and the fitness gain from a change of colour. It can be based on the measurement of some fitness-related trait, such as increased fecundity, survival or simply higher prey capture rate as a function of the degree of flower colour matching. This is a main piece of supporting evidence that is often missing and the latest results obtained by the Brechbühl *et al.* (2010), showing that colour-matched crab spiders do not have a higher prey encounter rate or capture success than conspicuous ones, do not support this hypothesis. We also need to assess the likelihood of the 'nearly perfect' matching of spiders to their flowers referred to earlier. This in turn, requires the sampling of the colour of *all* flowers in the neighbourhood of the one chosen by a spider. The latest results obtained from systematic field survey indicate that the matching of spider and flower colours is not different from a random assortment (Defrize *et al.*, 2010). Thus, supporting evidence for the second hypothesis is scant.

The third hypothesis is based on the observation that the major function of ommochrome in eyes is the protection of photosensitive visual cells against excessive scattered light, and also protection against photodestruction by intense UV light (Langer, 1975; Stavenga, 1989). Ommochromes participate in the antioxidative system in invertebrate photoreceptors, as melanin in the eyes of vertebrates (Dontsov *et al*., 1984; Ostrovsky *et al*., 1987; Sakina *et al*., 1987; Dontsov, 1999). The ommochromes are also effective inhibitors of free radical-induced lipid peroxidation. Lipid peroxidation is also produced by photooxidation and is indicative of photoreceptor damage, expressed in the retina by the deterioration of photoreceptor membranes (Ostrovsky & Fedorovich, 1994). The hypothesis that ommochromes in the tegument have a similar function deserves therefore much more attention for the following reasons. First, ommochrome precursors could be sufficient as screening pigments, as in the group of *chartreuse* mutants of *Apis mellifica* (Linzen, 1974). Indeed, the mutant group accumulates the yellow tinted but still translucent 3-OH-kynurenine in a granular form in the pigment cells of the compound eyes. That pigment precursor therefore assumes a pigment function (Linzen, 1974). The intensity of the yellow hue of spiders, due to the mix between 3-OH-kynurenine and ommochromes, might reflect the amount of screening against radiation. Second, *M. vatia* is both exposed for days to direct solar radiation on the top of flowers and has a transparent cuticle exposing the epidermal cells

to direct radiation. This transparency implies a need for protective means in the tissues situated beneath the cuticle, and ommochromes might act as such.

To support this conclusion we have analysed the presence of pigment granules in the epidermal cells of the juvenile instars of *M. vatia*. We found that the progranules of pigment precursors (Insausti & Casas, 2008) are already present in the second instar spiderlings, which have just emerged (**Fig. 2**). The spiderlings, when hatched, have a pale whitish-greenish coloration, except on the abdomen, where the brownish intestine and white spots of the crystals of guanine are visible through the translucent cuticle. The yellow coloration was never observed in spiderlings (Gabritschevsky, 1927), although the precursors of the ommochrome pigment are present. Thus, they are not some waste products of excessive tryptophan harvested from prey and are needed from birth on.

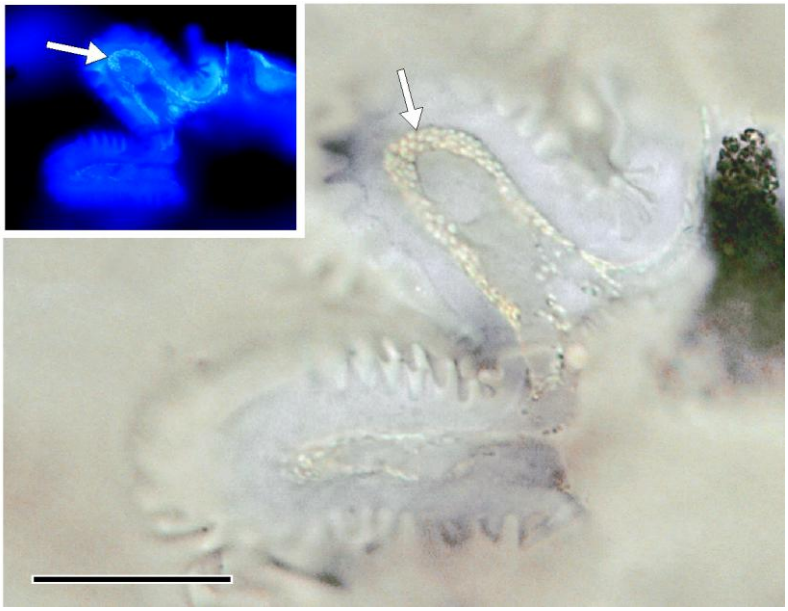

Figure 2: Light micrograph of an unstained cross section of the tegument of the second instar of *Misumena vatia*. The epithelial cells are full of granules (arrow). The inset shows the same region of tegument observed under UV light. The granules (arrow) show a strongly autofluorescence, a characteristic of ommochrome precursors. Scale bar, 15 µm.

The comparison with another crab-spider, *Synaema globosum*, reinforces the concept of the role of the ommochrome pigments and their precursors as photoprotectors of the

epidermal cells. This species that does not have a camouflage pattern also has a transparent cuticle and comes in three different colour types: white, yellow and red (**Fig. 3**).

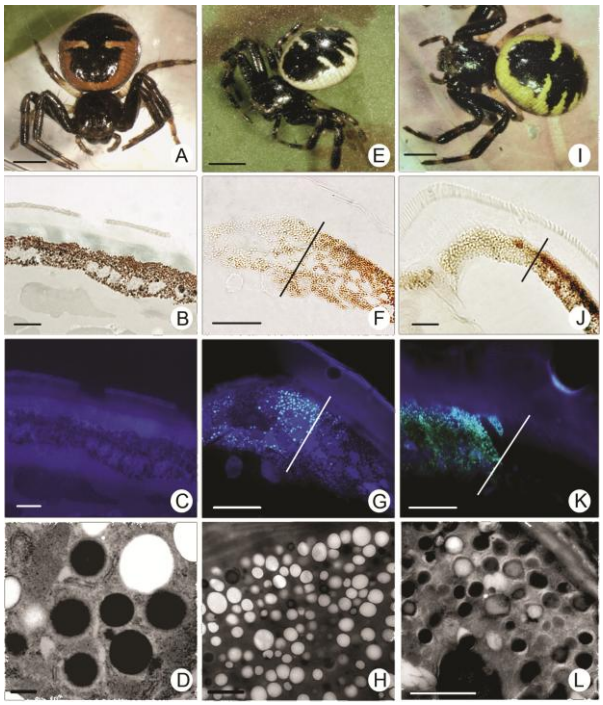

Figure 3: *Synaema globosum* individuals (*a-d*, *e-h* and *i-l*, respectively) of (*a*) red, (*e*) white and (*i*) yellow colours: (*a*, *e*, *i*) habitus, (*b*, *f*, *j*) unstained cross sections of the tegument under light microscopy, (*c*, *g*, *k*) under UV light and (*d*, *h*, *l*) electron micrographs of epithelial cells and pigment granules. The cuticle of both regions, black and coloured (*b*), is transparent. The absence of fluorescence in the red spider (*c*) is typical of ommochromes granules (*d*). In yellow spiders, there is a distinct difference between the black and yellow areas (on the right and left of the dividing mark), both under light microscopy (*j*) and under UV light (*k*). The black region contains two types of granules, red and black, whereas the yellow region contains also two types of granules, translucent and light brown (*l*). Only the yellow portion contains fluorescent granules. In white spiders, the white region (*f*) contains translucent, fluorescent granules only (*g*, *h*). As a result, the white coloration is produced by the guanine layer under the epithelium. Almost the totality of the granules is electron-lucent and homogeneous, indicative of kynurenine (granules type I, Insausti & Casas, 2008). There is thus a clear association between body colour and ommochrome metabolites in this non-cryptic crab spider. Scale bars, (*a*, *e*, *i*) 2 mm, (*b*, *c*, *f*, *g*, *j*, *k*) 10 µm, (*d*) 0.5µm and (*h*, *l*) 2 µm.

It is unknown whether this spider does change colour or whether these are different fixed phenotypes. We observed that both the brown-black and the yellow or red coloured parts of the epidermis contain ommochrome granules, as in *M. vatia*. The pigmentation of *S. globosum* is therefore another strong hint that the ommochrome coloration might be related to

the transparency of the cuticle in crab spiders. Camouflage profits from such a relationship, but may not be the driving force.

The surprisingly complex relationships between animal colour and background matching described here show how far an assessment of crypsis capacities against the substrates with regard of receiver visual systems provides useful information about how cryptic a given species really is, regardless of any human biases. As shown for this crab spider, a relevant and accurate assessment can be very complex to obtain due to several physiological and ecological constraints. This requires indeed (i) the exact measure of both substrate and individual colorations through spectroradiometric measurements or image analysis in the very location in which the behavioural interaction between prey and predator occurred; (ii) an account of the variability of the substrate visual characteristics encountered by the cryptic species in natural conditions (i.e. the sampling universe); (iii) the identity of the correct receivers, and (iv) a knowledge of their visual abilities. All these reasons explain why accurate measurements of the colour contrast in the perspective of a relevant receiver are so rare. The crab spider *M. vatia* is in these respects one of the best study models, outpacing much more famous examples (*Table 1*). Its potential for addressing fundamental questions in evolutionary physiology and behavioural ecology is not fully realised.

Species (author)	Sample	Spectral reflectance of exact location	Coverage of the variability of the used background(s)	Use of the correct receiver	Number of fulfilled conditions
Misumena vatia (Defrize *et al*., 2010)	N=126	Yes	Yes	Yes	3/3
Uca vomeris (Hemmi *et al*., 2006)	N=2	Yes	Yes	Yes	3/3
Sepia officinalis (Mäthger *et al*., 2008)	N=6	Yes	Yes	No	2/3
Thomisus onustus	N=10	Yes	No	Yes	2/3

(Théry *et al*., 2005)					
Ctenophorus decresii (Stuart-Fox *et al*., 2004)	N=23	Yes	Yes	No	2/3
Thomisus onustus (Théry & Casas, 2002)	N=10	Yes	No	Yes	2/3
Misumena vatia (Chittka, 2001)	N=2	Yes	No	Yes	2/3
Geomys bursarius (Krupa & Geluso, 2000)	N=41	Yes	Yes	No	2/3
Moths (Endler, 1984)	N=372 (belonging to 321 species)	Yes	Yes	No	2/3
Bradypodion taeniabronchum (Stuart-Fox *et al*., 2008)	N=16	No	No	Yes	1/3
Pagurus bernhardus (Briffa *et al*., 2008)	N=20	No	Yes	No	1/3
Misumena vatia (Théry, 2007)	N=8	No	No	Yes	1/3
Bradypodion transvaalense (Stuart-Fox *et al*., 2006)	?	No	Yes	No	1/3

Octopus vulgaris (Hanlon, 2007)	N=1	Yes (Video recording)	No	No	1/3
Rana muscosa (Norris & Lowe, 1964)	N=3	No	Yes	No	1/3
Uma scoparia (Norris & Lowe, 1964)	N=4	No	Yes	No	1/3
Uta stansburiana (Norris & Lowe, 1964)	N=1	No	No	No	1/3
Streptorausus mearnsi (Norris & Lowe, 1964)	N=1	Yes	No	No	1/3
Urosaurus ornatus (Hamilton *et al.*, 2008)	N=19 (male) N=11 (female)	No (Image analysis)	No	No	0/3
Hyla cinerea (King *et al.*, 1994)	N=16	No	No	No	0/3
Dipsosaurus d. dorsalis (Norris & Lowe, 1964)	N=3	No	No	No	0/3

Table 1: Overview of quantitative studies assessing background colour matching. For each species, we asked four questions: how many individuals were taken into account in the study, is the spectral reflectance of the background measured at the exact or generic location of the individual, does the study takes into account the variability of the used background(s) of the species and finally, is the colour contrast measured in the correct receiver visual system? The last grey column indicates the total score of fulfilled conditions. Only studies that measured background matching through a colorimetric assessment of the colour contrast of a species against its

background were included. Thus, several studies based on human colour qualitative assessment are not reported, nor are the numerous works on background matching of computer generated prey.

Related puzzling aspects of coloration in spiders are the widespread fluorescence and UV reflectance. The former aspect has being only recently assessed (Andrew *et al*., 2007; Lim *et al.*, 2007). We doubt that the fluorophores observed by these authors are located in the haemolymph, as stated by Andrews *et al.* (2007), and rather interpret their results and picture as indicative of a pigment located in the epidermis. Several ommochrome precursors based on the tryptophan pathway located in the epidermis are indeed fluorescent (Insausti & Casas, 2008) and fluorescence might simply be a side effect of the widespread occurrence of ommochromes in spider colours. On the basis of several behavioural tests and ingenious experiments using both native and European bees, it was conclusively demonstrated that UV reflective body colours of Australian crab-spiders attract prey (i.e. bees) to the flowers they are positioned on (Heiling *et al*., 2003; Heiling & Herberstein, 2004; Heiling *et al*., 2005*a*, *b*, 2006; Herberstein *et al*., 2009). While the tropical and subtropical distribution of UV reflectance in crab spiders raises a number of very exciting evolutionary questions about coevolution and trait evolution, the much higher amount of UV radiation received in Australia compared with Europe (Godard, 2005) should not be forgotten as an easier potential explanation. UV reflectance might act as protective means in tropical and subtropical regions.

6. Spiders mimic ants

More than 300 species of spiders, belonging to 13 families, mimic ants (Cushing, 1997; Nelson & Jackson, 2007*a*). Myrmecomorphic species are defined as spiders mimicking ant morphology and/or behaviour. Morphological adaptations include colour and form modification, which make the spider look as though it has three body segments instead of two, and long slender legs instead of shorter robust legs (review by Cushing, 1997). Adaptation of the chelicerae, spinnerets and cuticle coloration allow the spider to mimic the mandibles, sting, compound eyes and antennae of their ant model. Behavioural adaptation includes ant-like erratic movements and the raising of a pair of legs to mimic the movements of ant antennae. Several species of myrmecomorphic spiders evolved transformational mimicry in which successive instars mimic different ant models. Also, several ant-mimicking spiders use polymorphic mimicry in which each morph mimics a different ant morph or species. Some species have each sex mimicking a different ant model. The limited space for

this paper precluded us from doing full justice to movement camouflage that needs more studies in general, as it seems the most striking type of camouflage spiders have used in the course of evolution.

A minority of spider myrmecomorphs are aggressive mimics (McIver & Stonedahl, 1993; Cushing, 1997), and use their morphology and behaviour to attract and prey on ant models. A myrmecomorphic spider, *Myrmarachne melanotorsa*, is also an aggressive mimic but relies on other salticids or on hersilid spiders to mistake them for ants and flee, leaving these araneophagic spiders (Nelson & Jackson, 2009*a*) access to eggs and post-embryos (Nelson & Jackson, 2009*b*). However, in order for the myrmecomorphic spider to be considered an aggressive mimic by the ant species, the ant model must be a selective agent able to see resemblance of the mimic. This is unlikely for the majority of ant species that have poor eyesight or which do not investigate the spider myrmecomorphs (Cushing, 1997). Most myrmecomorphic spiders are considered as Batesian mimics because ant unpalatability offers protection against generalistic arthropod predators. Both direct and indirect evidence support this hypothesis (review in Cushing, 1997; see also Nelson *et al*., 2005, 2006 *a*-*c*; Nelson & Jackson, 2006*a*, *b*, 2007*a*, *b*, 2009*b*, *c*; Jackson *et al.* 2008). Recent experimental studies in the genus *Myrmarachne* have shown that salticid spider resemblance to ants holds in the eyes of their predators, other salticid species and mantises (Nelson & Jackson, 2006*b*; Nelson *et al*., 2006*b*, *c*). It has also been demonstrated that an ant-mimicking jumping spider is able to discriminate between ant models, conspecifics and prey by sight alone (Nelson & Jackson, 2006*b*, 2007*b*). A recent unpublished study using a physiological model of bird vision has shown that although head and thoracic regions of *Myrmarachne gisti* are visible to bird predators from a long distance, this myrmecomorphic spider is unlikely to be detected at short distance (D. Li 2008, personal communication). By giving the choice between living *M. gisti* and its and model ants under light conditions with and without UV, specialised ant-eating salticids are able to distinguish between ant-mimics and ants based on *M. gisti*'s specific display behaviour but not on coloration. These findings provide evidence that this classic ant mimicry has extended into UV light wavelengths, and that Batesian mimicry of *M. gisti* is an effective defence against avian predators.

7. Future prospects

Spider camouflage and mimicry is attracting attention, mainly from the behavioural ecologist quarters. While we enthusiastically welcome this renewed interest, we caution

against glossing over physiological mechanisms. As so often with integrative biology, we need both more detailed mechanistic studies within the animal, on the biochemical pathways or the colour perception processes for example, and evolutionary behavioural or ecological work, both in the laboratory and in the field. As an example to the point, it is still unclear whether a crab spider changes colour to match its background or chooses an appropriate flower colour to match its imminent colour change.

Our paper identified major advances and gaps in our understanding and an untapped potential of studying mimicry and camouflage in spiders. Recent studies do take into account the visual systems of prey and predators and light environments. This approach is necessary, and has clearly improved our knowledge on the functions of web, decoration and spider coloration. By contrast, we still lack a comprehensive understanding of colour vision in the very same spiders, an approach which requires painstaking electrophysiological work, furthermore on all four pairs of eyes. The study of mimicry and camouflage centred on the classical models systems, such as *Octopus* or *Heliconius*, is plagued with the recurring difficulty to observe and quantify the ecological impact and evolutionary forces of the predators on the studied traits. Spiders, by being comparatively immobile and constructing trapping devices which often contain a portion of their predatory history, represent an excellent model devoid of the above difficulties. The almost complete lack of theoretical studies of colour mimicry and camouflage using spiders is therefore even more striking.

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Jérémy DEFRIZE

Camouflage chez les araignées crabe: Approche sensorielle, comportementale et écologique

Résumé

Misumena vatia est supposée, depuis plus d'un siècle, adapter sa couleur à celle de son substrat pour diminuer sa probabilité d'être détectée par des proies et des prédateurs. Il existe cependant un décalage entre la quantité de travaux sur son écologie, sa notoriété en tant qu'experte du camouflage, et la connaissance réelle sur son camouflage et le changement de couleur. Le but de cette thèse était d'aborder le camouflage d'un point de vue sensoriel, à une échelle communautaire, en combinant plusieurs approches. Il a été ainsi démontré que si *M. vatia* était indétectable dans l'achromatique à longue distance, le niveau de contraste chromatique à courte distance était dépendant du substrat et de l'identité du receveur. Des études électrophysiologiques et comportementales montrent de manière convergente que *M. vatia* possède la vision des couleurs. Les juvéniles utilisent cette habilité pour choisir des substrats qui les rendent peu détectable pour les proies. Enfin, les résultats de cette thèse sont replacés dans un contexte évolutif et physiologique plus général.

Mots-clés: *Misumena vatia*, Camouflage, Ecologie sensorielle des communautés, Contraste chromatique, Contraste achromatique, Préférence colorée, Sensibilités spectrales

Abstract

Misumena vatia is assumed for more than a century to adapt its colouration to the colour of its substrate in order to decrease the risk of being detected by prey and predators. However, a discrepancy exists between the large quantity of works on its ecology, its fame as an expert of camouflage and the empirical knowledge about its cryspis and colour change mechanisms. The aim of this thesis was therefore to study crypsis from a community sensory perspective, using an approach combing physiology, behaviour and colour vision models. We showed that if *M. vatia* was undetectable at long distance through achromatic vision, the chromatic contrast value is quite dependent of both substrates and receiver identities. Electrophysiological recordings and behavioural choices all concur to show that *M. vatia* is able to see colours. Spiderlings use this ability for making choices among coloured backgrounds diminishing its conspicuousness to potential prey. Finally, the results of this thesis are discussed in an evolutionary and physiological context.

Key-words: Misumena vatia, Crypsis, Community sensory ecology, Chromatic contrast, Achromatic contrast, Colour preference, Spectral sensitivities