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Author(s): Lyndon Alexander Jordan, Hanna Kokko, and Michael Kasumovic

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Reproductive Foragers: Male Spiders Choose Mates by Selecting among Competitive Environments

Lyndon Alexander Jordan,^{1,2,*} Hanna Kokko,³ and Michael Kasumovic¹

1. Evolution and Ecology Research Centre, University of New South Wales, Sydney, New South Wales 2052, Australia; 2. Department of Integrative Biology, University of Texas, Austin, Texas 78712; 3. Research School of Biology, Australian National University, Canberra, Australian Capital Territory 0200, Australia

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ABSTRACT: Mate choice frequently operates differently for males and females as a consequence of male competition for mates. Competitive interactions can alter the fitness payoffs of choice and the realization of preferences under natural conditions, yet the majority of male choice studies still use binary trials that ignore social factors. Here we test the importance of contest dynamics in male choice using a framework in which females are considered analogous to foraging patches that are subject to competition. We track the mate choices and interactions of 640 spiders (*Nephila plumipes*) before and after manipulation of competition within enclosures, modeling the expected fitness payoffs of each male's actual choices and comparing these with all alternative choices. Many males choose new mates once social conditions change and achieve higher fitness than predicted under random movement. Males do not simply move to larger females but choose favorable competitive environments that balance competition and female fecundity, thereby increasing their fitness payoffs. Further, we show for the first time that prior-residence effects, which are known to influence male contests, also have a strong influence in male reproductive contests and can shape male mate choice. These results highlight the importance of situating male choice studies in the relevant social context, as intrasexual interactions can have profound effects on the realization and payoffs of male mate-choice strategies.

Keywords: male, mate choice, foraging, resident effect, prior residence.

Introduction

The costs of male reproduction are relatively low compared with those of female reproduction, and competition among males for access to mates can be intense (Andersson 1994). Moreover, males often provide little or no parental care and so can theoretically maximize fitness by mating with all available females (Bateman 1948; Trivers 1972).

* Corresponding author; e-mail: lyndonjordan@gmail.com.

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Because of this, the evolution of male choosiness has been considered unlikely in the past (Parker 1972), especially in comparison with female choice. Recent theoretical models and empirical studies, however, have made a compelling case that male choice can be expected under a relatively wide range of conditions (Rowell and Servedio 2009; Venner et al. 2010), and male choice is now known to be taxonomically widespread (Amundsen 2000; Bonduriansky 2001; Edward and Chapman 2011).

Although choice plays an important role in both male and female reproductive behaviors, one important facet distinguishes male and female choice: male reproduction is typically a competitive endeavor, in which the presence of rivals moderates the extent to which males can choose preferred mates. This important aspect of male reproductive biology is generally overlooked in male mate-choice studies, which often emulate traditional female choice experiments by using dichotomous choice trials precluding social interactions. Thus, although empirical studies show male preferences for larger, more fecund females in a variety of taxa (e.g., moths [Xu and Wang 2009], newts [Verrell 1985], finches [Jones et al. 2001], and *Drosophila melanogaster* [Byrne and Rice 2006]), it is difficult to ascertain whether preferences determined using binary approaches are representative of the actual choices that would occur under natural conditions (Jennions and Petrie 1997; Werner and Lotem 2006). Given the important role that social interactions can play in shaping mating strategies (Oh and Badyaev 2010), ignoring the rich sexual selection literature demonstrating the importance of male competition (Andersson 1994) will lead to a distortion of our understanding of male choice and our ability to distinguish between preferences and realized choices.

An important consequence of including competitive interactions in analyses of male choice is that it helps to explain why males mate and pair with nonpreferred females and how alternative mating strategies are maintained

(Neff and Svensson 2013). Because competition among males can mediate choice, selection does not easily favor identical male mating preferences for all males, as the mean mating value of a female declines as the number of males she attracts increases (Servedio and Lande 2006; Servedio 2007). Because of this, male mate choice evolves considerably more easily when males can alter their mate preferences and reproductive behavior in response to the level of competition (Fawcett and Johnstone 2003; Härdling and Kokko 2005; Rowell and Servedio 2009; Venner et al. 2010). Empirically, males are known to change their mate preferences in response to social factors such as competition from rival males (Bel-Venner et al. 2008; Candolin and Salesto 2009), their recent history of mate encounters (Jordan and Brooks 2012), or the reactions of courted females (Patricelli et al. 2002). By modifying their mate preferences, males that are not competitive in one context may increase their fitness by moving to social environments in which they are more likely to successfully compete (Härdling and Kokko 2005; Härdling et al. 2008; Wada et al. 2010), even if this means mating with females that may not be preferred in isolation.

Yet despite their potential effect on the evolution of reproductive behavior, social factors are rarely addressed in male mate-choice studies, possibly because they present a prohibitive experimental challenge. Consequently, we do not have—for any species—a thorough investigation of how mate choice operates in changing competitive environments and do not know whether changes in the competitive environment cause male mate choices to deviate from baseline preferences. The effect of changing social conditions is multifaceted since variable social conditions may provide the opportunity for males to move to better selective environments, but competitive interactions may also prevent males from reaching these places of higher fitness payoffs. A clear example of this is the establishment of dominance hierarchies based on order of arrival: often first-arrived individuals enjoy a prior-residence effect, enabling them to occupy preferred positions or spatial locations in an environment (Hardy and Field 1998; Kokko et al. 2006).

Here we measure how male mate choice varies in changing social conditions using a hybrid approach that combines an ideal free distribution framework with an assessment of the prior-residence effect. In this framework, females are analogous to foraging patches, with an inherent value that declines as a result of competition. We use the golden orb-web spider (*Nephila plumipes*), an excellent system in which to study the influence of social factors on male mating behavior. At maturity, males search for a female's web on which to settle and mate (Kasumovic et al. 2007). Settlement decisions are therefore equivalent to mate choice in this species, making measurement of male

choice straightforward and unambiguous. Previous studies strongly suggest that males do not move once they have settled on a female's web in the wild (Kasumovic et al. 2007) or in captivity (Schneider et al. 2008), and our own pilot observations show that male settlement decisions are stable in the absence of male-male competition. Once on a female's web, males wait until the female captures a prey item before attempting to assume a mating position (Elgar and Fahey 1996; Schneider et al. 2008). Males may attempt to placate females by web plucking, but females typically react aggressively to all males that they detect on the web, and males that attempt to approach females without a current prey item are killed and eaten (Elgar and Fahey 1996; L. A. Jordan, personal observation). Females settle together, creating aggregations of interconnected webs (Herberstein and Elgar 1994; Kasumovic et al. 2008), thereby allowing males to choose among multiple potential mates in a small area. Female size is correlated with fecundity in the genus *Nephila* (Miyashita 1986), and males generally prefer older and larger females (Kasumovic et al. 2007; Kasumovic and Jordan 2013). Mating order is based on male proximity to the female, and larger/heavier males secure a position closer to a female in dichotomous competition trials (Elgar and Fahey 1996; Elgar et al. 2003). Females mate multiply, and paternity share is determined by mating order in a predictable distribution, with males that mate first siring a greater proportion of the offspring compared to males that mate second and third (Schneider and Elgar 2001; Elgar et al. 2003).

Male choices among females in *N. plumipes* thus resemble foraging decisions between patches, in which a male's success will depend on female fecundity, competition, his own fighting ability relative to rivals (including effects of prior residence), and his predicted paternity share. To examine the relative importance of social and competitive interactions in male mate-choice decisions, we examine initial and subsequent male mate choices before and after experimentally increasing intrasexual competition within experimental enclosures that mimic wild conditions. We then compare the choices males actually make with every alternative choice they could have made and calculate the fitness payoffs of male mate-choice decisions under changing social environments. In this way, we can test hypotheses about male reproductive behavior that cannot be addressed using traditional binary approaches.

Methods

Each week between January 15 and February 28, 2011, we collected ~50 female and ~150 male *Nephila plumipes* from a large population found over ~0.735 km² at North Head Sanctuary in Manly, New South Wales, Australia. From those collected each week, we used 12 focal males, 8 fe-

males, and 12 further competitor males in each of four trials per week. We conducted a total of 20 trials and used 240 males as experimental subjects, with a further 240 males used as competitors, choosing among the webs of 160 female spiders. The additional competitor males contributed only to an initial analysis of the relationship between weight and rank (see below), while the calculation of payoffs or competition males faced was based on only the initial 12 males released. Females collected varied with respect to age and mating status, reflecting their natural distribution in the wild. We held males in 50-mL plastic sample jars and the substantially larger females in 400-mL plastic food containers until required for experiments. Not all collected individuals were used. We conducted experiments in two $2.5 \times 2.5 \times 2.5$ -m (15.625-m^3) wooden frame enclosures covered with shade cloth that allowed air to flow but prevented spiders from escaping. These enclosures were placed in isolated rooms within a large glass house so there was no mixing of pheromones between enclosures. We simultaneously ran two trials in two separate enclosures and completed a total of four trials each week. We weighed and individually marked each male and female on the abdomen using nontoxic, water-based gouache paint (Reeves, Harrows, England). We released all used individuals at the field site and collected new individuals each week. Previously used individuals were easily identified and excluded due to their markings. We ensured that males were all adult virgins by checking for the presence of a full embolus on each of the two pedipalps (mating organs found on the cephalothorax). Each embolus has a sclerotized tip that breaks off after mating, such that males cannot reuse their pedipalps (Schneider et al. 2008).

We weighed and photographed each individual against a 1×1 -cm grid 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. Within each trial, we visually separated juvenile, penultimate, and adult females (by examination of the epigynum; Kasumovic et al. 2009) and introduced two to three females of each age and a distribution of sizes in all trials. On day 1 of each replicate, between 1600 and 1700 hours, we randomly and equally distributed eight females throughout the enclosure by placing two females 80 cm apart on the base of each wall. We allowed the females to settle anywhere within the enclosure and build webs overnight. The following morning, between 0900 and 1000 hours, we randomly selected 12 males from the wild-caught individuals and released 3 males 60 cm apart at the base of each wall. After 6 h (~ 1400 hours), we returned to the enclosure and measured the three-dimensional coordinates of each male and female and noted which males were on each female's web (this time point is denoted $t = 1$). Male rank was determined

by comparing the linear distance to the female with which he settled relative to other males on the same web. The average distance traveled by males prior to initial settlement was 232.59 ± 49.13 cm (mean \pm SD), which was significantly further than the distance to the nearest female, 186.70 ± 36.08 cm ($t = 12.747$, $df = 1, 153$, $p < .0001$).

After recording the locations of all individuals, we released a second batch of 12 males. These males were all assigned newcomer status in all subsequent analyses but did not contribute to the data set. We returned after 1 h to record the locations of all 24 males (~ 1500 hours) and then returned again the following day at 1600 hours to once again record the coordinates of all males and females (this is time point $t = 2$). The coordinate data for all males and females at $t = 1$ and $t = 2$, as well as their weights, are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2qp1v> (Jordan et al. 2014). After completing sampling, we removed all the surviving males and females and brushed the enclosure to remove all webbing before beginning a new trial. By using two different male release times, our experiment mimicked the progression of maturation and mate location found in natural environments. Although males are generally sedentary on female's webs, our pilot studies showed that a pulse of competition can make males shift between webs, and we sought to use this response to test hypotheses about male settlement decisions. Due to sexual cannibalism ($\sim 60\%$; Schneider and Elgar 2001), their possession of only two sperm transfer organs (emboli) that are lost during mating, and a 76% mortality rate during mate searching (Kasumovic et al. 2007), *N. plumipes* males are largely limited to a single mating event. Thus, a male's lifetime reproductive output is well described by the reproductive success of his first choice and mating event.

Calculation of Fitness Payoffs

Previous studies of *N. plumipes* show that male rank on a web is determined by its proximity to the female and that this rank influences its share of paternity (Elgar and Fahey 1996; Schneider and Elgar 2001; Servedio and Lande 2006). Males ranked first on a web (i.e., closest to the female) attain the majority of fertilization success. In double mating trials, first males gain an average of 54% paternity (Elgar et al. 2003). The paternity of the first and second males is somewhat diluted in mating trials involving three males, with the first, second, and third males gaining an average of 43%, 32%, and 23% paternity, respectively (Elgar et al. 2003). Although males ranked fourth and lower may gain some paternity in natural situations, fourth matings are rarely observed in captivity (Elgar et al. 2003), and we assigned males ranked fourth or lower with no paternity. To calculate a male's expected

fitness payoff at his chosen web and compare this against the payoffs of alternative choices, we determined how male rank is decided. A previous study (Elgar and Fahey 1996) showed that heavier males win in dyadic contests over web position, and a field study demonstrated strong selection for male size when competition is more intense (Kasumovic et al. 2008). These results suggest a correlation between male size and rank; however, our own analysis with the males from this study showed no such relationship, neither for males at $t = 1$ when competition was low ($r = 0.21$, $n = 153$, $p = .072$) nor for all males that made a choice at $t = 2$ ($r = 0.57$, $n = 274$, $p = .345$).

We subsequently used Akaike Information Criteria (AIC) approaches to determine which factors predicted male rank at $t = 2$ in our experiment. Males were classified as stayers or movers depending on whether they switched locations between time points 1 and 2 (thus, a male could be a newcomer at a site either because he was a mover or because he was one of the newly introduced males with no location at $t = 1$). We tested among four models: model A, the null model, in which neither residence status nor male weight predicts male rank; model B, in which residence status predicts male rank but male weight does not; model C, in which male weight predicts male rank but residence status does not; and model D, the full model, in which both weight and residence status predict male rank. In model D, the propensity of each male obtaining his observed rank is calculated as pe^{aw} , where w is the male's weight, a is a parameter determining the strength of the weight-rank relationship, $p = 1$ if the male is a stayer (i.e., resident) and $p = P \leq 1$ if he is a mover. The values for the parameters a and p were established by numerically searching for the maximum of the log-likelihood function, that is, the sum of all male-specific $\log(pe^{aw})$ values. All models use this same structure, but they differ in the number of estimated parameters because P and a can either be set to predetermined values (indicating no effect of the relevant variable) or estimated based on data. The male's weight has no effect if $a = 0$, and residence status has no effect if $p = 1$ for all males (i.e., if $P = 1$). Thus, in model A, we set $a = 0$ and $P = 1$; in model B, we set $a = 0$ and estimated P ; in model C, we estimated a and set $P = 1$; and in model D, we estimated both a and P . Note that the maximum likelihood method estimates single values for a and P across all trials.

As the AIC approach gave high support for models B and D (see "Results") and both agree that male weight has minimal effect while the prior-residence effect is strong, we assumed in our subsequent analysis that weight does not matter but that residence status does (with the estimate of p chosen as the maximum likelihood value obtained in model B). We used a randomization approach to establish expected payoffs for males released at $t = 1$. Payoffs were

calculated for one of three settlement locations: (i) the expected fitness payoff on the female the male was with at time $t = 2$ (i.e., his actual choice, hereafter "chosen"), (ii) the expected fitness payoff had he stayed on the female he had originally chosen at time 1 (hereafter "original"), (iii) the average expected payoff of all the other choices a male had available to him (hereafter "random"). Note that values (i) and (ii) are identical if the male did not move between times 1 and 2 and that (iii) excludes the chosen female.

For each male, we estimated the expected fitness payoff using a randomization approach. The approach assumes that the fecundity of a female is proportional to her weight (e.g., Miyashita 1986); that a male can have paternity (translating into a proportion of the female's fecundity) according to published results (Elgar et al. 2003) if he is of rank 1, 2, or 3 with this female; and that rank is determined through a process in which ranks 1, 2, and 3 are sequentially assigned to males that are present on a particular female's web. If there are more than three males present, some will remain without paternity (rank 4 onward). A male's propensity to be assigned the currently available rank position is 1 if he is a prior resident (i.e., a stayer) and P if he is a newcomer to this female's web. Males were drawn, without replacement, to fill in rank positions with probabilities proportional to their propensities, until there were no more males competing for a female or all ranks 1, 2, and 3 were filled.

Each male for which we had recorded a position at $t = 1$ and $t = 2$, whether a stayer or a mover in reality, was given a new rank this way 10,000 times for three different situations: (i) if he was assumed to have stayed with his original choice ($t = 1$, original), with all other males' positions following that of $t = 2$, including all newcomers; (ii) if he was assumed to be with his actual choice at $t = 2$ (chosen), again with all other males' positions following that of $t = 2$; and (iii) if he was with a randomly chosen female other than his actual choice (random), again with all other males' positions following that observed at $t = 2$. Six male-specific means, based on 10,000 randomized trials each, were thus generated: (i) the expected fitness payoff for each male, (ii) the weight of the female, (iii) male rank on the web, (iv) the number of males on the female's web, (v) the total competition faced by each male, and (vi) the number of prior residents on the web. The total competition was calculated using the number of prior residents (stayers) or newcomers (movers or newly introduced males) on each web, such that a web with two resident males (competition = 2×1.0) was assigned a competition level approximately twice as high as a web with two newcomer males (competition = 2×0.53 ; see "Results"). The number of prior residents was calculated as the number of males that stayed on their web between

$t = 1$ and $t = 2$ and necessarily includes each male that was specified as a stayer in the count. Because we are interested only in the comparison between the choice a male did make and the other choices he could have made (original or random), we performed these pairwise contrasts for each of the six response variables using t -tests. Equal variances were not assumed because one group of data are based on actual observations, while the other two are based on 10,000 simulations and therefore have different variance structures.

Results

Male Behavior

Of the 240 males initially released into the enclosures, 154 (64.17%) had settled on a female's web at $t = 1$. Males that had settled away from webs, for example, on support strands or on the enclosure walls, were not considered to have chosen females and so were not included in further analyses. After competition was experimentally increased, 105 of the males (43.75%) had made choices at both $t = 1$ and $t = 2$. If males had not settled with a female at $t = 1$ but had settled with female at $t = 2$, then they were not included in analyses as no comparison between choices could be made. Males either stayed with the same female at both time points ($n = 48$) or moved to a new female at $t = 2$ ($n = 57$). The mean (\pm SE) number of males on each female's web was 2.1 (± 0.8) at $t = 1$, and at $t = 2$, the mean number of original males was 1.67 (± 0.11) on each female's web. The mean number of males released after $t = 1$ as competitors that settled on female's webs at $t = 2$ was 1.67 (± 0.10).

AIC Analysis

The ultimate settlement pattern of males in our experiments indicated no relationship between weight and rank ($r = 0.57$, $n = 274$, $p = .345$). Rather, we found a strong prior-residence effect, which had a greater effect on male rank than did male size. In an AIC analysis, the model with the best support (table 1) predicted that weight does not predict male rank but that prior-residence effect is

strong; the next best model with $\Delta\text{AIC} < 2$ repeated the same message, with an extremely small negative effect of weight on rank acquisition propensities (estimated $a = -6.312 \times 10^{-4}$) and a very similar estimate for P : $P = .5385$ in the best model and $P = .5295$ in the only other model with $\Delta\text{AIC} < 2$. The biological interpretation is that a moving male is approximately half as competitive as a male that stays with the same female after competition increases (i.e., a prior resident). This suggests a significant cost of moving from female to female in response to increased competition.

Although weight did not have an appreciable impact on male rank acquisition, it did have a strong influence on the likelihood that a male moved away from his initial female choice after competition was increased (fig. 1; logistic regression $\beta = -0.0079$, $\chi^2 = 7.97$, $P < .005$).

Calculation of Expected Fitness Payoffs

We found that males that stayed with the same female after we increased competition had higher expected fitness payoffs if they had settled with a random female other than their original choice ($t = 3.20$, $\text{df} = 55$, $P = .002$; fig. 2A). In contrast, males that moved away from their originally chosen female had lower, but not significantly so, expected fitness payoffs on the new female with which they settled ($t = 1.560$, $\text{df} = 82$, $P = .123$; fig. 2A). However, the average payoff for movers was significantly higher than expected had these males settled randomly with any female other than the original one ($t = 2.208$, $\text{df} = 81$, $P = .006$; fig. 2A). This result was not driven by males simply moving to larger females after competition was increased, as there was no difference between the average weight of females that males chose and that of random females ($t = 1.142$, $\text{df} = 71$, $P = .257$) or between chosen and original females ($t = 1.036$, $\text{df} = 111$, $P = .302$; fig. 2B). Both staying and moving males settled on webs where their ranks were significantly lower (i.e., closer to the female) than on random webs (stayers: $t = 4.488$, $\text{df} = 88$, $P < .001$; movers: $t = 4.553$, $\text{df} = 108$, $P < .001$; fig. 2D). Moving males settled on webs with significantly greater numbers of rival males than on the webs of

Table 1: Akaike Information Criterion (AIC) results in order of model support

Model	a	P	$\log(L)$	AIC	ΔAIC
B. Only prior residence matters	0	.5385	-175.275	352.544	0
D. Full model	-6.312×10^{-4}	.5295	-175.186	354.373	1.83
A. Null model	0	1	-177.540	355.081	2.54
C. Only weight matters	-1.8×10^{-3}	1	-177.533	357.066	4.52

Note: All models use the likelihood structure Pe^{aw} , where w is male weight, a represents the effect of weight on rank acquisition, and P represents the effect of prior residence on rank acquisition. Values a and P are either fixed to a value that indicates no effect (0 for a and 1 for P) or estimated from data. $\log(L) = \log$ likelihood.

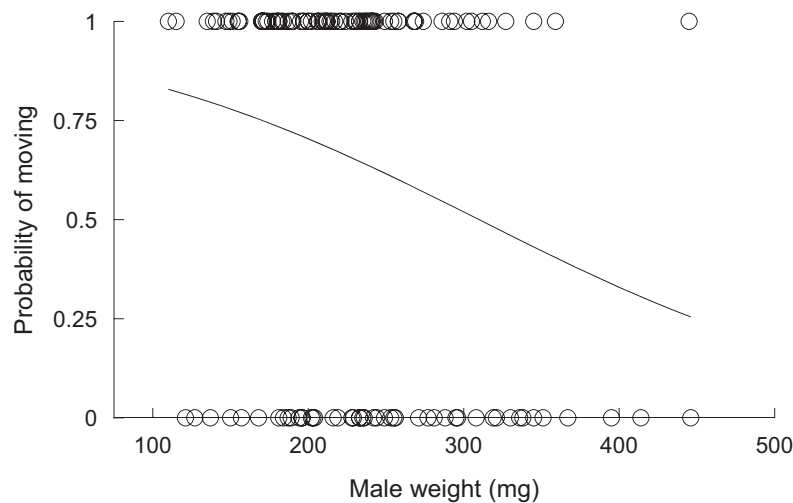


Figure 1: Logistic regression for the probability that a male left his original choice and moved to a new female when competition was increased as a function of male weight.

their original female choice ($t = 3.138$, $df = 111$, $P = .002$) or on the webs of random females ($t = 3.966$, $df = 73$, $P < .001$; fig. 2C). Despite this, when accounting for effects of prior residence, competition for a mover male's final choice of female was significantly lower than for random females ($t = 2.582$, $df = 68$, $P = .012$; fig. 2E). The number of prior residents on the webs chosen by moving males was significantly lower than on either their original web ($t = 5.157$, $df = 108$, $P < .001$) or the webs of random females ($t = 9.966$, $df = 108$, $P < .001$; fig. 2F), while for stayers there was no difference in the number of prior residents on chosen versus random webs ($t = 0.284$, $df = 54$, $P = .778$; fig. 2F).

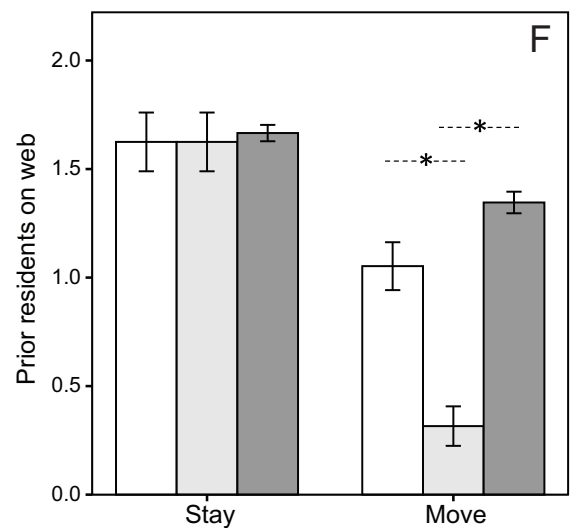
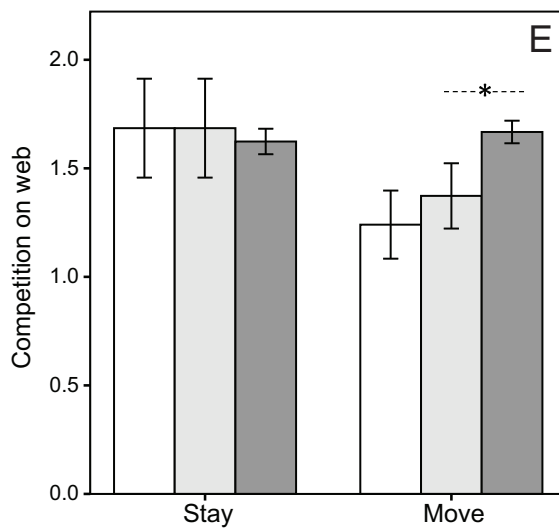
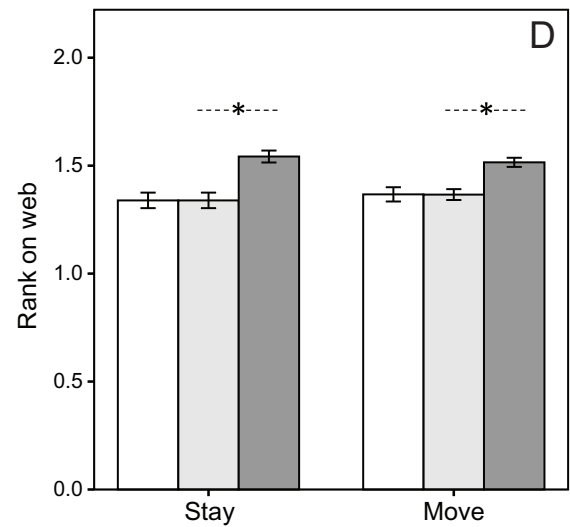
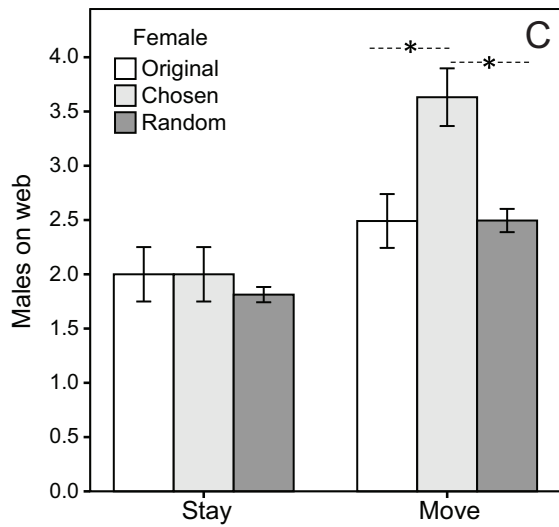
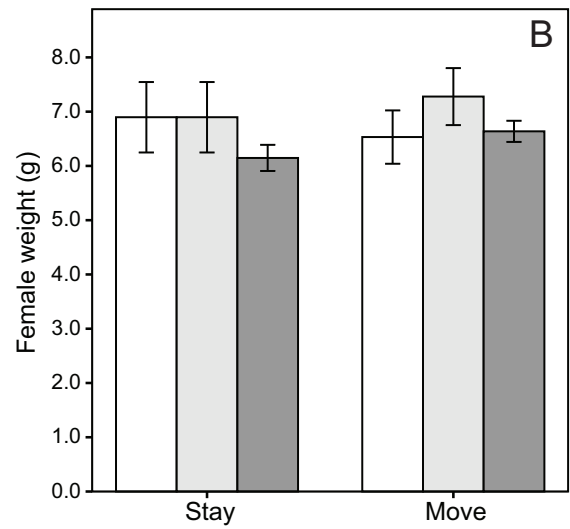
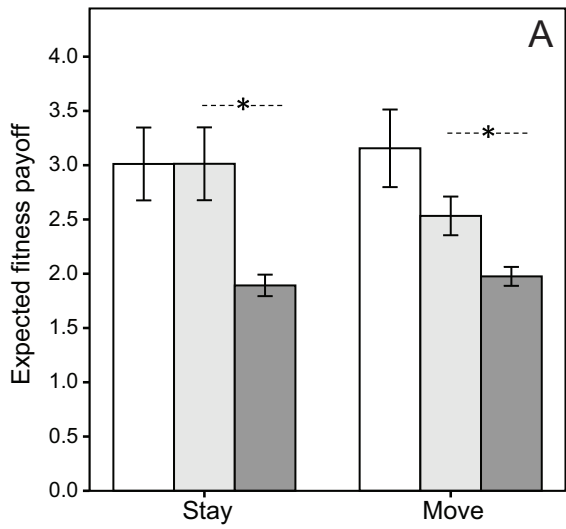
Of the 240 males used, 15.4% initially settled on females that changed their own position between $t = 1$ and $t = 2$ (see Kasumovic and Jordan 2013 for an analysis of female movement). For these males, prior-residence advantage was lost and movement to a new female occurred as a consequence of female behavior. In four cases (1.6%), the male followed the moving female and retained prior-residence advantage in our analysis. Because this female movement is biologically meaningful (see Kasumovic and Jordan 2013) and because these females were still available to choosing males, they were retained in the data set.

Discussion

A fundamental difference between male and female mating behaviors is that in most systems, males face increased competition for mating opportunities (Andersson 1994; but see Nelson-Flower et al. 2013). Despite this, male choice is rarely examined in the relevant social context,

giving a skewed perception of how male mate-choice strategies operate under natural conditions. Here we used a novel experimental approach based on foraging theory to examine how males respond to changing payoffs of their mate-choice decisions as their social environment (number and distribution of male competitors) changes. We find two main results that fundamentally change how we view male competition and male mate choice under natural conditions. By calculating the fitness payoffs of each male's actual choice and comparing this to the payoffs of all alternative choices, we find that males actively shift their mate choice as social conditions change in a way that increases their fitness returns, rather than having immutable preferences for, for example, larger females (Bonduriansky 2001). We show that prior-residence effects, a well-known factor in foraging behavior, also have a strong influence in male reproductive contests and can shape the expression of male mate choice. Our findings demonstrate the importance of situating male choice studies in the relevant social setting, as both inter- and intrasexual interactions have profound effects on the expression and fitness payoffs of different male mate-choice strategies.

When we examined male behavior in realistic social conditions, we found that predictions based on dichotomous trials did not hold true. Larger males of our study species (*Nephila plumipes*) almost exclusively displace smaller males in dyadic contests (Elgar and Fahey 1996), and dichotomous competition trials across numerous other species demonstrate the importance of increased size, weight, and weaponry in contest outcomes (Andersson 1994). However, the ultimate settlement pattern of males in our experiments indicated no relationship be-



tween weight and rank on a female's web (table 1; fig. 3). This mismatch between the results of traditional binary trials and choices made under more realistic social conditions suggests that other social factors are important in male contest outcomes. Using AIC analysis, we found a strong prior-residence effect in male settlement on a female's web. This prior-resident advantage had a greater effect on eventual male rank than did male weight and meant that males that moved were approximately half as competitive as males that stayed with the same female after competition was increased (i.e., prior residents). Dominance hierarchies based on order of arrival are common in nature, most often being observed in foraging contexts (Hardy and Field 1998; Kokko et al. 2006), and prior residence can have a strong effect on contest outcomes (Johnsson et al. 1999; Fayed et al. 2008; Kasumovic et al. 2011). The prevalence of mate-guarding strategies across taxa (e.g., Møller and Birkhead 1991; Jormalainen 1998; Prenter et al. 2003) demonstrates the potential for prior-residence effects to have widespread consequences in mating contexts. While residence effects have been observed in contests for resources used in breeding (Davies 1978; Bergman et al. 2007; Sacchi et al. 2009), our results are the first to directly show the importance of prior residence in male mate choice. When combined with the effects of previous experience on contest outcomes (i.e., winner and loser effects; Whitehouse 1997; Hsu et al. 2009; Kasumovic et al. 2010) and resource value (Enquist and Leimar 1987; Arnott and Elwood 2008; Kasumovic et al. 2011), social factors may have a more important effect on male mate choice than previously appreciated.

Although male weight did not have an appreciable impact on male rank acquisition, it did have a strong influence on the likelihood that a male moved away from his initial female choice after competition was increased (fig. 1). The fact that lighter males were far more likely to leave their original choice than heavier males suggests two possibilities. Rather than leaving voluntarily to search for higher fitness payoffs, small males may be forced off their chosen webs when larger competitors arrive. In this scenario, when males are similar sized or larger than newly arriving competitors, they are able to maintain their position, while males below a relative threshold size are unable to hold their position when challenged by larger com-

petitors and instead leave in search of a new female. Alternatively, the movement of males may reflect decision making under sensory limitation. In nature, a plausible reaction to locally increased competition is to voluntarily leave the web and attempt to move to a place of lower competition. In our experiment, males may be unaware of the fact that increased competition now applies throughout the experimental web system. Males may make suboptimal decisions as a result of imperfect knowledge of the global level of competition if their perception is limited to local conditions. In classical foraging theory, uncertainty about foraging patch quality can greatly influence decision making (Stephens and Krebs 1986), leading to suboptimal distribution of individuals throughout the foraging environment (Abrahams 1986; Beauchamp et al. 1997). The same may also be true in a reproductive context, in which limited knowledge about alternative reproductive options can lead to mate choices that deviate from those expected under the assumption of perfect information when all potential mates are known.

We next assessed the fitness outcomes of male settlement decisions by comparing the expected fitness payoff of male mate choices. We modeled the payoff for each male's actual choice of female, their payoff had they stayed with their initial choice of female, and their average payoff with random females in the population. The loss of a prior-residence advantage meant that moving away from an initially chosen female carried a significant cost in terms of achieving a high-ranking position near a new female. Yet when moving males settled on a subsequent web, they attained a rank similar to the rank they would have attained if they had stayed with their original choice (a difference of only 0.001; fig. 2D). Perhaps more remarkably, the rank of moving males was almost identical to that of males that had stayed with their original choice (moving males' mean rank = 1.36, staying males' mean rank = 1.33). Consequently, males that moved suffered only a mild reduction in expected fitness payoff compared with if they had stayed with their original choice (fig. 2A). However, the average payoff of their subsequent mate choices was significantly higher than expected had these males settled randomly with any available female (fig. 2A). This result was not driven by males simply moving to heavier females after competition was increased, as there was no difference in

Figure 2: Mean (\pm SE) values generated from 10,000 randomization runs for males that stayed with their original female choice (stay, $n = 48$) or males that moved from their original female choice (move, $n = 57$) after male competition was experimentally increased between times $t = 1$ and $t = 2$. Open bars represent the expected payoff a male would have received at $t = 2$ if he had stayed with the same female he had chosen at $t = 1$ (original). Light-gray bars represent the actual payoff at $t = 2$ with the female a male had chosen at $t = 2$ (chosen). Dark-gray bars represent the payoff a male would have gained with a random female at $t = 2$, not including the female actually chosen (random). A, Expected fitness payoffs for mating, accounting for female fecundity and male rank (hence paternity share; see "Methods"). B, Female weight (grams). C, Number of males on a female's web. D, Male rank on a female's web. E, Level of competition on a female's web, accounting for male prior-residence effects. F, Number of prior residents on a female's web.

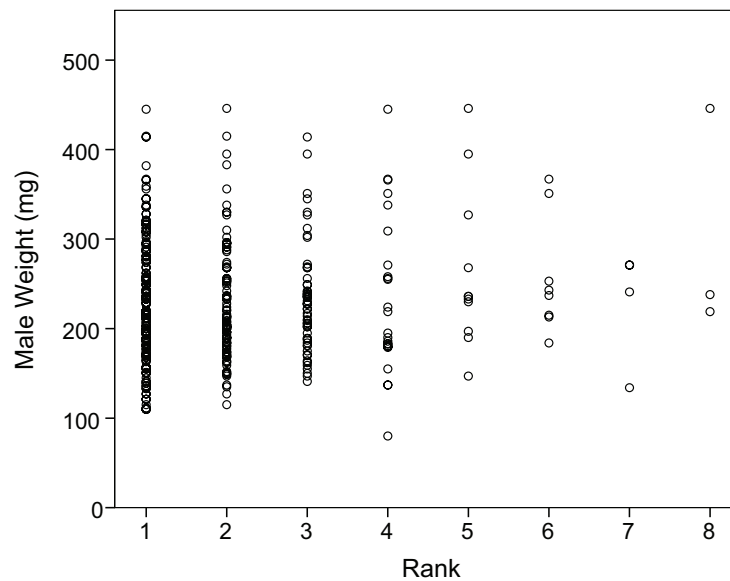


Figure 3: Scatterplot comparing male rank to male weight for all males that made a choice at $t = 2$.

the weight of chosen and alternative females (fig. 2B). Rather, male mate choice operated in a very similar way to ideal free distribution of food foragers; males struck a balance between female fecundity and competition when choosing mates.

The assessment of the trade-off between patch value and competition is a vital aspect of foraging decisions. In a mate-choice context, there is some evidence that individuals are able to assess competition for potential mates: when given a choice between females that are associated with other males and hence the subject of higher perceived sperm competition, males of some species prefer females subject to lower competition, for example, *Poecilia reticulata* (Dosen and Montgomerie 2004) and *Gambusia holbrooki* (Wong and McCarthy 2009). Further, previous studies of a closely related species to that used in this study, *Nephila senegalensis*, show that males avoid webs of females that have been previously visited by other males (Schneider et al. 2011). However, in our experiments, males on average moved to places with more competitors than would be encountered under random movement. Despite this, when we included the effects of prior residence on the competitiveness of males that moved or stayed, the actual competition males faced for their choice of female was significantly lower than that for random females (fig. 2D). This is explicable, because prior-residence effects predict that not all webs with the same number of competitors present an equally strong competitive environment since some competitors are newly arrived. This likely also applies to other species; the number of rivals for potential mates

may not be an accurate representation of the level of competitive risk due to residence effects. In *Gammarus pulex* (Franceschi et al. 2010) and mosquitofish *G. holbrooki* (Callander et al. 2012), males do not appear to account for competition, and it is possible that, as we show here, a more nuanced assessment of competition than raw numbers of competitors is being used.

Moving males tended to settle on webs with many other competitors (fig. 2D), yet avoiding the webs of females harboring prior residents (fig. 2F), rather than settle disproportionately on webs with other newly arriving males. This canceled the relative disadvantage of the male moving (a newcomer himself), and as a net effect, movers settled with females where competition was lower than average (fig. 2E) even though the number of competitors was higher than average. This pattern of male choice also explains why there is no relationship between male weight and the likelihood of achieving a high-ranking position in our study, despite the fact that smaller males are more often displaced from their preferred webs. Moving males face a choice between taking a low-ranking position on a web that offers high fecundity but much competition and a high-ranking position on a web that offers lower fecundity but reduced competition. By moving to initially less preferred females and avoiding more competitive prior residents, moving males were able to avoid competition from residents and achieve ranks equivalent to those of males that stayed. Our results thus demonstrate that males can increase their fitness by choosing a more appropriate

partner rather than a more attractive partner (Griffith et al. 2011).

Our study examines emergent patterns arising from thousands of interactions between rivals and potential mates and so provides robust information about the factors shaping male reproductive behavior in social settings. While we focus here on the behavior of males, any form of mate choice inevitably involves both sexes and so the settlement patterns we observe here must be considered in the context of all social interactions, including those with females. Although female settlement in *N. plumipes* can act as a level of female choice (Kasumovic and Jordan 2013), males in our experiments are released and allowed to settle after females have completed this stage, thus minimizing the impact of female behavior. Yet while we do find strong evidence that males are responsive to their social context, the underlying behavioral mechanisms that cause these emergent patterns of male response are still to be elucidated. Individuals may use prior experience to guide subsequent behavior (Jordan and Brooks 2012), and in the context of our own and many similar experiments, wild-caught individuals may have differing social histories that affect their mate-choice decisions. Moreover, in complex social settings, there are numerous factors that can shape mate choice. Males may, for example, react only to the behavior of rival males, use some form of sampling rule (Janetos 1980), or respond to female's reactions (Patricelli et al. 2002). A potential mechanism we did not test directly is the movement of males even under low competition. While we have evidence from previous studies that male movement is limited unless competition is increased (Kasumovic et al. 2007; Schneider et al. 2008), it would be interesting to compare the level of movement under different competitive regimes (including a treatment with no new males added). Indeed, the patterns we observe may be consistent across social contexts and not only a consequence of our competition treatment; males might make adjustments to their choices even when competition is low, using the same behavioral patterns we observe here to increase the fitness payoffs of their choice among potential mates. Whether the processes we see here occur only when competition is high or are a consistent behavioral trait across social conditions remains a testable question worthy of future study. More generally, future studies examining the fine-scale detail of social interactions among rivals and potential mates in this and other species will be a fruitful avenue of inquiry into the mechanisms underlying the broad patterns of social reproductive behavior we describe here.

Male mate choice has been described in multiple species with intense intrasexual reproductive competition (Amundsen and Forsgren 2001; Jones et al. 2001; Reading and Backwell 2007; Bel-Venner et al. 2008; Hoefler et al. 2009), em-

phasizing the potential role of interactions with rivals in the mate-choice process. Indeed, in many cases, increased competition among males can select for male choice through assortative choice or competition avoidance (Fawcett and Johnstone 2003; Härdling and Kokko 2005; Venner et al. 2010). Yet when experimental designs preclude the possibility of male-male interactions by emulating female-choice designs, the findings from these experiments may not reflect the natural mate-choice processes they are intended to examine. We found that males changed their initial mate choice to settle in places of relatively low competitive pressure once social conditions changed. In this way, males may be able to alter the selection acting on them by changing their own mate choice to suit the prevailing social conditions, moving to microenvironments that differ in their selective regimes (Odling-Smee et al. 1996; Noe 2001) and increasing the fitness returns of their mate-choice decisions. This study offers a framework to study male choice in the relevant social context, allowing a more comprehensive understanding of the factors shaping male mating behavior in natural conditions across taxa.

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A female (left) and male (right) Australian golden orb-web spider (*Nephila plumipes*) in the wild. Note the considerable sexual size dimorphism; females are larger than the palm of a man's hand. Photo credit: M. Kasumovic and L. A. Jordan.