COLOR CHANGE AND ECOLOGY IN FEMALE *MISUMENOIDES FORMOSIPES* CRAB SPIDERS

A THESIS SUBMITTED TO THE GRADUATE SCHOOL IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE MASTER OF SCIENCE

BY

ALISSA G. ANDERSON

ADVISOR: DR. GARY DODSON

BALL STATE UNIVERSITY

MUNCIE, INDIANA

MAY 2013

COLOR CHANGE AND ECOLOGY IN FEMALE *MISUMENOIDES FORMOSIPES* CRAB SPIDERS

A THESIS SUBMITTED TO THE GRADUATE SCHOOL IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

MASTER OF SCIENCE

BY

ALISSA G. ANDERSON

ADVISOR: DR. GARY DODSON

Committee Approval:

Committee Chairperson	Date
Committee Member	Date
Committee Member	Date

Departmental Approval:

Departmental Chairperson	Date
Dean of Graduate School	Date

BALL STATE UNIVERSITY
MUNCIE, INDIANA
MAY 2013

TABLE OF CONTENTS

LIST OF FIGURES

Figure Page

CHAPTER 2

LIST OF TABLES

Table Page

CHAPTER 2

ABSTRACT

THESIS: Color change and ecology in female *Misumenoides formosipes* crab spiders

STUDENT: Alissa G. Anderson

DEGREE: Master of Science

COLLEGE: Science and Humanities

DATE: May 2013

PAGES: 45

Female *Misumenoides formosipes* crab spiders, unlike their highly mobile, short-lived male counterparts, are relatively sedentary predators that forage long after the males have died off. Associated with their foraging ability is a phenomenon rare amongst animals: the capacity for a reversible change in body color. This color change ability, exhibited by several species of crab spiders, has historically been interpreted as an adaptation providing enhanced crypsis during movement between hunting substrates (inflorescences). *Misumenoides formosipes* females were relocated onto matched and mismatched substrates in the field to assess their propensity for color change, the rate at which it occurs, and any impact on foraging success. Yellow females transferred to white inflorescences were the only category that did not remain in their new location. White females changed to yellow over a 9 day period. We found conflicting evidence as to whether or not foraging success was enhanced for females on matched backgrounds.

ACKNOWLEDGEMENTS

I first thank Ball State University, the Ball State Chapter of Sigma XI, Indiana Academy of Science and the American Arachnological Society for grants to aid in this research. Thanks to Hans Kellogg for his expert help with the photographic techniques and Wendy Fleenor, Michelle Taylor and Jessica Jordan for their time spent aiding with data collection. For statistical help I thank Dr. David LeBlanc and Stephen Jaquemin. Thanks to Dr. Timothy Carter and Dr. Randy Bernot for their time spent serving as valuable committee members for this thesis project. Last, I thank my advisor Dr. Gary Dodson for his expertise, time, guidance and support throughout the entirety of the research.

CHAPTER 1: Life history and ecology in female *Misumenoides formosipes* crab spiders

Abstract- A number of crab spider species, including *Misumenoides formosipes,* are ambush predators of insects on a variety of inflorescences. Differential allocation of reproductive effort in male and female crab spiders is reflected in their extreme sexual size dimorphism as well as contrasts in their life histories. In *M. formosipes* the small, mobile adult males expend substantial energy finding and attempting to mate with females, whereas the large females are mostly sedentary and dedicated to foraging long after the males have died off. Gaining detailed information on the ecology of this species has allowed for the testing of a variety of hypotheses rooted in behavioral ecology theory.

INTRODUCTION

Misumenoides formosipes is a crab spider belonging to the widely distributed Thomisidae family. Thomisids fall within a larger group of true spiders that do not use webs to hunt their prey. Instead, they are typically ground or plant dwelling predators, and specifically in the case of many Misumeninae species are ambush predators that employ a sit-and-wait strategy upon a variety of plant species (Gertsch, 1939). The majority of thomisids have laterigrade limbs, which allow them to walk both sideways and backwards, giving weight to the name crab spiders (Gertsch, 1939). Extreme sexual dimorphism is characteristic of the entire crab spider family (Head, 1995; Morse, 2007), and *M. formosipes* males are only one-quarter the size of females (Pollard *et al*., 1995). In addition to the sexual size dimorphism, protandry is common among crab spiders where males undergo one less molt and mature faster than females. Another notable characteristic found in some thomisid species is the reversible color change capability found only in females (Gertsch, 1939; Schmalhofer, 2000; Chittka, 2001; Théry & Casas, 2002; Heiling *et al.,* 2004), which will be the topic discussed in the subsequent chapter.

DISTRIBUTION AND LIFE HISTORY

Misumenoides formosipes occurs throughout the USA and Canada (Gertsch, 1939) where they are commonly found hunting on a variety of inflorescences in open fields (Beck & Conner, 1992). Adult females mature mid to late summer and produce their clutches in the late summer to early autumn. Spiderlings overwinter and emerge

in early spring (Gertsch, 1939; Beck & Conner, 1992; Schmalhofer, 1999; A. G. Anderson, personal observations).

MATING SYSTEM AND REPRODUCTIVE BEHAVIORS

The mating systems of crab spiders reflect gender divisions with regard to reproductive roles and this is most readily demonstrated by their extreme sexual size dimorphism. Within the mating system of *M. formosipes* the smaller adult males expend substantial energy finding and attempting to mate with one or multiple females (Beck & Conner, 1992; Dodson & Beck, 1993; Dodson & Schwaab, 2001; Stellwag & Dodson, 2010) whereas the large females are mostly sedentary and dedicated to foraging long after the males have died off. As the population transitions to adult instars, the operational sex ratio is heavily male biased (G. N. Dodson, L. Stellwag, and A. G. Anderson, unpublished data).

Male navigation and contests

Once males mature they must often travel and locate penultimate females within a complex and patchy habitat. Males make use of both floral olfactory cues and visual cues (at closer distances) to aid in their search of females (Stellwag & Dodson, 2010; Dodson *et al*., 2013). Males are attracted to the volatile floral chemicals of *Rudbeckia* spp. but not to the scent of *Daucus carota*, even though both are common substrates for females (Dodson *et al*., 2013). Once a penultimate female is located, males compete for the alpha (closest) position relative to the female through a series of contests (Dodson & Beck, 1993). Mating takes place soon after the female undergoes her final molt. Virgin females typically do not resist the first male

that approaches her, which highlights the importance for males to maintain the alpha position (Dodson & Beck, 1993). If *M. formosipes* expresses first male sperm priority as predicted (Austad, 1982; Dodson & Beck, 1993), then winning contests should result in higher reproductive success.

Male contests often involve degrees of physical contact between two male opponents, and typically results in a retreat by the losing male (Dodson & Schwaab, 2001). Larger males win significantly more contests and in the field the largest males reside in the alpha guarding position (nearest the female), supporting the notion that there is a reproductive advantage to males of larger size (Dodson & Beck, 1993). However, there is strong evidence that prior experience (previously winning or losing a contest) is a more significant predictor of outcomes of future contests than size differences (Hoefler, 2002). A life saving tactic commonly used within male contests is leg autotomy where males may essentially 'give up' a leg if it is grasped by another male as a strategy to combat the spread of venom (Dodson & Beck, 1993). Losing a leg does not affect the ability of a male to win future contests and be reproductively successful (Dodson & Schwaab, 2001).

Female reproductive behavior

After mating, females continue to forage until at least one egg clutch is laid, and females have been observed remaining on and possibly guarding their egg clutches (Beck & Conner, 1992; G. N. Dodson, unpublished observations). Egg clutches have occasionally been located on the leaves of *Toxicodendron* radicans, *Loncera* spp., and *Duchensnea indica* (Beck & Conner, 1992). Foraging success and clutch size have a direct positive correlation in *M. formosipes* (Beck & Conner,

1992). The majority of weight gain in females (>60%) is a result of foraging as an adult (Beck & Conner, 1992).

FORAGING ECOLOGY AND FEEDING BEHAVIOR

Female foraging

As *M. formosipes* males devote themselves to the roles of searching complex habitats for females, guarding females nearing their adult molts, and mating; female activities both pre- and post-copulatory are focused on the predatory success that dictates their fecundity. Females are ambush predators on various inflorescence types. Inflorescences include: *Daucus carota*, *Erigeron strigosus, Rudbeckia hirta*, *R. triloba*, *Helianthus decapetalous*, *Coreopsis tripteris*, *Ratibida pinnata*, *Solidago* spp. and *Silphium integrifolium* (Dodon & Beck, 1993; A. G. Anderson and G. N. Dodson, unpublished data).

Females forage both nocturnally and diurnally; however, most prey captures occur diurnally (Schmalhofer & Casey, 1999). Schmalhofer reported that the majority of prey items are hymenopterans and dipterans, and the next most commonly captured prey were lepidopterans, hemipterans, orthopterans, and araneans (Schmalhofer & Casey, 1999; Schmalhofer, 1999; Schmalhofer, 2001). Foraging females remain motionless as they hold their first two pairs of larger raptorial legs at an approximate 45° angle from the substrate surface, while using the back two pairs of smaller legs to grip onto the substrate surface (Schmalhofer & Casey, 1999). Females wait for potential prey to approach within a few millimeters, at which point they will strike the prey and attempt to bite directly behind the head (Gertsch, 1939;

Schmalhofer & Casey, 1999). This process takes only a few seconds, and because crab spider venom is powerful and fast acting (Gertsch, 1939) prey are typically subdued within 30 s (Schmalhofer & Casey, 1999). The venom and feeding technique employed by *M. formosipes* and other thomisids allow them to catch prey items much larger than themselves (Gertsch, 1939). *Misumenoides formosipes*, and thomisids in general, inject digestive enzymes into the body of their prey so that the spider can feed by sucking the liquefied contents (Foelix, 1982; Pollard, 1990).

Male nectar feeding

During the course of locating and guarding penultimate females, adult males drink nectar (Pollard *et al.*, 1995). *Misumenoides formosipes* was the first spider for which this phenomenon was recognized, but nectarivory has since been recorded for a number of other species (Taylor & Pfannenstiel, 2008). Nectar feeding is beneficial to males in that it provides energy at low cost. Males must rely on the energy reserves from feeding in pre-adult stages and nectar is likely a source of extra energy gain that may be beneficial before male contests. Drinking nectar may also allow a male to avoid desiccation if other water sources are not readily available while guarding a female (Pollard *et al.*, 1995). Evidence suggests that *M. formosipes* females also feed on nectar, but is either much less common or less beneficial to females (Pollard *et al.*, 1995).

REFERENCES

Austad, S.N. (1982) First male sperm priority in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer). *Evolution,* 36, 777-785.

Beck, M.W. & Connor, E.F. (1992) Factors affecting the reproductive success of the crab spider *Misumenoides formosipes*: the covariance between juvenile and adult traits. *Oecologia*, 92, 287-295.

Chittka, L. (2001) Camouflage of predatory crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae / Hymenoptera: Apidae). *Entomologia Generalis*, 25, 181-187.

Dodson, G.N. & Beck, M.W. (1993) Precopulatory guarding of penultimate females by male crab spiders, *Misumenoides formosipes. Animal Behavior*, 45, 289-299.

Dodson, G.N., Lang, P.L., Jones, R.N. & Verspille, A.N. (2013) Specificity of attraction to floral chemistry in *Misumenoides formosipes* crab spiders. *Journal of Arachnology*, In press.

Dodson, G.N. & Schwaab, A.T. (2001) Body size, leg autotomy, and prior experience as factors in the fighting success of male crab spiders, *Misumenoides formosipes*. *Journal of Insect Behavior*, 14, 841-855.

Foelix, R.F. (1982) *Biology of Spiders*. Harvard University Press, Cambridge, Mass.

Gertsch, W.J. (1939) A revision of the typical crab-spiders (Misumeninae) of America north of Mexico. *Bulletin American Museum of Natural History*, 76, 277–442.

Head, G. (1995) Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Aranea). *Evolution,* 49, 776-781.

Heiling, A.M., Cheng, K. & Herberstein, M.E. (2004) Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). *Behavioral Ecology*, 15, 321–326.

Hoefler, C.D. (2002) Is contest experience a trump card? The interaction of residency status, experience, and body size on fighting success in *Misumenoides formosipes* (Araneae: Thomisidae). *Journal of Insect Behavior*, 15, 779-790.

Morse, D.H. (2007) Mating Frequencies of Male Crab Spiders, *Misumena vatia.* (Araneae, Thomisidae). *Journal of Arachnology*, 35, 84-88.

Pollard, S. (1990) The feeding strategy of a crab spider, *Diaea* sp. indet. (Araneae: Thomisidae): post-capture decision rules. *Journal of Zoology*, 222, 601 – 615.

Pollard, S.D., Beck, M.W. & Dodson, G.N. (1995) Why do male crab spiders drink nectar? *Animal Behaviour*, 49, 1443-1448.

Schmalhofer, V.R. (1999) Thermal tolerances and preferences of the crab spiders *Misumenops asperatus* and *Misumenoides formosipes* (Araneae, Thomisidae). *Journal of Arachnology*, 27, 470-480.

Schmalhofer, V.R. (2000) Diet-induced and morphological color changes in juvenile crab spiders (Araneae, Thomisdae). *Journal of Arachnology*, 28, 56-60.

Schmalhofer, V.R. (2001) Tritrophic interactions in a pollination system: impacts of species composition and size of flower patches on the hunting success of a flower-dwelling spider. *Oecologia*, 129, 292-303.

Schamlhofer, V.R. & Casey, T.M. (1999) Crab spider hunting performance is temperature insensitive. *Ecological Entomology,* 24, 345-353.

Stellwag, L. & Dodson, G.N. (2010) Navigation by male crab spiders *Misumenoides formosipes* (Araneae: thomisidae): floral cues may aid in locating potential mates. *Journal of Insect Behavior*, 23, 226-335.

Taylor, R.M. & Pfannenstiel, R.S. (2008) Nectar feeding by wandering spiders on cotton plants. *Environmental Entomology*, 37, 996-1002.

Théry, M. & Casas, J. (2002) Predator and prey views of spider camouflage. *Nature*, 415, 133.

CHAPTER 2: Color change ability and its effect on prey capture success in female *Misumenoides formosipes* crab spiders

Abstract- Changing between white and yellow body color allows *Misumenoides formosipes* females to match the background color of the inflorescence on which they are hunting and, hypothetically, appear cryptic to prey and/or their own predators. Potential costs and benefits of color change were investigated with respect to foraging opportunities and prey capture success along with the rate of color change in female *M. formosipes.* Females were moved onto white and yellow inflorescences to test the effect of being matched or mismatched with their background. Digital photos of females were used to quantify color in the Lab color space component of Adobe Photoshop. Insect visits (potential prey) were quantified on inflorescences with and without spiders and with females matched and mismatched to their background. The tendencies of yellow females to abandon white inflorescences and white females to remain and undergo color change on yellow inflorescences provided support that the costs of color change differs between the two directions. Female departures from white flowers was apparently not due to a lack of insect visitation, as white inflorescences had higher visitation rates than did yellow. An increase in the prey capture success of females who transitioned from white to yellow against a yellow background supported the prey deception hypothesis.

INTRODUCTION

The ability to undergo a change in body color in relation to its background is a rare trait in animals overall, but known to occur in multiple species across several families of spiders (Oxford & Gillespie, 1998). Best known among the spider cases are those within the flower inhabiting crab spiders of the family Thomisidae. The leading interpretation regarding the evolution of this phenomenon since at least the 19th century has been the presumed advantage of being cryptic on different backgrounds, an idea illustrated by Angus (1882) who described the "protective change of color in a spider." Proposed advantages of crypsis include both prey deception and avoiding detection by one's own predators (Oxford & Gillespie, 1998; Chittka, 2001; Théry & Casas, 2002). In the last ten years, however, multiple studies have provided new insights suggesting that 1) the matches between spiders and their chosen backgrounds (inflorescences on which they capture prey) were not as good as previously thought (Brechbuhl *et al*., 2009; Defrize *et al.*, 2010); 2) reflectance or absorption of UV light differs among species and affects their degree of visibility to prey (Heiling *et al.*, 2005a, 2005b; Herberstein *et al.*, 2009; Llandres *et al.*, 2011; Llandres & Rodríguez-Gironés, 2011); and 3) certain prey appear to be attracted to spider locations due to a visible contrast between spider and substrate (i.e. deception of a different type) (Heiling *et al.*, 2003, 2005a, 2005b; Bhaskara *et al.*, 2009).

Five thomisid species are reported to be capable of color change, and most of the literature concerns *Misumena vatia* (e.g. Gabritschevsky, 1927; Chittka, 2001), *Thomisus onustus* (e.g. Heckel, 1891; Théry & Casas, 2002), and *T. spectabilis* (e.g. Heiling *et al.*, 2004, 2005b). Color change in the other two species (*Misumenops*

asperatus and *Misumenoides formosipes*) has been examined in the lab for the effect of diet on body color in juveniles (Schmalhofer, 2000). Our study is the first to examine the possible function of color change and background matching for *M. formosipes* in the field and the first to assess the rate of color change empirically for any of the five species.

Misumenoides formosipes females are capable of reverse color change between yellow and white depending on the inflorescence color (Beck & Conner, 1992; Schmalhofer, 2000). Although diet induced color change occurs in juvenile males (Schmalhofer, 2000), late instar and adult males do not change color in the field. This suggests that the adaptation arose in response to stronger selection for successful foraging over the adult lifespan of females. Color change of the type exhibited by crab spiders is considered to be a morphological rather than a physiological change, as it occurs over a number of days rather than instantly (Cott, 1940). The metabolic pathways producing color change in *M. vatia* have largely been identified (Insausti & Casas, 2008, 2009; Riou & Christidès, 2010) with the change from white to yellow involving the synthesis of ommochrome pigments immediately beneath the transparent cuticle (Insausti & Casas, 2008). The transition back to white (bleaching) requires the disassembly of those same pigment molecules, allowing the pre-existing guanine crystals to show through the translucent pigments in the epidermis (Insausti & Casas, 2009). The ability to change body color and thereby blend in to the background when switching between substrates has *a priori* adaptive value; and while it occurs within multiple phyla (Edmunds, 1974), it is still rare across the animal kingdom. This rarity suggests that significant costs might be

associated with the required physiological mechanisms. A primary aim of our study was to assess costs and benefits associated with *M. formosipes* females' color changing ability in order to add to our understanding of the phenomenon for crab spiders overall.

Gabritschevsky (1927) reported that it took 10 to 25 d for *M. vatia* to change from white to yellow and less time (2 – 6 d) to go from yellow to white. However, no quantification of color intensity was used, so the determination of yellow and white thresholds was subjective. In contrast, Théry (2007) reported that the time required for *M. vatia* to change from yellow to white under artificial light took longer than the reverse, and suggested that this inefficient matching might mean it is more costly to degrade the color compounds. The only report on color change in adult *M. formosipes* came from Schmalhofer (2001) who estimated a duration of 2 d for yellowing to take place. Preliminary observations from our first field season revealed that white *M. formosipes* females transferred to a yellow inflorescence appeared fully yellow within 4 to 8 d. Color change in the reverse direction was more rarely observed, but seemed to take longer. A difference in the time is takes to change color depending on the direction would support the idea of different costs being involved.

The cryptic predator (i.e. prey deception) (Bristowe, 1958) and prey attraction (Heiling, 2005a, 2005b) hypotheses both predict enhanced prey opportunities based on the degree of visual contrast between spider and background. The case for prey (honeybees) being attracted to *T. spectabilis* locations is associated with reflectance of ultraviolet light from the spider (Heiling, 2003). The UV properties of *M. formosipes* are not known at this time, which prevents us from directly testing the

prey attraction hypothesis currently. Nonetheless, measurement of prey visitation rates and prey capture success of female *M. formosipes* in relation to visible color matching and mismatching will provide insights into potential benefits and/or costs related to color change. The studies that have examined the responses of insects visiting inflorescences with matched or mismatched spiders highlight the variation that exists among color changing thomisid species. For example, Brechbuhl *et al*. (2009) found that solitary bees and syrphid flies avoided inflorescences containing either matched or mismatched *M. vatia* females, while all other insect visitors showed no response to spider presence. By contrast, color matching by the UV reflective *T. spectabilis* resulted in honeybees being attracted to the visual contrast of white spiders on either white or yellow flowers (Heiling *et al.,* 2005b).

Here, we quantified the rate of color change as well as examined prey opportunities and prey capture success of *M. formosipes* females that matched and mismatched their inflorescence background. The two hypotheses tested were: (1) costs of color change differ based on the direction of change and we predict that yellow females transferred to white background would take longer to convert their color than the reverse move; and (2) changing color to match the background functions in prey deception, with the prediction that females who match their background would have more predation opportunities and higher capture success than mismatched females. Also, we predicted based on optimality theory that females we transferred would be more likely to remain and forage on inflorescences they already matched than on mismatched color.

METHODS

Field site and study animal

The majority of the study, including all experimental trials, took place at Ball State University's Cooper Field Area, Delaware Co., IN, where a stable population of *Misumenoides formosipes* hunts along the woodland and prairie edges. Some of the insect visitor quantification (see below) and supplemental collection of females for subsequent trials took place at prairie plantings on private property in Henry Co., IN. Within both field sites, late instar and adult *M. formosipes* were most commonly found on the white inflorescence *Daucus carota*, and various yellow inflorescences (depending on the time of year) including: *Rudbeckia hirta* and *R. triloba*, *Helianthus decapetalous*, *Coreopsis tripteris*, *Ratibida pinnata*, and *Silphium integrifolium*. These also served as the inflorescences used in the color match/mismatch trials. Field work was conducted between July and September in 2011 and 2012 when females ranged from antepenultimate juveniles to adult instars.

Census of naturally occurring females

Daily searches for naturally occurring *M. formosipes* females were performed in 2011 to determine their tenure at a specific site, distribution relative to inflorescence types, and to estimate the frequency of prey capture. In 2012, each new female was photographed and her color, the plant species, and the presence/absence of a prey item were recorded. A total of 233 females were located, of which 163 were collected and used within 24 h in our color matching/mismatching trials.

Insect visitor quantification

Prey capture opportunities across the combinations of spider colors and inflorescence colors were assessed for 101 of the naturally occurring females prior to their collection. Females had to be found without prey and in a hunting position (i.e. settled on an inflorescence in a position to catch prey). Observations were made only in the absence of rain or high winds, and observers positioned themselves close enough to identify visiting insects. The female's location was then observed for 15 min, during which the number of insect visitors were recorded. Only flying insects in the immediate proximity of the inflorescence inhabited by the spider were included. Individual visitors were recorded as either a flight or a landing, but not both. Flights included both hovering and diverted flights (when the flight path of an insect diverted toward an inflorescence). Landings were categorized as greater than or less than 1 cm from the spider. All visitors were categorized as hymenopterans, dipterans or other/undetermined. Photos were not taken until after the observation period to limit disturbances prior to visitor quantification.

The effect of spider presence on insect visitation rates was assessed by observing a comparable hunting site with no spider present. Beginning a minimum of 2 m from each spider-occupied plant, we searched for the first plant that matched the original in terms of plant condition and inflorescence arrangement (i.e. the number, sizes, and condition of contiguous inflorescences). The 2 m distance was chosen to reduce the level of disturbance from the previous set of observations while keeping the hunting sites within the same general area and conditions. Insect visitation was

recorded in the same manner as described above, except that landings were not separated into two categories due to the absence of a spider.

The same females initially monitored for insect visitation were then collected for use in the subsequent color change trials. Each female was photographed immediately after being released onto a new inflorescence and then given a minimum of 15 min to settle into place. If she had assumed a hunting position on the inflorescence at that point, insect visitation rates were quantified in the same manner as above including the observations on a comparable inflorescence with no spider.

Color change trials

Females were moved from their original inflorescence to new ones that were in good condition (i.e. apparently attractive to pollinators) for two purposes. First, yellow and white females were relocated onto inflorescences of their opposite color in an effort to document the rate at which the full color change occurred. As a control for any effect on the relocation disturbance, additional yellow and white females were moved onto new inflorescences of like color. Second, this trial design allowed for prey capture opportunities to be compared between females matched and mismatched to their background color. Throughout this report, the four trial types are categorized by two letter codes (WW, YY, WY, and YW), whereby the first letter designates the spider color and the second letter the inflorescence color. Relocated females were checked at 08:00, 12:00, 16:00 and 20:00 each day to monitor spider residency, prey capture, and color change. A trial ended when the spider was no longer present on the inflorescence where it had been placed. However, to ensure it had not been

overlooked, the area was checked for an additional 2 d. Prey items were identified to order and their size (length) was measured from head to tip of abdomen.

Rate of color change was documented with digital photos taken at trial initiation and again each day at 08:00 with a Canon PowerShot G12 camera. All photographs were taken at -1 exposure using the flash to standardize light conditions. Color was quantified in Adobe Photoshop® using the Lab color space component, which provides an empirical representation of color independently of the device used to produce the image. The color values within Lab color space are represented as three numbers, with L* representing lightness, a* the red/green value, and b* the yellow/blue value (Margulis, 2005). For this analysis only the b* values were used.

Preliminary investigations revealed that each spider's legs, cephalothorax, and abdomen changed color simultaneously and any could be used to measure the rate of change. However, because the legs are more often in a position to be photographed without disturbance, a standardized point on the femur of the front legs was chosen. Photographs were not taken if excessive disturbance would have been required. Once images were opened in Photoshop, four guides were placed at each edge of the femur to form a rectangle. Two diagonal lines were then drawn from opposite corners to form an X. One horizontal guide and one vertical guide were placed at the point where the two diagonal lines cross. The lines were then deleted, as the color of the line would affect the color reading of the spider. The eyedropper tool was placed where the two new (colorless) guides crossed, and the color measurement was recorded using a 5 X 5 pixel sample.

Statistical Analysis

The proportions of prey caught by naturally occurring background-matched females residing on white versus yellow inflorescences were compared using chi-square analysis.

Two sample t-tests, were used to determine the difference between the numbers of insect flights and landings at 1) unoccupied white versus yellow inflorescences 2) white versus yellow inflorescences occupied by naturally occurring background-matched females, and 3) naturally occurring versus relocated females on matched yellow and white inflorescences. Relocated matched spider-occupied inflorescences and their matched-pair, unoccupied inflorescences were compared using paired t-tests to determine if spider presence had an effect on insect flights or landings. The proportions of flying insects that landed on inflorescences harboring a matched or mismatched spider were compared using chi-square analyses for both white and yellow inflorescences.

To eliminate variation across individuals, the b* value (color value) obtained at the initiation of each trial was subtracted from b* values on subsequent days resulting in an "adjusted b* value." The adjusted b* value across the first 9 d after trial initiation (at which time mean b* reached a peak) was used to determine rate of color change for white females on yellow inflorescences (WY). The duration of stay on inflorescences among all four trial types (WW, WY, YY, YW) was compared using Kruskal-Wallis ANOVA and Tukey-type multiple comparisons test for medians (Zar, 1996). The duration of stay for the subset of females who stayed more than 1 d was square root transformed to achieve normality and compared using one-way ANOVA. The YW trial type was omitted from this comparison due to its small

sample size (n=2). The proportion of females that stayed for more than 1 d was compared across the four trial groups using chi-square analysis and Tukey-type multiple comparisons test for proportions (Zar, 1996). The proportion of females observed with prey were compared using chi-square analysis. This comparison was restricted to the first 2 d of trials to ensure WY females were still mismatched to their background. Females that remained less than 2 d as well as the YW trial type (n=2) were excluded. Linear regression was used to determine if the rate of prey capture increased over time for white and yellow females placed on yellow inflorescences.

All statistical analyses were done in Minitab (ver. 16, 2013) except for the Kruskal-Wallis and chi-square multiple comparisons tests, which were conducted using hand calculations (Zar, 1996). Means and standard errors are reported throughout except where statistical tests call for comparisons of medians. Data distributions were tested for normality using the Anderson-Darling tests. Parametric tests were used in all cases except when data were not normally distributed and transformations could not achieve normality. Alpha was set at 0.05 for all tests of significance.

RESULTS

Census of naturally occurring females

Naturally occurring females remained on yellow inflorescences for 6.67 ± 1.73 d (n = 48), and on white inflorescences for 5.97 ± 0.93 d (n = 37) after we detected them. Tenure on other colors of inflorescences (red, purple, blue) averaged only 4.87 ± 0.98 d (n = 23). Departures were typically coincident with inflorescence

deterioration. All of these durations are minimums of actual mean tenure on inflorescences since they do not include any days spiders were present prior to our detection of them.

Of the 233 naturally occurring females sighted (Table 1), 96% were subjectively judged to match their background. Yellow females on yellow inflorescences were observed with prey more often than white females on white inflorescences (14.6% versus 4.6% of the sightings, respectively) ($\chi^2_1 = 6.347$, $p = 0.012$; Table 1) and no mismatched females had prey upon detection.

Insect visitor quantification

White inflorescences had more insect flights ($t_{92} = 3.26$, $p = 0.002$) and landings ($t_{95} = 2.52$, $p = 0.014$) than yellow inflorescences when no spider was present (Fig. 1a). When matched spiders were present, white inflorescences still had more insect flights ($t_{50} = 2.31$, $p = 0.025$) than yellow inflorescences, however there was no difference found for landings ($t_{81} = 0.78$, $p = 0.438$; Fig. 1b).

There were no significant differences in mean number of insect flights ($t_{52} = 0.82$, $p = 0.414$) or landings ($t_{51} = 1.06$, $p = 0.295$) between inflorescences with naturally occurring matched females versus inflorescences with our matched, relocated females. Likewise, insect visitation did not differ between inflorescences harboring our matched relocated females versus the unoccupied matched-pair inflorescences (flights: paired-t = 0.30, $p = 0.764$; landings: paired-t = 0.74, $p = 0.461$; see Table 2).

Within the relocation trials of matched/mismatched females, insects in flight around inflorescences housing color-matched females were no more likely to land

than those flying around inflorescences with mismatched females (Fig. 2a: white inflorescences, $\chi^2_1 = 2.78$, $p = 0.09$; Fig 2b: yellow inflorescences, $\chi^2_1 = 2.99$, $p = 0.08$). However, when naturally occurring females are included in the analysis, insects observed flying around white inflorescences were significantly more likely to land on inflorescences occupied by a mismatched yellow spider compared to a matched white spider ($\chi^2_1 = 5.94$, $p = 0.01$) and insects observed flying around yellow inflorescences were more likely to land on inflorescences occupied by a matched yellow spider compared to a mismatched white spider ($\chi^2_1 = 6.14$, $p = 0.01$).

Insects flying around inflorescences were often unidentifiable, although hymenopterans clearly outnumbered all other individual orders (Table 3). Upon landing identifications were much more reliable and the vast majorities were hymenopterans across all categories (Table 3).

Characteristics of prey items

The size of prey items observed with females varied throughout the season (Fig. 3), and mean prey size did not differ between white (6.53 ± 0.79 mm, n = 39) and yellow inflorescences (7.95 ± 0.49 mm, n = 133) ($t_{69} = -1.54$, $p = 0.12$). The majority of the prey items caught on white and yellow inflorescences were hymenopterans and dipterans (Table 4).

Color change trials

The change of females from white to yellow when placed on a yellow inflorescence began within 1 d, and some females reached the upper end of the range by day 3 (Fig. 4). Mean color value, i.e. the adjusted b* value, peaked at day 9 before

leveling off. The average color value for days 9-20 was 58.54 ± 0.68 (adjusted b*) and 72.42 ± 0.59 (non-adjusted b*). We used the slope of the initial 9 d period (y = 7.88x + 6.27) as a measure of the rate of color change, which represents an average rate of change of 11.1% per day.

Many of the relocated females (38.8%) left the inflorescence within the first day and 62.2% of those left within the first 4 h (Fig. 5). The proportion of females that remained for more than 1 d on the inflorescence where they were relocated differed across the four trial types ($\chi^2_3 = 46.89$, $p < 0.001$; Fig. 5). More YY females (90%) than WW females (55.6%) stayed for at least 1 d. The proportion of WY females remaining at least 1 d (72.4%) was statistically equivalent to YY and WW females, and fewer YW females (6.67%) stayed beyond 1 d than any other trial type. The median duration of stay differed across the four trial types ($H_3 = 39.02$, $p < 0.001$; Fig. 6a) and again the duration of stay was the least for YW compared to all other trial types. However, if the females that departed within 1 d are omitted from the analysis (thus eliminating the YW category), there were no differences in the mean durations of stay across the trial types ($F_{2,60} = 0.35$, $p = 0.71$; Fig. 6b).

There were no differences across trial types (with YW excluded) for the proportion of females observed with prey within the first two days of trials ($\chi^2_2 = 4.918$, $p = 0.086$; Fig.7). Following their relocation, the proportion of WY females with prey increased significantly across the days of the trial ($y = 0.019 + 0.013x$, $F_{1,18} = 22.9$, $r^2 = 0.56$, $p < 0.001$; Fig. 8a). No relationship was found between the

proportion of YY females with prey and trial durations ($y = 0.150 + 0.00052x$, $F_{1,18} = 0.02$, $r^2 = 0.001$, $p = 0.893$; Fig. 8b).

DISCUSSION

Preliminary observations of naturally occurring color change in *Misumenoides formosipes*, together with information on the biochemistry of these processes in other species, led us to hypothesize that the two directions of color change differ in their costs. Studies of *Misumena vatia* have demonstrated that the development of the yellow body color results from the formation of ommachrome pigment granules within epidermal cells (Insausti & Casas, 2008; Riou & Christidès, 2010), whereas the "bleaching" from yellow to white involves the degradation of those same pigments (Insausti & Casas, 2009). Théry (2007) suggested that the latter process might be more costly. Our plan to test the prediction that transitioning from yellow to white would take longer than the reverse was hampered when yellow females quickly abandoned white inflorescences in our trials. With respect to this rate of change comparison we can only say that the transition by females from white to yellow, while not as fast in our study as the 2 d estimated by Schmalhofer (2001), sometimes occurred as quickly as 3 d; whereas, the only two yellow females that remained on white substrates long enough to begin transitioning were not fully white even after 11 days (their b values measured 47 and 22 compared with a mean of 9.93 for white females collected in the field; smaller numbers reflect a more intense white). Paradoxically, the very behavior preventing a full quantitative comparison of the rates of color change, i.e. departures by yellow females from white flowers, can itself be interpreted as supportive of the differential costs hypothesis. We propose that the

reluctance of these females to remain and change colors could be a response to "expected" foraging tradeoffs. Relatively lower predation opportunities and/or high-energy costs for the transition to white body color would be plausible reasons to move to another location.

The substrate preferences exhibited by *M. formosipes*, with both color morphs of spiders accepting yellow flowers but only white spiders staying on white flowers, raised an interesting comparison with the Australian crab spider *Thomisus spectabilis.* In field censues, 94% of yellow *T. spectabilis* females were located on yellow inflorescences, while white females occupied both yellow and white inflorescences (69% to 31% respectively) (Heiling *et al.*, 2005b). Our own census of naturally occurring females likewise revealed 95% of yellow females on yellow backgrounds; however, we did not observe the split distribution of white females. Almost all (97%) of our white morph females were found on white flowers despite their acceptance of yellow flowers during our relocation trials. Heiling *et al.* (2005b) were able to offer an intriguing explanation for the differing distributions of their two spider morphs following experimental trials that revealed yellow spiders on white flowers to be the only combination avoided by honeybees. Schmalhofer (2001) reported that honeybees are also a preferred prey item of *M. formosipes*, so if a similar avoidance occurred in our population it could explain the departures by yellow females relocated onto white flowers. It should be noted that no honeybees were observed visiting *Daucus carota* (our white inflorescence) even with no spider present. Also, the cue for detection by honeybees of the yellow *T. spectabilis* on white flowers is purported to be the high

contrast resulting from UV reflectance by that crab spider (Heiling *et al.*, 2005b). Whether or not *M. formosipes* reflects or absorbs UV light is unknown at this time.

Our other predictions from an optimality perspective were that females would be more likely to remain and forage on inflorescences they already matched than on mismatched backgrounds, and that hunting success would be higher for color-matched females. We obtained contrasting results with respect to these predictions. Females on white flowers behaved according to our expectation (only matched females remained on the flowers after relocation), while females on yellow flowers persisted at the same rate whether matched or not. With regard to foraging success, our measures of flying insect visitation rates revealed no differences between matched and mismatched circumstances, while the proportions of landings supported the prey deception hypothesis on yellow flowers but not on white ones. Prey capture by mismatched white females was statistically equivalent to that of matched females of either color (although the non-significant capture rate was distinctly lower for the mismatched females).

The strongest support for the prey deception hypothesis came from the significant increase in prey capture success as white females transitioned into better matches on their yellow backgrounds. The possibility that improvement seen for these color changing females was due to recovery from the initial relocation disturbance is inconsistent with the fact that the yellow females we relocated to yellow flowers showed no improvement in capture rate during their trials. Overall, while our results were mixed with respect to assessment of the prey deception hypothesis, even the limited support contrasted with the findings of Brechbühl *et al*. (2009) for *M. vatia.* In

a rigorous study of insect prey potential across the four matched/mismatched categories, they found no advantages for matched spiders in either visitation rates or capture success.

Schmalhofer (2001) demonstrated that *M. formosipes* females can discriminate amongst flower patches of varying quality with respect to prey visitation and that the proportion of females on yellow flowers increased as the season progressed. Could yellow inflorescences simply have provided better foraging locations in comparison to white in our population, regardless of crypsis? Naturally occurring matched females caught prey more often on yellow inflorescences compared to matched females on white inflorescences. By contrast, matched females in color change trials did not differ in their prey capture success. Prey sizes were the same regardless of floral color. Finally, white inflorescences actually had more flying insects than yellow inflorescences regardless of spider presence, and insect landings occurred at a higher rate on inflorescences with yellow spiders regardless of floral color.

Floral architecture, symmetry, UV reflectance, and patch size can all affect the number and type of insects visiting inflorescences (Schmalhofer, 2001); therefore, it is important to consider that the inflorescences used in our study differed beyond color. The umbel of *D. carota* provides a broader surface for pollinators to obtain nectar rewards in comparison to all of the yellow aster species, which restrict pollinators to the center disk of tightly clumped disk florets (Schmalhofer, 2001).

In conclusion, our results provide general support for the notion that the two directions of transitioning between yellow and white body color have differing costs

and benefits. Therefore, when *M. formosipes* females search for a new hunting site the decision on when to stop may not be predicated solely on the condition of the inflorescence or distance to it, but also on its color. Future research with this species should offer females the opportunity to choose between immediately adjacent yellow and white inflorescences in the field while controlling for all other differences possible. We predict that as with similar lab trials with *T. spectabilis* (Heiling *et al*., 2005b) yellow *M. formosipes* will consistently choose the yellow background whereas white females will exhibit mixed results with some choosing their match and others choosing to transition to yellow. We further suggest that if such trials are conducted across the season, preference for the yellow inflorescences would increase as the season progressed and as female size increased. This prediction is based on the fact that in our population the main late season white inflorescence is *D. carota*, whose collection of individually small flowers (arranged into an umbel) attracts few larger pollinators. Thus, more mature females may be favored to locate yellow flowers.

The role that background color matching plays across the multiple thomisid species capable of color change continues to be challenging to interpret. As other researchers (e.g. Chittka, 2001; Théry & Casas, 2002; Heiling *et al.*, 2005a, Théry *et al*., 2005; Defrize, *et al.*, 2010) have pointed out, we have to consider the visual capacities of the animals involved when attempting to evaluate hypotheses regarding predator crypsis. It is increasingly clear that the absorption or reflection of UV light by these spiders is a factor in the predator/prey relationships and apparently plays different roles depending on the species (e.g. Herberstein *et al*., 2009). Evidence

suggests that UV-associated contrasts between spiders and their background can be an attractant for prey as well as a cue that prey will avoid (Heiling *et al.*, 2003, 2005a, 2005b; Heiling & Herberstein, 2004; Llandres *et al.*, 2011; Llandres & Rodríguez-Gironés, 2011). The UV properties of *M. formosipes* are unclear at this time, however, we have shown that color contrasts accessible to the human eye are sufficient to predict how this species will behave on differently colored backgrounds.

REFERENCES

Angus, J. (1882) Protective change of color in a spider. *American Naturalist*, 16, 1010.

Beck, M.W. & Connor, E.F. (1992) Factors affecting the reproductive success of the crab spider *Misumenoides formosipes*: the covariance between juvenile and adult traits. *Oecologia*, 92, 287-295.

Bhaskara, R.M., Bruesh, C.M., Ahmed, S., & Borges, R.M. (2009) Perception of ultraviolet light by crab spiders and its role in selection of hunting sites. *Journal of Comparative Physiology A*, 195, 409-417.

Brechbuhl, R., Casas, J. & Bacher, S. (2009) Ineffective crypsis in a crab spider: a prey community perspective. *Proceedings of the Royal Society B: Biological Sciences*, 277, 739–746.

Bristowe, W.S. (1958) *The World of Spiders*. London: Collins.

Chittka, L. (2001) Camouflage of predatory crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae / Hymenoptera: Apidae). *Entomologia Generalis*, 25, 181-187.

Cott, H.B. (1940) *Adaptive Colouration in Animals.* Methuen Ltd, London.

Defrize, J., Théry, M. & Casas, J. (2010) Background colour matching by a crab spider in the field: a community sensory ecology perspective. *Journal of Experimental Biology*, 213, 1425-1435.

Edmunds, M. (1974) *Defence in Animals. A Survey of Anti-predator Defences* Longman Group, Harlow, U.K.

Gabritschevsky, E. (1927) Experiments on color changes and regeneration in the crab-spider, Misumena vatia. *Journal of Experimental Zoology*, 47, 251-267.

Heckel, E. (1891) Sur le mimétisme de *Thomisus onustus*. *Bulletin Scientifique de la France et de la Belgique*, 23, 347-354.

Heiling, A.M., Cheng, K., Chittka, L., Goeth, A. & Herberstein, M. (2005a) The role of UV in crab: spider signals: effect on perception by prey and predator. *Journal of Experimental Biology*, 208, 3925-3931.

Heiling, A.M., Chittka, L., Cheng, K. & Herberstein, M.E. (2005b) Colouration in crab spider: substrate choice and prey attraction. *Journal of Experimental Biology*, 208, 1785-1792.

Heiling, A.M., Cheng, K. & Herberstein, M.E. (2004) Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). *Behavioral Ecology*, 15, 321–326.

Heiling, A.M. & Herberstein, M.E., (2004) Predator – prey coevolution: Australian native bees avoid their spider predators. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, 196-198.

Heiling, A.M., Herberstein, M.E., & Chittka, L. (2003) Crab-spiders manipulate flower signals. *Nature*, 421, 334.

Herberstein, M.E., Heiling, A.M. & Cheng, K. (2009) Evidence for UV-based sensory exploitation in Australian but not European crab spiders. *Evolutionary Ecology* 23, 621-634.

Insausti, T.C. & Casas, J. (2008) The functional morphology of color changing in a spider: development of ommochrome pigment granules. *Journal of Experimental Biology*, 211, 780-789.

Insausti, T.C. & Casas, J. (2009) Turnover of pigment granules: cyclic catabolism and anabolism of ommochromes within epidermal cells. *Tissue Cell*, 41, 421-429.

Llandres, A.L., Gawryszewski, F.M., Heiling, A.M. & Herberstein, M.E. (2011) The effect of colour variation in predators on the behaviour of pollinators: Australian crab spiders and native bees. *Ecological Entomology*, 36, 72–81.

Llandres, A.L., & Rodríguez-Gironés, M.A. (2011) Spider movement, UV reflectance and size, but not spider crypsis, affect the response of honeybees to Australian crab spiders. *PLoS One*, 6, e17136.

Margulis, D. (2005) *Photoshop LAB color: The canyon conundrum and other adventures in the most powerful colorspace*. Peachpit Press.

Morse, D.H. (1981) Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three common native flowers. *American Midland Naturalist*, 105, 358-367.

Oxford, G.S. & Gillespie, R.G. (1998) Evolution and ecology of spider coloration. *Annual Review of Entomology*, 43, 619–643.

Riou, M. & Christidès, J. (2010) Cryptic color change in a crab spider (*Misumena vatia*): identification and quantification of precursors and ommochrome pigments by HPLC. *Journal of chemical ecology*, 36, 412-423.

Schmalhofer, V.R. (2000) Diet-induced and morphological color changes in juvenile crab spiders (Araneae, Thomisdae). *Journal of Arachnology*, 28, 56-60.

Schmalhofer, V.R. (2001) Tritrophic interactions in a pollination system: impacts of species composition and size of flower patches on the hunting success of a flower-dwelling spider. *Oecologia*, 129, 292-303.

Théry, M. (2007) Colours of background reflected light and of the prey's eye affect adaptive coloration in female crab spiders. *Animal Behaviour*, 73, 797-804.

Théry, M. & Casas, J. (2002) Predator and prey views of spider camouflage. *Nature*, 415, 133.

Théry, M., Debut, M., Gomez, D. & Casas, J. (2005) Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behavioral Ecology*, 16, 25-29.

Zar, J.H. (1996) *Biostatistical Analysis,* 3rd edn. Prentice Hall, Inc., Upper Saddle River, New Jersey.

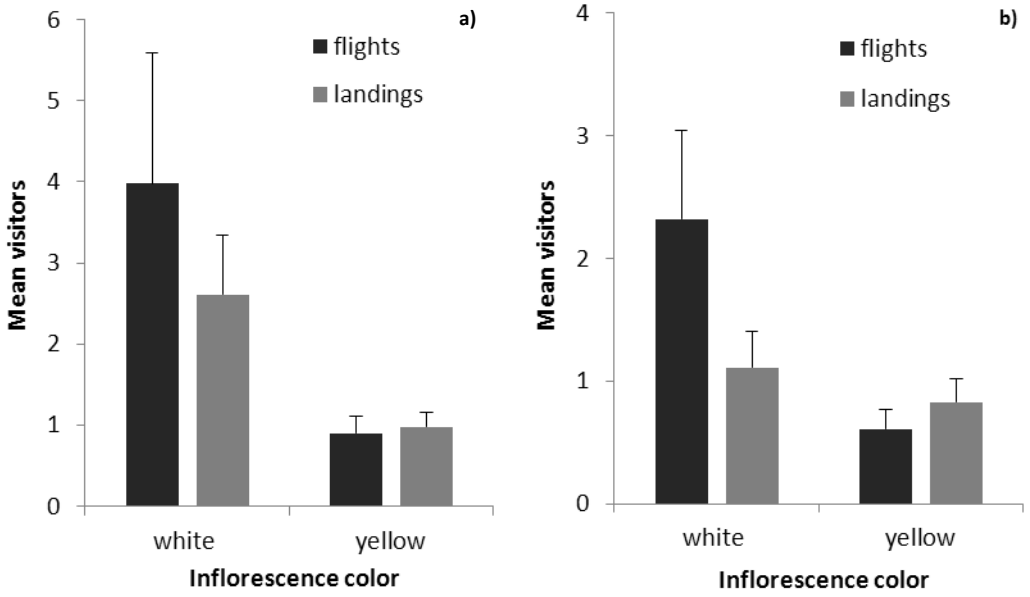

Fig. 1. Mean (+SE) number of flights and landings by insects at white (a: n=87; b: n=47) and yellow (a: n=100; b: n=54) inflorescences with a) no spider and b) matched spider present.

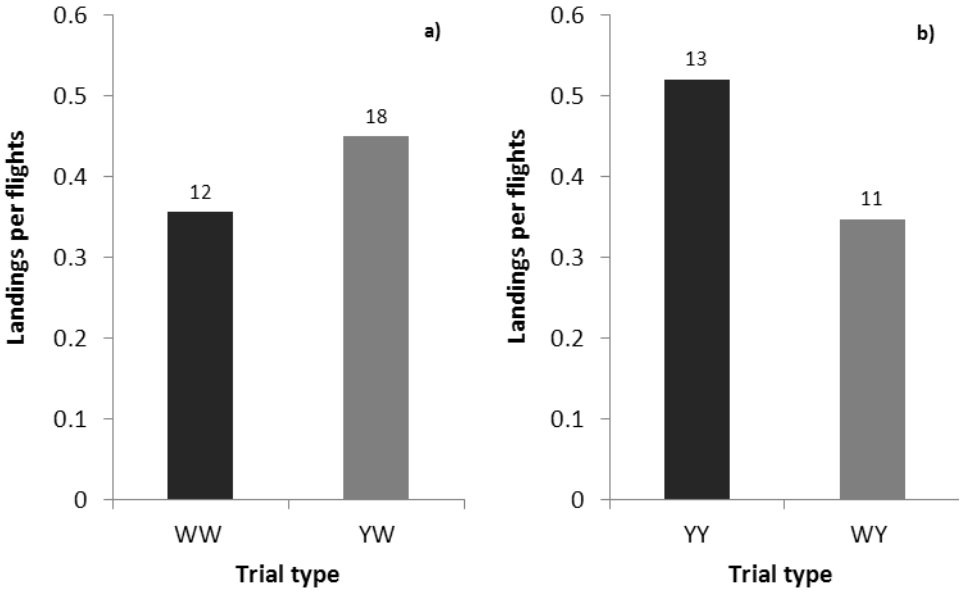

Fig. 2. Proportion of flying insects that land on (a) white and (b) yellow inflorescences occupied by a relocated, matched (■) or relocated mismatched (■) spider. Sample sizes are reported above each bar.

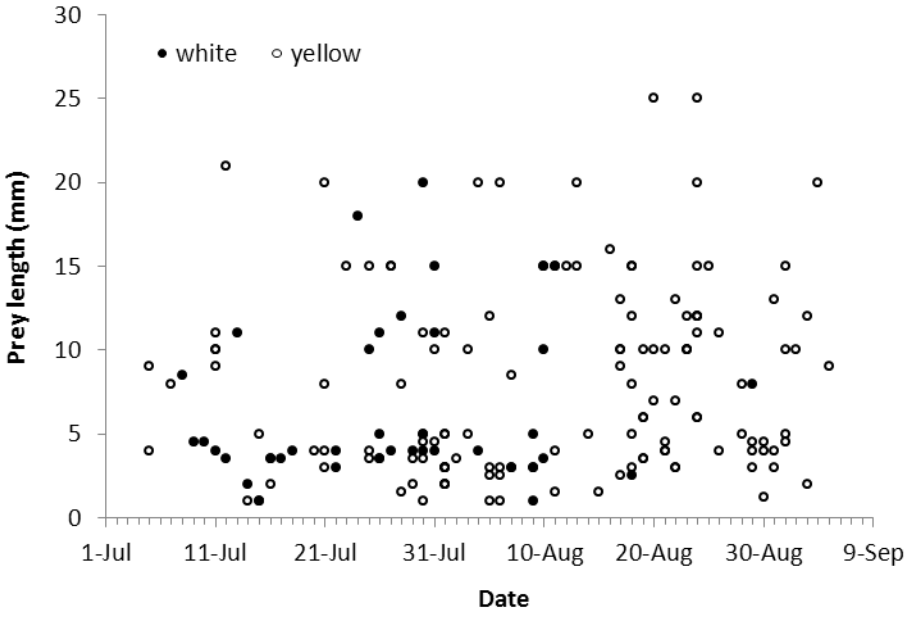

Fig. 3. Size (length in mm) of prey items observed across days for *M. formosipes* females on white and yellow inflorescences.

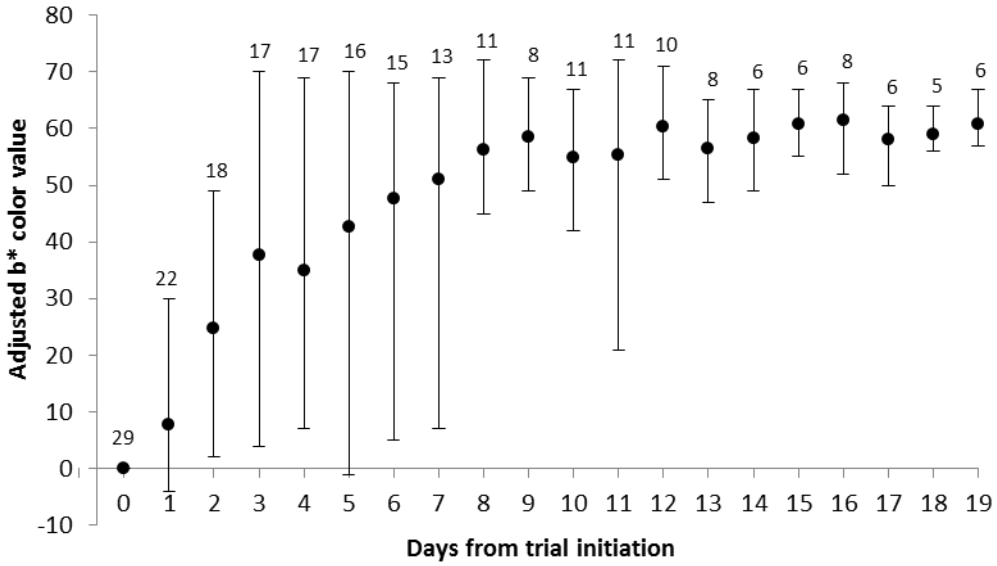

Fig. 4. Mean adjusted b* color value for white *M. formosipes* females placed onto yellow inflorescences. Bars show range of measurements per female and sample sizes are reported above each range.

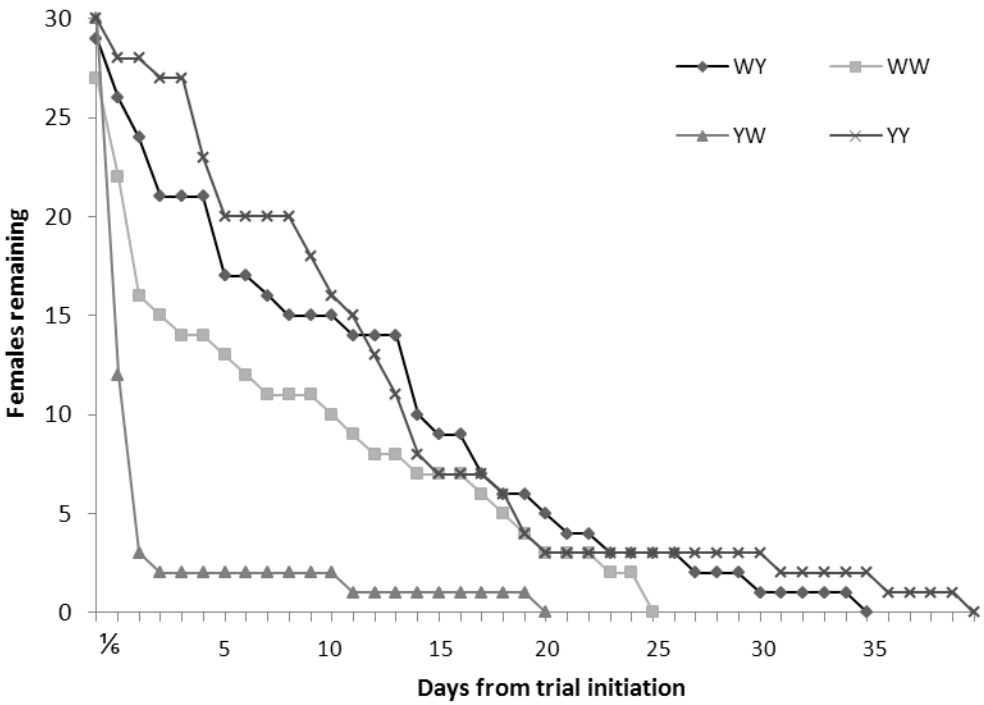

Fig. 5. Number of *M. formosipes* females remaining across days of trials after being placed onto yellow or white inflorescences that either matched or mismatched their body color. The continued presence of each female was checked 4 h after her release (shown as 1/6 day on the x-axis) and then at ca. 0800h each subsequent day.

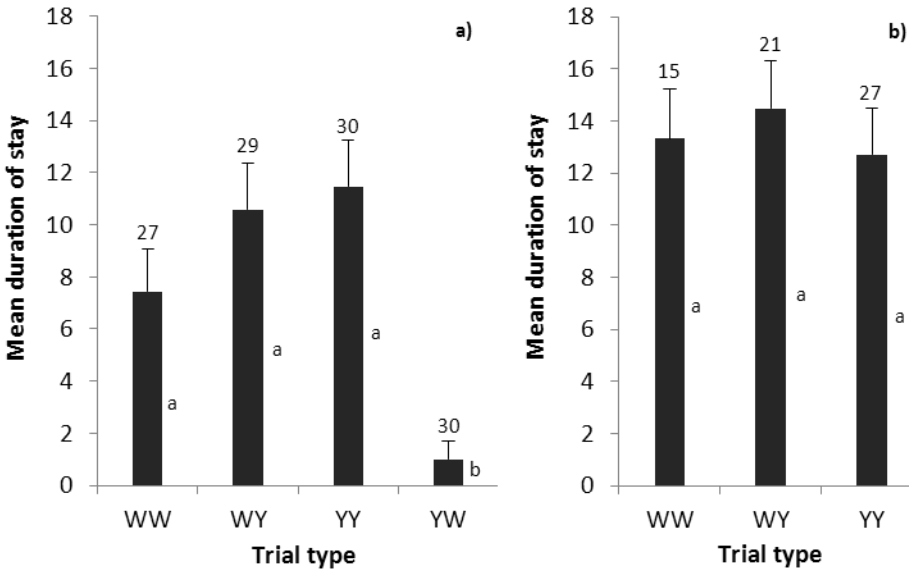

Fig. 6. Mean (+SE) duration of stay on inflorescences that either matched or mismatched body color for (a) all white and yellow females from trial initiation and (b) the subset of females that remained on the inflorescence for >1 d. Sample sizes are reported above each bar. Bars sharing the same letter were not significantly different at p = 0.001.

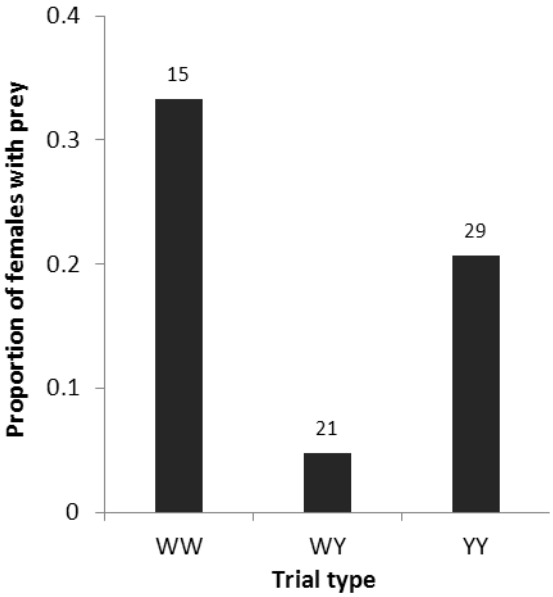

Fig. 7. Proportion of *M. formosipes* females staying >2 d observed with prey over first 2 d of trials. Sample sizes are reported above each bar.

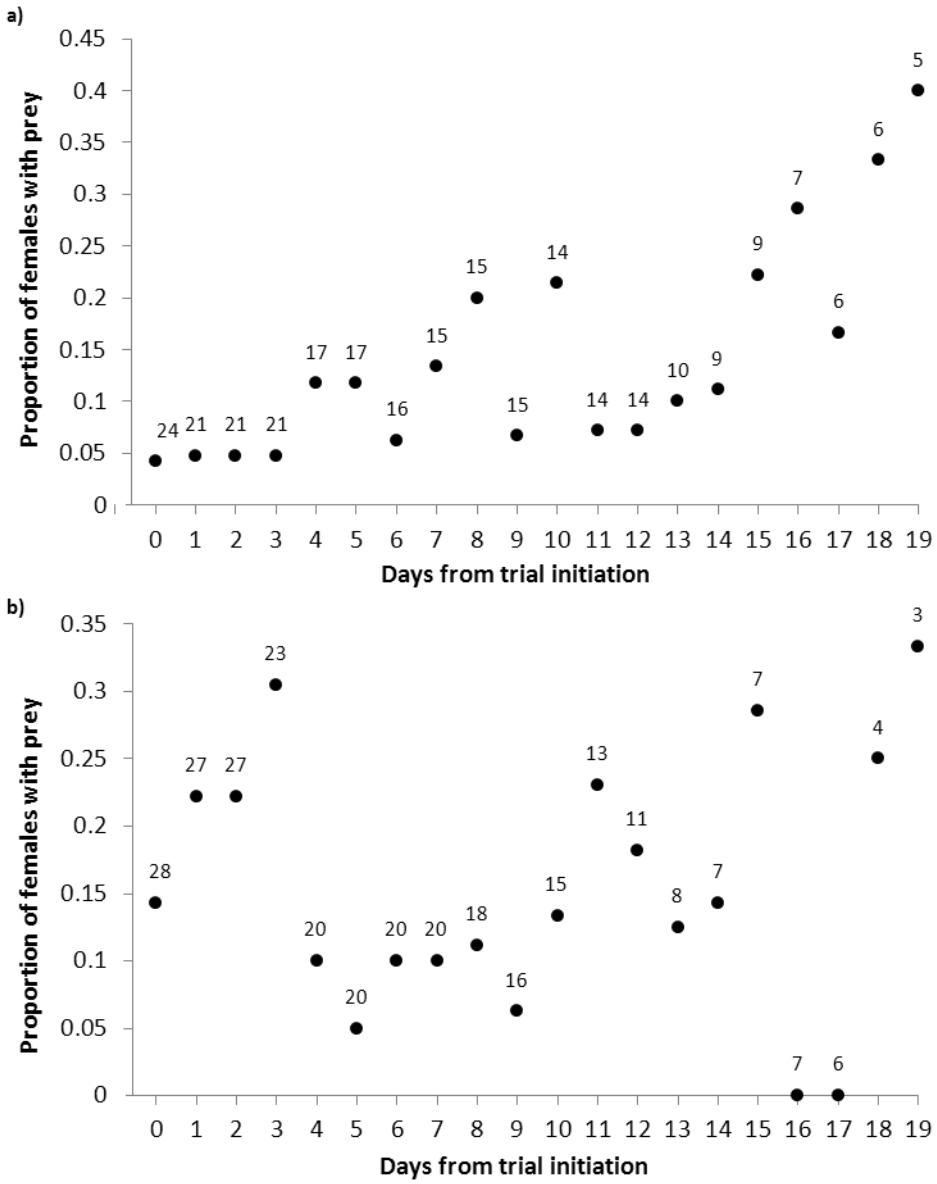

Fig. 8. Proportion of a) white and b) yellow *M. formosipes* females observed with prey each day after being placed onto yellow inflorescences. Sample sizes are reported above each data point.

body/inflorescence color	total	with prey
white on white	108	5
white on yellow	3	0
yellow on yellow	116	17
yellow on white	6	0

Table. 1. Number of naturally occurring *M. formosipes* females discovered on inflorescences that matched or mismatched their body color, and the numbers possessing prey.

	Color*	*n*	flights	landings	landings <1cm
Spider present	WW	19	4.47 ± 2.65	2.47 ± 1.31	0.00 ± 0.00
	WW (nat.)	47	2.32 ± 0.72	0.96 ± 0.27	0.09 ± 0.59
	YW	21	4.71 ± 1.98	3.67 ± 1.68	0.19 ± 0.15
	YY	26	0.89 ± 0.38	0.77 ± 0.23	0.19 ± 0.10
	YY (nat.)	54	0.61 ± 0.16	0.61 ± 0.14	0.22 ± 0.11
	WY	20	1.60 ± 0.62	0.80 ± 0.26	0.05 ± 0.22
Spider absent	White	87	3.98 ± 0.93	2.61 ± 0.63	
	Yellow	100	0.90 ± 0.18	0.98 ± 0.15	

Table. 2. Mean (±SE) number of flights, landings, and landings within 1 cm of the spider for the four relocation trial types, naturally occurring females (nat.) on matched backgrounds, and unoccupied white and yellow inflorescences. *First letter denotes spider body color and second letter denotes inflorescence color. Sample sizes (n) reflect the number of observation periods.

		Flights (%)			Landings (%)		
	Color*	Hymenop-tera	Diptera	other/ unknown	Hymenop-tera	Diptera	other/ unknown
Spider present	WW	29.4	2.4	68.2	83.0	8.5	8.5
	WW (nat.)	44.0	10.1	45.9	76.9	3.8	19.2
	YW	34.3	0.0	65.7	90.1	3.7	6.2
	YY	47.8	8.7	43.5	52.0	4.0	44.0
	YY (nat.)	30.3	36.4	33.3	75.6	13.3	11.1
	WY	40.6	12.5	46.9	58.8	5.9	35.3
Spider absent	White	40.8	2.9	56.4	89.0	4.4	6.6
	Yellow	53.3	21.1	25.6	59.2	14.3	26.5

Table. 3. Percentage of insect orders in the categories of flights and landings for the four relocation trial types, naturally occurring females (nat.) on matched backgrounds, and unoccupied white and yellow inflorescences. *First letter denotes spider body color and second letter denotes inflorescence color.

Inflorescence color	order	% of total observed	mean size (mm)	size range (mm)
white (*n=39*)	Diptera	30.77	8.38 ± 1.39	3 - 15
	Hymenoptera	53.85	5.24 ± 0.90	1 - 20
	Lepidoptera	2.56	11.00 ± 0.00	11
	Orthoptera	5.13	14.50 ± 3.50	11 - 18
	unknown	7.69	1.33 ± 0.33	1 - 2
yellow (*n=133*)	Diptera	27.07	7.39 ± 0.66	1.5 - 15
	Hymenoptera	38.35	7.445 ± 0.70	1 - 20
	Lepidoptera	13.53	13.17 ± 1.71	3.5 – 25
	Orthoptera	9.02	11.08 ± 1.57	4 - 20
	Hemiptera	4.51	3.50 ± 0.58	2 - 6
	unknown	7.52	2.10 ± 0.40	1 - 5

Table. 4. Percentage, mean size (±SE) and size range of prey items categorized into orders observed with *M. formosipes* females on white and yellow inflorescences.