VOL. 182, NO. 4 THE AMERICAN NATURALIST OCTOBER 2013

Social Factors Driving Settlement and Relocation Decisions in a Solitary and Aggregative Spider

Michael M. Kasumovic* and Lyndon A. Jordan

Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia

Submitted October 16, 2012; Accepted May 15, 2013; Electronically published July 31, 2013

Dryad data: http://dx.doi.org/10.5061/dryad.3723v.

ABSTRACT: Both ecological and social factors play an important role in determining the structure of animal settlement patterns. While the ecological factors determining animal settlement are generally well known, the relative importance of social factors in mediating fine-scale settlement choices is poorly understood. As a result, we have little knowledge of why individuals choose to settle near specific neighbors. Here we used a web-building spider (*Nephila plumipes*) that settles both solitarily and next to neighbors within aggregations to examine the specific social factors that influence settlement decisions. Within experimental enclosures, we observed the settlement patterns of females pre- and postmale release. This allowed us to compare two models of aggregative settlement in lekking species—the hotshot and preferences models—to examine the relative importance of a female's phenotype and mate attraction to further dissect settlement and relocation decisions. We show that mate attraction increased with aggregation size and that larger females were generally preferred, supporting both the hotshot and preference models of aggregative settlement. We further demonstrate that smaller females that attracted fewer males within an aggregation were most likely to relocate. Our results demonstrate how social feedback can affect initially state-dependent settlement decisions, thereby highlighting the dynamic nature of settlement.

Keywords: aggregations, settlement patterns, mate attraction, *Nephila plumipes*.

Introduction

Territory establishment is constrained by a number of biotic and abiotic factors. Although habitat requirements are undoubtedly important in determining whether settlement occurs, there are a number of secondary factors that are essential in determining individual settlement patterns. For example, the presence of predators can determine how closely individuals aggregate (Lima 2009), and social factors such as population density can determine territory size (Erlinge et al. 1990; Sommaro et al. 2010). While such factors can explain the spatial layout of territories, they fall short of explaining why individuals choose to settle near particular neighbors. Understanding neighbor choice requires a specific focus on the social factors that drive settlement patterns.

Social factors, in particular, appear to drive settlement patterns in species where individuals settle in clustered territories despite abundant available habitat. Such aggregations are epitomized by lekking species where males create ephemeral aggregations for the sole purpose of acquiring matings (birds, Höglund and Alatalo 1995; lizards, Stamps 1988). Such aggregative settlement, however, is also commonly found outside of lekking species. Males are known to settle in display territories, where they attract mates but also care for offspring (e.g., fish, Breder and Rosen 1966; crabs, Christy 1988). Even species such as socially monogamous pairs of birds are known to settle in tightly packed territories occurring within pockets of widely available habitat (e.g., hidden leks, Tarof et al. 2005; Wagner 1993). Social elements seem particularly important in regulating aggregative patterns outside of true lekking species, as such settlement can be triggered by the presence of conspecifics (Muller et al. 1997), and males within aggregations may prefer certain neighbors over random individuals (Booksmythe et al. 2010). Given that aggregative settlement patterns are common across a wide variety of taxa, it is both interesting and important to understand how different social factors influence and alter individual settlement decisions.

Of particular utility in examinations of settlement patterns are those species in which settlement decisions influence multiple facets of life history. Web-building spiders are ideal for such examinations, as both sexes build webs used for prey capture, and web location and the size of the web can affect resource acquisition (Herberstein et al. 1998; Herberstein and Fleisch 2003). More importantly, males leave their natal webs upon maturity to search for

---

* Corresponding author; e-mail: m.kasumovic@unsw.edu.au.

Am. Nat. 2013. Vol. 182, pp. 532–541. © 2013 by The University of Chicago. 0003-0147/2013/18204-54186$15.00. All rights reserved.
DOI: 10.1086/671930

females' webs, which are used for mate attraction and form the mating and competitive arena. Although many web-building spiders are solitary, some species are known to aggregate to various degrees, from simply sharing support strands to colony building and interactive prey capture. The genus *Nephila* is a particularly fitting example because although females each have their own distinct web to protect, they have a tendency to settle nearby one another, thereby creating aggregations (Higgins 1990; Herberstein and Elgar 1994; Kasumovic et al. 2008; Rittschof and Ruggles 2010). Aggregations contain females of varying age and mating status, ranging from early instar juveniles to mated adults (Kasumovic et al. 2008, 2009). Females of all ages are known to attract males (Kasumovic et al. 2008), although evidence suggests that males alter their preference for the female they settle with in response to their own phenotype (Elgar et al. 2003; Kasumovic et al. 2007).

One interesting facet of individual settlement patterns within the genus *Nephila* is that females also settle solitarily and are known to switch between solitary and aggregative settlement as the breeding season progresses (Rittschof and Ruggles 2010). Moreover, although settlement decisions in *Nephila* can be determined by the presence of kleptoparasites and predators (Elgar 1989; Rittschof and Ruggles 2010), the availability of prey (Rypstra 1981; Vollrath 1985), and the possible benefits of prey capture (Uetz 1989), there is evidence that aggregation formation is also determined by social factors (Vollrath and Houston 1986; Rittschof and Ruggles 2010). Furthermore, *Nephila* is easily housed within controlled environments, allowing simple manipulation of social situations. Given these characteristics, the genus *Nephila* is particularly useful for examining how social factors specifically affect settlement patterns and how labile settlement decisions are in response to changing social environments.

Here we use the golden orb-web spider (*Nephila plumipes*) to examine the role of the social environment in determining female settlement. Although the aggregative settlement patterns formed by *N. plumipes* are not true leks because females' webs are all-purpose territories used for mate attraction and foraging, two specific hypotheses incorporating social factors to explain settlement patterns in leks may provide a guide toward examining which social factors drive aggregation formation and neighbor selection in *N. plumipes.* The first hypothesis is the hotshot model, where aggregations are predicted to occur when inferior individuals (in this case, females) settle around a single high-quality individual in hope of increasing their mate attraction through spatial spillover effects (Beehler and Foster 1988). The key assumption of this model is that attraction is skewed to particular females regardless of where females are located. The second hypothesis is the preference model, which suggests that searching individuals (in this case, males) prefer to visit and mate with individuals in aggregations (Bradbury 1981). The key assumption of this model is that male attraction to aggregations should increase with aggregation size. Each model makes particular assumptions about what the mate searching sex prefers. In the hotshot model, males are searching for specific females; while in the preference model, males prefer larger aggregations. The predictions from each model are not mutually exclusive and may function in concert, for example, if males prefer larger females within larger aggregations. However, if the preference model alone is driving aggregative settlement, then, along with attraction being positively correlated with aggregation size, there should be little or no variance in attraction between females within an aggregation.

In this experiment, we aimed to examine what social factors drive female settlement patterns and what factors specifically affect relocation decisions. To examine the role of female phenotypes and intra- and intersexual interactions in female settlement patterns, we released females of varying size, age, and mating status in an artificial enclosure and allowed them to freely settle. We then released two distinct groups of 12 males separated by a 6-h interval to examine how relocation decisions overnight are affected by a combination of both mate attraction and female traits. This experimental design also allowed us to use the assumptions of the hotshot and preference models of lek formation to explore settlement patterns in *N. plumipes.*

Material and Methods

We collected spiders for this experiment at the North Head Sanctuary in Manly, New South Wales, Australia. Each week, we randomly collected 48 females of various ages and mating statuses (i.e., mated and virgin) and 144 males from a large population found on ~0.735 km^2 of property. Males were collected from the webs of females ranging from immature to adult. We ensured that all males were adult virgins by checking for the presence of a full embolus on each of the two pedipalps (mating organs found on the head). Each embolus has a scleritized tip that breaks off after mating, such that males cannot reuse their pedipalps (Schneider et al. 2009). Upon return to the laboratory, we aged females according to the color of their epigynum (the outer covering of the female's genitalia; Kasumovic et al. 2008, 2009) and separated females into three age classes (juvenile, subadult [one molt from maturity], and adult). We then visually separated each age into a continuous distribution of size and ensured that each trial consisted of approximately the same number of females of each age class (1 juvenile, 2–3 subadults, and 4–5 adults), depending on what was available for collection at any given time. We chose to use such a distribution of females because aggregations in the field normally contain females of varying age, size, and mating status (Kasumovic et al. 2008, 2009).

We weighed all females and then used nontoxic water-based gouache paint (Reeves, Harrows, UK) to mark females on the abdomen for individual identification in batches of eight. We also photographed each female to measure the patella-tibia length of the first pair of legs, the length and width of the cephalothorax, and the length and width of the abdomen. We marked males for individual identification in batches of 24 and weighed them, measured their cephalothorax width, and the patella-tibia length of the first pair of legs.

We built two 2.5-m^3 wooden frame enclosures and covered the frames with shade cloth to create an enclosure that allowed air to flow through but prevented spiders from escaping (fig. 1). We separated the inside of the enclosure into thirds and placed two wooden beams (1 × 2.5 cm) centered horizontally and vertically at each third to allow a greater space for movement and web construction by females. Given the amount of substrate, all females would be able to avoid other females and build solitary webs in the enclosure if they so desired.

We used a greenhouse for our experimental enclosures, which allowed the use of natural light. Although males use pheromones to locate and choose between females (Gaskett 2007), it is unclear whether females also use pheromones to make settlement decisions. Nevertheless, we minimized the spread of pheromones by placing each enclosure in a separate room and cleaning the enclosures of webbing between trials. We simultaneously ran two trials in two separate enclosures and completed a total of four trials each week. We released all the individuals used back to the field site and collected new individuals each week. We ensured that we collected new individuals each time, as we could identify previously released individuals by their markings. The trials ran for 5 weeks in January and February 2011.

Each replicate took 3 days to complete (fig. 2). On day 1 of each replicate, we randomly and equally distributed eight females throughout the enclosure by placing two females on the base of each wall. We allowed females to settle anywhere within the enclosure and allowed them to build webs overnight. The morning of day 2, we collected information on the settlement patterns of each female by measuring the *x*-, *y*-, and *z*-coordinates of the hub of each female's web. We then randomly and evenly distributed 12 males throughout the enclosure by releasing 3 males at the base of each wall. After ~6 h, we returned to the enclosure and measured the coordinates of each female and noted the males on each female's web. After noting the location of all the individuals, we released a second batch of 12 males randomly at the same release sites. We returned 1 h later and noted the coordinates of all the females and noted the males on each female's web to examine the initial preference of the newly introduced males.

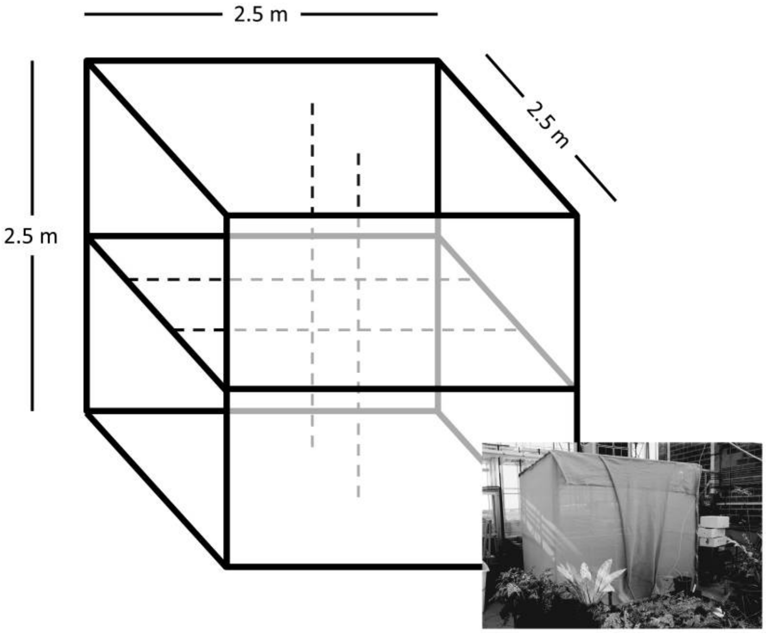

Figure 1: Schematic of the screened-in enclosures and photograph of an enclosure (inset). The horizontal and vertical pairs of dotted lines are the horizontal and vertical wooden beams at each third within the enclosures.

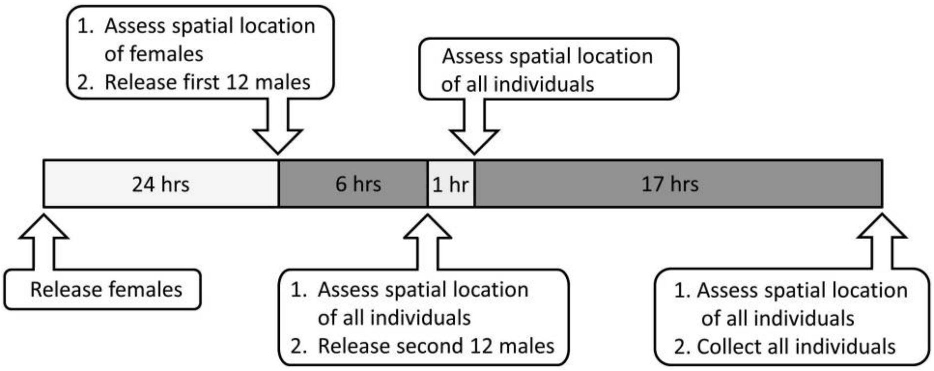

Figure 2: Schematic of the release schedule of females and males throughout each trial and when spatial measurements were taken.

We chose this time frame because competition with rivals after initial settlement affects whether a male remains on a web (L. A. Jordan, H. Kokko, and M. M. Kasumovic, unpublished manuscript). As our goal was to examine the effect of a female's phenotype and position on her relative attraction (i.e., a male's initial preference), we wanted to ensure that males made a settlement decision (which occurs in ~30 min) that was not yet influenced by rival competition. On the morning of day 3, we returned to note the coordinates of each female and noted the males on each female's web. After completing all three sampling events, we removed all the surviving males and females and brushed the enclosure to remove all webbing before beginning a new trial. This ensured that newly released individuals were not following draglines from previous trials. By staggering male release times, our experiment mimicked the progression of maturation and mate location found in natural environments.

Although we had information on the movement patterns of each male given that all males were individually marked, we focused on female attraction for this experiment and discuss male preferences and settlement decisions in a separate paper (L. A. Jordan, H. Kokko, and M. M. Kasumovic, unpublished manuscript).

Statistics

All measured phenotypic traits were normally distributed. As all the phenotypic traits were highly correlated, we used a principal component analysis on the correlation matrix to create a set of new uncorrelated traits that described overall size and shape of individuals for further analyses. We performed the principal components analysis using JMP 8.0.2 (SAS Institute, Cary, NC).

We used a general linear mixed model with a binomial distribution and a logit link to examine whether a female's age or phenotypic traits could predict her settlement type (i.e., whether she settled solitarily or within an aggregation). We used a multiple regression to examine which factors best explained female attraction at the end of day after the second release of males. We used the number of males attracted as the dependent variable and a female's age, phenotypic traits, and settlement type as independent variables. To examine whether mate attraction affected female relocation decisions overnight, we used a general linear mixed model with a binomial distribution and a logit link with settlement type, age, and phenotypic traits as predictor variables. We also placed the total number of males attracted after the second release to examine whether females were basing relocation decisions on mate attraction. In the above three models, we placed collection batch as a random effect to control for any differences between individuals in different collection periods.

We used the lme4 package (Bates et al. 2008) in R v2.15.2 to examine the above models. For each question, we started with a biologically appropriate model and removed individual parameters in a stepwise fashion, each time performing a pairwise comparison to select the appropriate model. We used Akaike Information Criteria (AIC; Akaike 1983) to distinguish between the models and chose the reduced model only if it differed by two or more AIC units, as this provides a distinguishable level of support (Burnham and Anderson 2002). We then used a likelihood-ratio approach to determine significance of the factors remaining in each model. Results are in mean ± SE, unless otherwise stated.

We also examined the distribution of attraction of females within aggregations and compared it to the attraction of solitary females and examined whether attraction to aggregations was a function of aggregation size. Since female settlement patterns and attraction within a replicate were not independent of one another, we used subsampling (with replacement) and Monte Carlo simulations to calculate distributions and examine correlations, plus 95%

Table 1: Eigenvalues of each principal component (PC) axis and the loadings of each trait on each PC axis

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalues of each PC axis:						
Eigenvalue	4.72	.75	.24	.13	.10	.05
Percent	78.7	12.5	4.0	2.2	1.7	.8
Loadings of each trait on each PC axis:						
Weight	.3957	.3925	.7042	.4177	−.1376	−.0112
Leg length	.4110	−.4291	−.0899	−.0643	−.7231	.3338
Cephalothorax width	.4381	−.2781	−.0886	−.0158	.0346	−.8493
Cephalothorax length	.4037	−.4789	.1506	.0429	.6649	.3756
Abdomen width	.4033	.4399	.0155	−.7948	.0744	.0801
Abdomen length	.3956	.402	−.6821	.4332	.0972	.1394

confidence intervals (CIs) for comparisons where necessary. All subsampling was completed using PopTools in Excel.

We used a logistic regression to examine whether males settling on the closest female depended on the settlement type of that female. We used a *t*-test to examine whether the distance males traveled differed between males that chose females that settled solitarily or within aggregations. The data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3723v (Kasumovic and Jordan 2013).

Results

Collection and Descriptions

We ran a total of 20 trials using a total of 160 females and 480 males. Thirteen females were killed by neighbors before they built a web, and three more females were killed overnight after the final male release (mortality rate = 8%). The mortality was not biased toward females of a particular size or body condition (both P values $> .24$), but we could not determine the rivals that killed the females and, therefore, their relative phenotype. We used the remaining 144 females for further analyses. Of the surviving females, 19 were immature (2 or more molts from maturity), 29 were subadult (1 molt from maturity), and 96 were adults of varying mating status. These females represented the distribution of females found throughout the field site during any collection event.

Under natural circumstances, females within aggregations share support strands, as females continually replace old damaged webs with new webs (Herberstein and Elgar 1994; Kasumovic et al. 2008). Although females were settled next to one another as seen in natural aggregations (Herberstein and Elgar 1994; Kasumovic et al. 2008), females in our enclosures did not share support strands since they had only a single day to build webs. The mean distance (±SD) between hubs was 157.42 ± 25.17 cm prior to the addition of the second group of males and 164.89 ± 14.99 cm after. We thus classified females as part of an aggregation if any of their support strands were within 10 cm of one another or if the hubs were within 75 cm of one another (3 standard deviations below the mean), a distance of separation that is common in nature.

The first axis and principal component (PC1) explained 78.7% of the variation, and all the traits loaded positively and approximately equally, suggesting this axis is an indicator of overall size (table 1). The second axis explained a further 12.5%. In this second axis (PC2), patella-tibia length and cephalothorax width and length (traits that do not change after maturity) loaded negatively and approximately equally, while weight and abdomen width and length (flexible traits that change as females feed and begin producing eggs) loaded positively and approximately equally (table 1). This second axis was thus a good indicator of body condition or resource abundance, as females with a positive PC2 value would be heavier for their size. As all the other components explained less than 4% of the variance (table 1), they were not used in any further analyses.

Social Factors Affecting Settlement

To examine the initial factors that affected female settlement decisions prior to male release, we examined female settlement as a function of female age, size (PC1), and body condition (PC2). We also added interactions between age and both traits, as females of different ages can also vary in size and shape. After stepwise model reduction, only the model with size differed from the original model by more than 2 AICs (original: 162.34; reduced: 159.69). There was a trend toward females settling within aggregations being larger (PC1: 0.17 ± 0.21) than females that settled solitarily (PC1: −0.59 ± 0.35; $\chi^2 = 3.18$; df $= 1, 144$; $P = .08$). The random effect explained less than 0.01% of the variance.

To examine how settlement and female traits affected attraction, we placed settlement type, female age, size, and body condition in a multiple regression, with the number of males attracted after the second release period as the dependent factor. We examined interactions between settlement type and age, size, and body condition, as the importance of each variable may differ depending on settlement patterns. The only model that had a lower AIC than the original model excluded the age × settlement type interaction (original: 589.63; reduced: 586.2). Juvenile and adult females attracted significantly more males than penultimate females (2.11 ± 0.49, 2.04 ± 0.20, and 1.24 ± 0.27 males, respectively). Larger females attracted more males, and this pattern was stronger for solitary rather than aggregative females (significant size × settlement type interaction; table 2; fig. 3). There was a trend of females in better body condition attracting more males when settled solitarily (body condition × settlement type interaction; table 2; fig. 3). The random effect explained 0.05% of the variance.

To determine which females were more likely to move overnight, we examined movement as a function of female age, size, body condition, attraction, and settlement type. We also added interactions between settlement type and age, size, body condition, and attraction, as females of different settlement types may have different assessment rules of whether or not to move. The model with the lowest AIC consisted of size, attraction, settlement type, and a settlement type × attraction interaction (original: 210.21; reduced: 199.29). Further model reduction did not significantly reduce the AIC. Females in aggregations (60/111) were significantly more likely to relocate overnight than solitary females (11/33; table 3), and the likelihood of relocating was further increased if females attracted fewer males (significant settlement type × attraction interaction; table 3, fig. 4). The random effect explained 0.05% of the variance. Although relocating females varied in where they settled, both solitary (9/11) and aggregative (43/60) females equally preferred relocating to aggregations ($\chi^2 = 0.52$; $P = .47$).

Table 2: Results from a multiple regression examining how various factors affected attraction after the second release period

Factor	df	*F*	*P*
Settlement type	1, 134	12.68	**.005**
Age	2, 134	6.71	**.03**
PC1 (size)	1, 134	19.26	**.0001**
PC2 (body condition)	1, 134	1.61	.20
PC1 × settlement	1, 134	8.92	**.003**
PC2 × settlement	1, 134	3.15	.08

Note: Settlement type, female age, and size significantly affect mate attraction. There was also a significant size × settlement type interaction. Values in bold are significant.

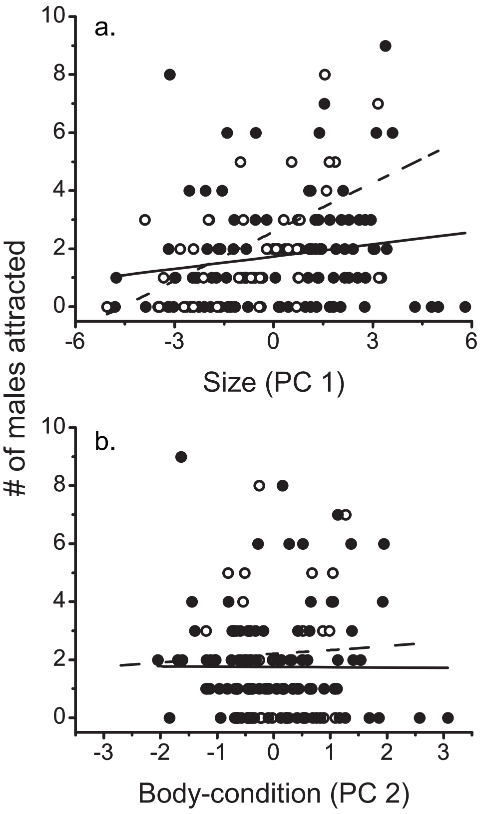

Figure 3: Regression of male attraction on size (*a*) and body condition (*b*) for females that settled within aggregations (filled circles, solid line) and solitarily (open circles, dashed line). Raw data were used to plot this figure.

Monte Carlo Examinations of Attraction

As the 37 aggregations (mean aggregation size = 3.75, range 2–7) on average attracted more males than the 47 females that settled solitarily, we next examined the role settlement (aggregation vs. solitary) played in mate attraction. Since a female's settlement or mate attraction within each replicate was not independent of other females, we randomly subsampled a single female from each replicate (with replacement) 10,000 times, noted her settlement, and created a distribution of mean attraction for both aggregations and solitary females. Aggregations attracted a mean of 5.39 males (variance = 0.78; 95% CI = 4.00–6.88), while solitary females attracted a mean of 1.64 males (variance = 0.23; 95% CI = 0.90–2.50), which was significantly different ($P = .014$). However, when we controlled for the number of females within an aggregation, the average number of males attracted per female within an aggregation (1.97; variance = 0.13; 95% CI = 1.43–2.59) did not differ from solitary females (1.63; variance = 0.22; 95% CI = 0.90–2.45; $P = .98$).

Table 3: Results from a generalized linear model with a binomial distribution and a logit link demonstrating that females within aggregations were more likely to relocate overnight (significance of settlement type) and that females that attracted a greater number of individuals within aggregations were more likely to stay (significant attraction × settlement interaction)

Factor	df	χ^2	P
PC1 (size)	1, 132	2.21	.13
Number of males attracted	1, 132	5.50	.06
Settlement type	1, 132	8.74	**.01**
Attraction × settlement	1, 132	4.26	**.03**

Note: Values in bold are significant.

Since a female's attractiveness was significantly correlated with size, we examined the distribution of attractiveness of 102 females that settled within an aggregation by ranking females by size. Since a female's rank within an aggregation is dependent upon other females' settlement, we subsampled a single female from each replicate (with replacement) 10,000 times and calculated the correlation between rank and attraction. Since we predicted a negative correlation (larger females are ranked lower and attract more males), we examined whether the correlation was greater than zero for each sample. There was a significant negative correlation between rank and attraction (-0.74; variance $= 0.15$, 95% CI $= -1.39$ to -0.14; $P = .022$; fig. 5).

Since aggregations attracted more males than solitary females, we next examined whether attraction within aggregations was correlated with aggregation size. Since aggregations within a replicate were not independent of one another, we subsampled a single aggregation from each replicate (with replacement) and regressed the number of males attracted against aggregation size 10,000 times to calculate an average regression coefficient and level of significance. The level of mate attraction was significantly correlated with aggregation size, with larger aggregations attracting a significantly greater number of males ($r^2 = 0.51$; $F = 19.08$; $P = .0008$).

Male Movement Patterns

Of the 273 males that selected a female, only 63 settled on the closest female. Whether males settled on the closest female did not depend on whether that female was part of an aggregation ($\chi^2 = 1.37$; df $= 1, 272$; $P = .24$). However, males that settled within aggregations traveled significantly further (237.8 ± 44.6 cm; mean ± SD) than males that settled on the webs of solitary females (218.5 ± 52.3 cm; $t = 2.83$; df $= 1, 272$; $P = .003$). Both distances traveled were greater than the average distance to the closest female (184.8 ± 35.5 cm), suggesting that males were looking for specific females.

Discussion

Habitat use by female golden orb-web spiders (*Nephila plumipes*) depends on several ecological characteristics including habitat availability (Herberstein and Elgar 1994; Kasumovic et al. 2008), the presence of kleptoparasites (Elgar 1989; Rittschof and Ruggles 2010), prey availability (Rypstra 1981; Vollrath 1985; Rittschof and Ruggles 2010), and prey capture (Uetz 1989). While ecological factors can affect broadscale settlement patterns, we demonstrate that both intra- and intersexual social interactions are sufficient to explain fine-scale settlement patterns and site fidelity. More importantly, we demonstrate that settlement decisions are dynamic, with females selecting and shifting settlement patterns and locations in response to a combination of rapid changes in the social environment and their own phenotype.

We examined two specific hypotheses from the hotshot and preference models used to explain aggregative settlement in lekking species to explore which social factors may be important in shaping female settlement patterns in *N. plumipes*. We demonstrate that the largest females attracted the most males, with large solitary females being particularly attractive (fig. 3). Combined with the fact that attraction was strongly skewed toward larger females within aggregations, our results support the hotshot hypothesis of aggregation formation. The hotshot model assumes that individuals join aggregations to increase their chances of attracting males through spatial spillover effects. Our results, however, demonstrate that females ranked sec-

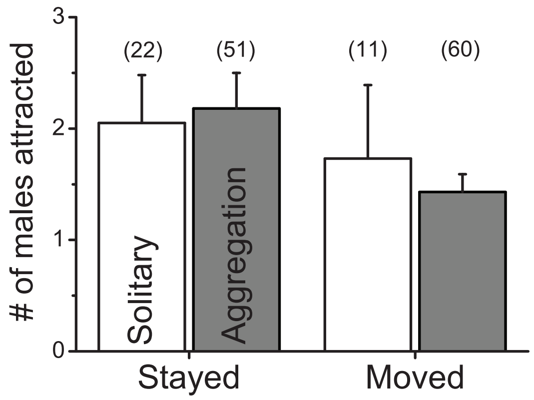

Figure 4: Number of males attracted by solitary (open bars) and aggregative (gray bars) females that stayed and moved overnight. Females within aggregations were more likely to move, and this effect was amplified by the number of males attracted. Numbers above each bar are the sample size for that particular group.

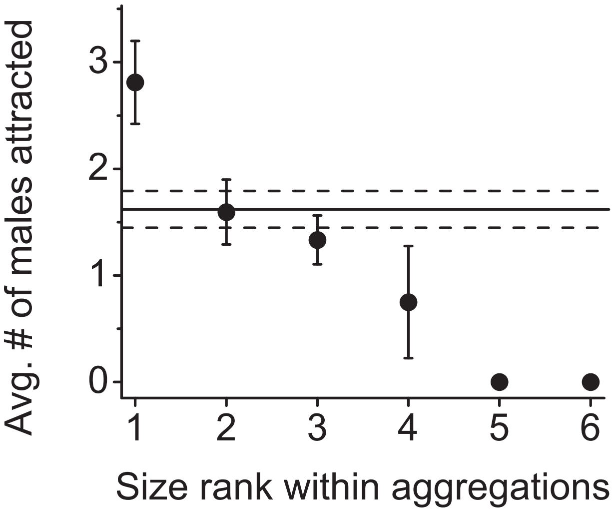

Figure 5: Observed average number of males attracted by all females in the third sampling period. Females within each enclosure are ranked by relative size (*X*-axis), with females becoming smaller as they increase in rank. The horizontal line shows the mean (dashed lines = standard error) number of males attracted by solitary females.

ond or third in relative size within an aggregation attracted approximately as many males as did solitary females, bringing into question why these females choose to settle within aggregations. In *N. plumipes*, females become unreceptive after several matings (Elgar and Fahey 1996; Schneider and Elgar 2001, 2002), and males may move off their initial choice of female if competition increases (L. A. Jordan, H. Kokko, and M. M. Kasumovic, unpublished manuscript). Females ranked second or third may therefore benefit from spillover effects when the largest female is no longer receptive and have a baseline attractiveness equal to that of solitary females. In contrast, this benefit may not occur for the smallest females within an aggregation (those ranked below third; fig. 4), which would explain why these females were most likely to leave. Interestingly, most females that relocated settled in new aggregations, suggesting aggregative settlement is the preferred settlement pattern for smaller females.

In addition to a strong preference for larger females, we show that males traveled further to reach aggregations and that the number of males attracted increased with aggregation size. These results support the preference model of aggregative settlement, even though we cannot distinguish between whether larger aggregations were specifically preferred or whether males more easily found larger aggregations (i.e., they cover a larger area) and therefore settled on them. This preference for larger aggregations may be a consequence of a combination of a high mate-searching cost (80% mortality; Kasumovic et al. 2007) and the fact that males are known to change their initial choice of female as a consequence of increased competition (L. A. Jordan, H. Kokko, and M. M. Kasumovic, unpublished manuscript). When searching for mates, males may be unaware of the intensity of competition they will encounter on any given female's web and may prefer to be in aggregations that minimize distances between alternative females. Settling within a larger aggregation may allow males to more easily change their mate choice and dramatically decrease the cost of searching.

It is currently unclear how females are locating aggregations since web-building spiders have such poor vision. However, given that females produce both long-distance, cuticular, and web-based pheromones that males use to locate females (Gaskett 2007), this information may also be used by wandering females. In addition, we could not determine the order in which females arrived to aggregations, and, as a result, we cannot surmise which females (smaller or larger) are founding aggregations. We can, however, say that smaller females are more likely to leave and join other aggregations, suggesting that smaller females may be settling around already established larger females. Further studies are required to determine this conclusively. Another fruitful avenue for future studies is to examine potential costs of aggregation. For example, there may be increased costs of predation and parasitism (Uetz and Hieber 1997; McCrate and Uetz 2010) and a mortality cost to defending a territory against larger females within aggregations (Rypstra 1985). Our study did not take into consideration costs of predation or parasitism, and although we did assess female mortality in our study, we could not determine whether mortality was skewed toward females of a particular size. As a result, our experiment could not detect any fitness costs of aggregating, and we explore the phenotype-specific benefits of differential settlement.

Our results provide evidence that aggregations in *N. plumipes* are driven by a combination of the preference and hotshot models of aggregation formation, generally agreeing with other studies that argue that multiple factors drive aggregative settlement (e.g., Jiguet and Bretagnolle 2006; Young et al. 2009). As in previous studies of aggregating animals, smaller females were more likely to be part of aggregations than to settle on their own, a common strategy in response to phenotypic factors such as age (Alonso et al. 2010), body condition (Sardà-Palomera et al. 2011), or size (Höglund and Robertson 1990). Our results, however, provide greater insight into aggregation formation and attrition. Smaller females relocated after initial settlement, suggesting that females are using phenotype-specific settlement strategies that are initially state dependent (McNamara and Houston 1996) and then refine these decisions with social feedback.

As most studies examining aggregative settlement focus on longer-lived vertebrates that generally encounter similar challenges within a single season, it is not surprising that individuals display age-specific reproductive tactics where tactics remain constant within a breeding season (Mainguy and Côté 2008; Alonso et al. 2010; Ponjoan et al. 2012). However, even in species where an individual's state (i.e., age, phenotype) may remain relatively constant within a season, social feedback is known to affect changes in mating strategies (Royle and Pike 2010; Jordan and Brooks 2012). The flexibility in settlement tactics demonstrated by *N. plumipes* females may be a result of their short life span and changes in age and state, coupled with the fact that the social environment varies rapidly, resulting in within-season changes in selective pressures (e.g., Kasumovic et al. 2008; Punzalan et al. 2010). Our results thus suggest that social feedback has the capacity to alter individual settlement tactics in a similar manner to mating tactics, such that settlement tactics can be a gradient of responses (Dingemanse and Wolf 2013) rather than being a dichotomy (i.e., alternative reproductive strategy; Gross 1996) as seen in colonial web-building species (Pruitt and Riechert 2011). How much these initial decisions are based on early developmental environments and experiences (Kasumovic 2013) is currently unknown. However, given that early social environments can affect developmental decisions (Kasumovic and Brooks 2011; Kasumovic 2013) and mating preferences (Hebets and Vink 2007; Bailey and Zuk 2008), examining the effect of early environments on settlement tactics and decisions may also prove fruitful.

Acknowledgments

We would like to thank N. Hughes, the Australian Wildlife Conservancy, and the Sydney Harbour Trust for access to the North Head Sanctuary. We also thank R. Brooks, D. Elias, and six anonymous reviewers for helpful comments on the manuscript. The final two reviewers were especially helpful and constructive during the review process; their comments and ideas were greatly appreciated.

Literature Cited

Akaike, H. 1983. Information measures and model selection. Bulletin of the International Statistical Institute 44:277–291.

Alonso, J. C., M. Magaña, C. Palacín, and C. A. Martín. 2010. Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort. Behavioral Ecology and Sociobiology 64:1589–1600.

Bailey, N. W., and M. Zuk. 2008. Acoustic experience shapes female choice in field crickets. Proceedings of the Royal Society B: Biological Sciences 275:2645–2650.

Bates, D., M. Maechler, and B. Dai. 2008. lme4: linear mixed-effects models using S4 classes. R package. Version 0.999375–28. http://lme4.r-forge.r-project.org/.

Beehler, B. M., and M. S. Foster. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. American Naturalist 131:203–219.

Booksmythe, I., M. D. Jennions, and P. R. Y. Backwell. 2010. Interspecific assistance: fiddler crabs help heterospecific neighbours in territory defence. Biology Letters 6:748–750.

Bradbury, J. 1981. The evolution of leks. Pages 138–172 *in* R. D. Alexander and D. W. Tinkle, eds. Natural selection and social behavior: recent research and theory. Chiron, New York.

Breder, C. M., Jr., and D. E. Rosen. 1966. Modes of reproduction in fishes. FH, Jersey City, NJ.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference. Springer, New York.

Christy, J. H. 1988. Pillar function in the fiddler crab *Uca beebei.* 1. Effects on male spacing and aggression. Ethology 78:53–71.

Dingemanse, N. J., and M. Wolf. 2013. Between-individual differences in behavioural plasticity within populations: causes and consequences. Animal Behaviour 85:1031–1039.

Elgar, M. A. 1989. Kleptoparasitism: a cost of aggregating for an orb-weaving spider. Animal Behaviour 37:1052–1055.

Elgar, M. A., M. J. Bruce, F. E. C. de Crespigny, A. R. Cutler, C. L. Cutler, A. C. Gaskett, M. E. Herberstein, S. Ramamurthy, and J. M. Schneider. 2003. Male mate choice and patterns of paternity in the polyandrous, sexually cannibalistic orb-web spider *Nephila plumipes*. Australian Journal of Zoology 51:357–365.

Elgar, M. A., and B. F. Fahey. 1996. Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). Behavioral Ecology 7:195–198.

Erlinge, S., I. Hoogenboom, J. Agrell, J. Nelson, and M. Sandell. 1990. Density-related home-range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. Journal of Mammalogy 71:597–603.

Gaskett, A. C. 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews 82:26–48.

Gross, M. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution 11:92–98.

Hebets, E. A., and C. J. Vink. 2007. Experience leads to preference: experienced females prefer brush-legged males in a population of syntopic wolf spiders. Behavioral Ecology 18:1010–1020.

Herberstein, M. E., K. E. Abernethy, K. Backhouse, H. Bradford, F. E. de Crespigny, P. R. Luckock, and M. A. Elgar. 1998. The effect of feeding history on prey capture behaviour in the orbweb spider *Argiope keyserlingi* Karsch (Araneae: Araneidae). Ethology 104: 565–571.

Herberstein, M. E., and M. A. Elgar. 1994. Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Aranea: Araneoidea): nocturnal and diurnal orb-weaving spiders. Australian Journal of Ecology 19:451–457.

Herberstein, M. E., and A. Fleisch. 2003. Effect of abiotic factors on the foraging strategy of the orb-web spider *Argiope keyserlingi* (Araneae: Araneidae). Austral Ecology 28:622–628.

Higgins, L. E. 1990. Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes* (Araneae: Araneidae). Journal of Insect Behavior 3:773–783.

Höglund, J., and R. V. Alatalo. 1995. Leks. Princeton University Press, Princeton, NJ.

Höglund, J., and J. G. M. Robertson. 1990. Female preferences, male decision rules and the evolution of leks in the great snipe *Gallinago media.* Animal Behaviour 40:15–22.

Jiguet, F., and V. Bretagnolle. 2006. Manipulating lek size and composition using decoys: an experimental investigation of lek evolution models. American Naturalist 168:758–768.

Jordan, L. A., and R. C. Brooks. 2012. Recent social history alters male courtship preferences. Evolution 66:208–287.

Kasumovic, M. M. 2013. The multidimensional consequences of the juvenile environment: towards an integrative view of the adult phenotype. Animal Behaviour 85:1049–1059.

Kasumovic, M. M., and R. Brooks. 2011. It's all who you know: the evolution of socially cued anticipatory plasticity as a mating strategy. Quarterly Review of Biology 86:181–197.

Kasumovic, M. M., M. J. Bruce, M. C. B. Andrade, and M. E. Herberstein. 2008. Spatial and temporal demographic variation drives within-season fluctuations in sexual selection. Evolution 62:2316–2325.

Kasumovic, M. M., M. J. Bruce, M. E. Herberstein, and M. C. B. Andrade. 2007. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). Behavioral Ecology 18: 189–195.

———. 2009. Evidence for developmental plasticity in response to demographic variation in nature. Ecology 90:2287–2296.

Kasumovic, M. M., and L. A. Jordan. 2013. Data from: Social factors driving settlement and relocation decisions in a solitary and aggregative spider. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.3723v.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.

Mainguy, J., and S. D. Côté. 2008. Age- and state-dependent reproductive effort in male mountain goats, *Oreamnos americanus.* Behavioral Ecology and Sociobiology 62:935–943.

McCrate, A. T., and G. W. Uetz. 2010. Kleptoparasites: a twofold cost of group living for the colonial spider, *Metepeira incrassata* (Araneae, Araneidae). Behavioral Ecology and Sociobiology 64:389–399.

McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. Nature 380:215–221.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). American Naturalist 150:650–661.

Ponjoan, A., G. Bota, and S. Mañosa. 2012. Ranging behaviour of little bustard males, *Tetrax tetrax*, in the lekking grounds. Behavioural Processes 91:35–40.

Pruitt, J. N., and S. E. Riechert. 2011. Within-group behavioral variation promotes biased task performance and the emergence of a defensive caste in a social spider. Behavioral Ecology 65:1055–1060.

Punzalan, D., F. H. Rodd, and L. Rowe. 2010. Temporally variable multivariate sexual selection on sexually dimorphic traits in a wild insect population. American Naturalist 175:401–414.

Rittschof, C. C., and K. V. Ruggles. 2010. The complexity of site quality: multiple factors affect web tenure in an orb-web spider. Animal Behaviour 79:1147–1155.

Royle, N. J., and T. W. Pike. 2010. Social feedback and attractiveness in zebra finches. Behavioral Ecology and Sociobiology 64:2015–2020.

Rypstra, A. L. 1981. The effect of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes.* Oikos 37:179–182.

———. 1985. Aggregations of *Nephila clavipes* (L.) (Araneae, Araneidae) in relation to prey availability. Journal of Arachnology 13: 71–78.

Sardà-Palomera, F., M. Puigcerver, D. Vinyoles, and J. D. Rodríguez-Teijeiro. 2011. Exploring male and female preferences, male body condition, and pair bonds in the evolution of male sexual aggregation: the case of the common quail (*Coturnix coturnix*). Canadian Journal of Zoology 89:325–333.

Schneider, J. M., and M. A. Elgar. 2001. Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. Behavioral Ecology 12: 547–552.

———. 2002. Sexual cannibalism in *Nephila plumipes* as a consequence of female life history strategies. Journal of Evolutionary Biology 15:84–91.

Schneider, J. M., M. E. Herberstein, M. J. Bruce, M. M. Kasumovic, M. L. Thomas, and M. A. Elgar. 2009. Male copulation frequency, sperm competition and genital damage in the golden orb-web spider (*Nephila plumipes*). Australian Journal of Zoology 56:233–238.

Sommaro, L. V., A. R. Steinmann, M. B. Chiappero, and J. W. Priotto. 2010. Effect of high density on the short term *Calomys musculinus* spacing behaviour: a fencing experiment. Acta Oecologia 36:343–348.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. American Naturalist 131:329–347.

Tarof, S. A., L. M. Ratcliffe, M. M. Kasumovic, and P. T. Boag. 2005. Are least flycatcher (*Empidonax minimus*) clusters hidden leks? Behavioral Ecology 16:207–217.

Uetz, G. W. 1989. The "ricochet effect" and prey capture in colonial spiders. Oecologia (Berlin) 81:154–159.

Uetz, G. W., and C. S. Hieber. 1997. Colonial web building spiders: balancing the costs and benefits of group living. Pages 458–475 *in* J. C. Choe and B. J. Crespi, eds. The evolution of social behaviour in insects and arachnids. Cambridge University Press, Cambridge.

Vollrath, F. 1985. Web spider dilemma: a risky move or site dependent growth. Oecologia (Berlin) 8:69–72.

Vollrath, F., and A. Houston. 1986. Previous experience and site-tenacity in the orb spider *Nephila* (Araneae, Araneidae). Oecologia (Berlin) 70:305–308.

Wagner, R. H. 1993. The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. Journal of Theoretical Biology 163:333–346.

Young, K. A., M. J. Genner, D. A. Joyce, and M. P. Haesler. 2009. Hotshots, hot spots, and female preference: exploring lek formation models with a bower building cichlid fish. Behavioral Ecology 20:609–615.

Associate Editor: Maria R. Servedio
Editor: Judith L. Bronstein