

Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*)

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Mate searching is a risky behavior that decreases survival by increasing predation risk and the risk of energy depletion. However, few studies have quantified actual mortality during mate search, making it difficult to predict mate searching and mating strategies. Using a mark and recapture study, we examined mate-searching success in a highly sexually dimorphic species, the golden orb-web spider (*Nephila plumipes*). We show that despite the high-density aggregations of this species, male survival during mate searching is extremely low (36%) and is phenotype independent. Surprisingly, males that survived mate search were in better condition after recapture than prior to release, most likely due to kleptoparasitism on females' webs. In a complementary release experiment in a field enclosure, we show that males are choosy and adjust their choice of female depending on their own condition and weight. Thus, the high mortality rate of searching males in the field may be a cost of choosiness because released males traveled further than necessary to settle on females. Although males were choosy about female phenotypes, they did not avoid webs with rival males already present. This suggests that the cost of continued searching outweighs the cost of competition but not the cost of mating with certain females. Further examinations of mate-searching risk in other species in reference to their mating system and environmental conditions are necessary to determine the occurrence and effects of high mortality rates during searching. *Key words*: mate choice, mate search, *Nephila plumipes*, searching mortality. [*Behav Ecol*]

Before courtship and mating can begin, individuals must locate a mate. Although mate-searching costs can be significant, they are rarely quantified in field studies. Mate searching is an energetically costly endeavor and only those individuals in good condition can afford to begin searching (Proctor 1992). This cost can be increased if individuals do not replenish their resources during searching, like in web-building spiders (Foelix 1982). In addition to energetic costs (Byers et al. 2005), searching individuals must also deal with an increased risk of predation. Studies that have examined mate-searching costs show that predation rates can be high and that mortality is often biased toward the sex that does the searching (Sakaluk and Belwood 1984; Gwynne 1987; Norrdahl and Korpimäki 1998; Gwynne and Bussière 2002; but see Su and Li 2006). This is because searching individuals are more conspicuous and because their greater activity increases the probability of encountering predators (Sakaluk and Belwood 1984; Gwynne 1987; Gwynne and Bussière 2002). It is therefore no surprise that increased predation risk leads to individuals decreasing search times and activity (DeRivera et al. 2003) or changing mate-searching patterns and habitat use altogether (Sih 1988).

Despite evidence demonstrating the costs of searching (Sakaluk and Belwood 1984; Gwynne 1987; Gwynne and Bussière 2002; Byers et al. 2005), there are only a few studies that estimate survival rates during mate search. This limits the ability to associate a direct risk with mate searching, making it difficult to determine individual mate-searching costs, and thus, to predict searching and mating strategies. The few studies that have quantified mate-searching risk and the traits associated with searching success demonstrate that male mor-

tality can be extremely high during searching (approximately 80% in 2 species of spiders: Vollrath 1980; Andrade 2003) and that successful mate-searching males tend to be larger and in better condition than average (Vollrath 1980; Andrade 2003; Foellmer and Fairbairn 2005b). As mate search costs could impose a considerable constraint on multiple mating by males, it is essential that mate search mortality be measured under natural conditions in a range of systems to determine whether such high costs are common.

Here we examine mate-searching survival in the golden orb-web spider (*Nephila plumipes*). There were 3 goals of this study. First, we used a mark-recapture experiment to determine whether male mate search mortality in this aggregative species (Elgar 1989) is similar to other spiders with sparser web distributions (*Latrodectus hasselti*: 80–93% mortality, Andrade 2003; *Nephila clavipes*: 88% mortality, Vollrath 1980). Mate search mortality in spiders may be mainly due to predation and exhaustion (e.g., Andrade 2003), so the cumulative risk should increase with time spent searching. Thus, it might be expected that mortality would be lower in a species with aggregated webs. Second, we examined whether male phenotype affected searching mortality. Third, we used a field-enclosure study to determine whether males are choosy during mate searching as this could elevate mortality rates. Male *N. plumipes* are monogynous due to a high frequency of injury and sexual cannibalism after attacks by their first mate (Elgar and Fahey 1996; Schneider and Elgar 2001). Recent work by Elgar et al. (2003) shows that males did not choose females based on mating status or weight; however, males that chose virgin females were significantly heavier than those that chose mated females. Thus, males may be choosy about female phenotype or mating status to ensure that their single mating has the highest payoff possible (Bonduriansky 2001; Andrade and Kasumovic 2005).

MATERIALS AND METHODS

Female *N. plumipes* build large orb webs, which can be part of aggregations or can occur solitarily (Elgar 1989), and are

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located at varying heights above the ground (Herberstein and Elgar 1994). Males mature either on or near the webs of females within these aggregations, or on their own orb web separate from any aggregations (Kasumovic MK, personal observation). Once mature, males leave their web in search of females. Although male orb-web spiders are not known to feed while searching (Foelix 1982), *N. plumipes* males can kleptoparasitize prey from a female's web once cohabitation begins (Kasumovic MK, personal observation). While cohabiting with females, multiple males can settle on a single female's web, remaining there until an opportunity to mate arises (when the female is occupied with a prey item: Elgar and Fahey 1996; Elgar et al. 2003). Males assort according to size with larger males closer to the hub, allowing them mating priority (Elgar and Fahey 1996). Although large size seems to play a role in mating success, direct competitions are rarely observed (Elgar and Fahey 1996).

We collected male *N. plumipes* from our field site in Bicentennial Park, Pymble in Sydney, New South Wales, Australia between February and March 2005. Although it is common for male *N. plumipes* to autotomize legs while escaping cannibalism (only 31% of 327 males collected had all legs intact) (Elgar and Fahey 1996), we only used males that had all eight legs to ensure no handicap in mate searching. Males can also break off the tip of the sclerotized portion of their intromittant organ (pedipalp) during copulation (Schneider et al. 2001). Because it is unclear if this affects male behavior, we selected only males with intact pedipalps for our experiments. All males and females used for the following experiments were released in nature once experiments were completed.

Mark and recapture

We completed 2 separate release experiments. In experiment 1, we released individual males ($N = 52$) throughout the field site to estimate survival. These males were marked using non-toxic fluorescent paint (Luminous paint, BioQuip Products, Rancho Dominguez, CA) on the abdomen and the tibia of both of the first pair of legs. Because males commonly autotomize legs and would thus be likely to lose part of this marking, we marked all males identically. One week later in experiment 2, we used a separate group of males ($N = 48$) to make a second estimate of survival and to determine the distance traveled to a female's web and how mate searching affected male condition and survival. We weighed and individually marked males by gluing (Tarzan's Grip, Selleys, New South Wales, Australia) numbered labels (2-point font printed on white paper approximately 2×3 mm in size) on their abdomen. Both marking techniques have been successfully used for tracking bees (e.g., Fewell and Bertram 2002). Size was measured as the average length of the patella-tibia of the first pair of legs (using calipers). In both experiments, males were anaesthetized using CO₂ to facilitate marking. We then monitored males for an hour after marking and for 5 min after release to insure that neither marking method had an affect on locomotion.

Males were released in a field site (approximately 845 m²) composed of 3 separate islands of vegetation (approximately 45, 200, and 600 m² in size) located on the Kuringai campus of the University of Technology campus in Sydney, New South Wales. The 3 islands consisted of predominantly Eucalypt forest and shrub and were less than 5 m apart, surrounded by parking lots in all directions. Females found at this site settled both solitarily and in aggregations of up to 9 spiders of various instars. Settlement of aggregations were similar in spacing to other described aggregations (Elgar 1989) and other aggregations in the area (Kasumovic MK, personal observation). Vehicular traffic was not observed during surveys and was

minimal throughout the study (completed during university holidays, February–March 2005).

We initially searched the entire site and located and mapped all females' webs. Although females were not marked, webs were found at the same locations during every survey. Males were released in the morning (08:00 AM) on the ground in groups of 8–10 individuals within 1 m of a conspecific female's web. Release locations were spread evenly throughout the field site. In experiment 1, 36 males were released in the largest island, and 16 males were released in the medium-sized island, whereas in experiment 2, 48 males were released in the largest island only. No males were released in the smallest island, as only 2 juvenile females' webs were found there. After release, we searched all 3 islands for marked males, surveying females' webs between 08:00 AM and 10:00 AM on each of the first 5 days, and then every 2 days for another 20 days. Any males found at this time were collected and returned to the laboratory. Males from experiment 1 were measured (tibia–patella length). Males from experiment 2 were measured and weighed to determine individual differences in condition (see below) before and after release.

Male mate choice experiment

If cannibalism reduces male mating opportunities, males might be predicted to be choosy about potential mates (Bonduriansky 2001; Andrade and Kasumovic 2005). To examine whether males in the field may be choosing specific females and thus increasing their search times, we performed a mate choice experiment in a $3 \times 3 \times 2.5$ -m screened outdoor enclosure. For this experiment, we collected 60 adult males, as well as 30 penultimate and 30 adult females from the field. Female instar was distinguished by examining the epigyne. Adult females have a protruding epigyne that has 2 clear openings, whereas penultimate females have the same protrusion, but the openings are covered. Although we could not identify the mating status (virgin or mated) of adult females collected, they were representative of the females available in the field at the time of the mark-recapture experiment and thus provided a representative sample of choices available to those males.

We ran 3 replicates of a male mate choice experiment where we randomly placed 10 juvenile and 10 adult females along the walls of the enclosure. We released females at 10:00 AM and allowed them to build their webs over 24 h. The following morning at 10:00 AM, we counted all the adult and penultimate females within the enclosure. All the females built their webs in the upper part of the enclosure using the walls and ceiling for support at similar heights to those found in the field. We then released 20 males evenly spaced along the base of each of the 4 walls of the enclosure (5 males per wall). Once again, we used only males that had all their legs and pedipalps intact. We returned to the enclosure 6 h later to collect all the females and any males found on each female's web. We also searched all the walls of the enclosure and each of the females' webs for dead males. Males and females were weighed and measured as above and we also calculated male condition after recapture.

Condition estimate

To estimate an index of body condition, we used a residual index (a regression of body weight on linear size) that has recently been proved to perform well and to be biologically relevant (Schulte-Hostedde et al. 2001, 2005). To determine the relationship between log(weight) and log(size) for *N. plumipes* males, we performed a reduced major axis regression

(Green 2001) on an independent group of males from a field-captured population ($N = 320$, Kasumovic MK, Bruce MJ, Herberstein ME, Andrade MCB, unpublished data). We regressed male $\log(\text{weight})$ on $\log(\text{size})$ and found the slope of the relationship to equal 4.22. We then used 4.22 as the exponent for the root of $\log(\text{weight})$ regressed on male $\log(\text{size})$ (for greater details, see Kasumovic and Andrade 2006).

We did not calculate a condition index for females because the relationship between size and weight did not correlate as strongly. This is most likely due to natural variance in female weight and size due to variance in the instar and mating status of the females used. Thus, for any analyses involving female traits, we only used weight and instar as the descriptive variables because females of different instars had significantly different sizes ($t = 7.961$, $df = 54$, $P < 0.001$).

RESULTS

Mark and recapture experiment

A total of 34 (34%) males were recaptured throughout both replicates. There was no difference in the proportion of males recaptured in the 2 release experiments (experiment 1: 19 males, 36.5%; experiment 2: 15 males, 31.3%; Fisher's Exact 2-tailed test = 0.67). There was also no difference in the proportion of males caught in each island in experiment 1 (large island: 14 males, 38.9%; medium island: 5 males 31.3%; Fisher's Exact 2-tailed test = 0.76). In experiment 2, males were only recovered in the large island where they were released, suggesting that males either limited their search for females within each island or that no males survived if they left the island. No males were found on the smallest island in either experiment. Of the 34 males recaptured, 21 (62%) were found together with rivals on a female's web; thus, competition over access to females may occur despite high male mortality rates. Up to 5 males (range 1–5, mean=1.3) were found cohabiting with the same female.

In the second experiment where we could follow individuals, the 15 recaptured males traveled an average of 9.91 ± 1.24 m to successfully find a female (range 2.4–17.8 m), even though they were released within 1 m of a conspecific female. Recaptured males from both experiments took an average of 3.38 ± 0.61 days to successfully find a female (range 1–15 days). We assessed whether male success at finding webs depended on the time elapsed following initial release by using a survival analysis (Sokal and Rohlf 1995). This analysis compares the observed pattern of male recapture over time with the expected pattern if there was an equal probability of discovering a male on each day following release (i.e., 1 or 2 males recovered each day until 34 males are recovered, Figure 1). This analysis suggests a much higher success rate for males that find a web quickly (survival analysis, $\chi^2 = 56.91$, $df = 2$, $P < 0.0001$).

Because only 34 males were recaptured, the power of parametric statistics to detect whether size is related to mate-searching success was limited. In a more powerful analysis, we used a subsampling technique to create a null distribution to determine whether the males recaptured were on average larger than the males that were released (Manly 1991). To create this null model, we randomly subsampled 34 males from the distribution of 100 released males and calculated the mean of this distribution. We repeated this subsampling a total of 10 000 times and used the mean calculated each time to create a null distribution of 34 randomly selected males. This allowed us to compare the actual mean of recaptured males with a null distribution to determine whether our observed sample differed from random (Figure 2). We also compared variances in male size before and after recapture to

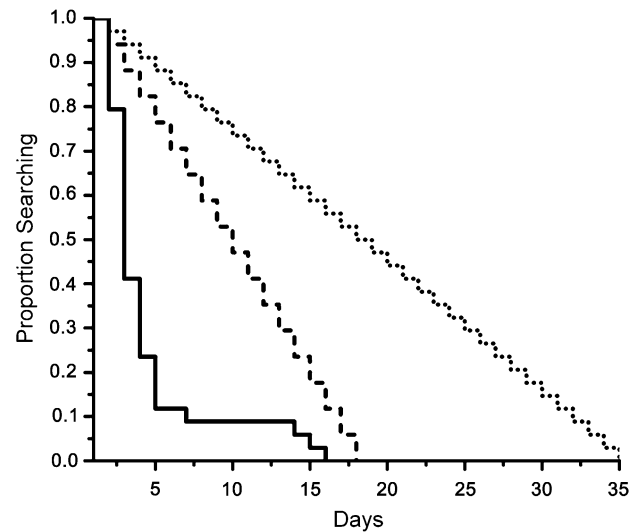


Figure 1

Survival analysis of rate of capture for all males that were eventually recovered in females' webs during 2 release experiments ($n = 34$). Actual recapture rate (solid line) is compared with null distributions that assume a constant recapture rate per day (dotted line = single male/day; dashed line = 2 males/day). Most males that successfully reached a female's web do so within a few days of release (by day 3, only 40% of males that will eventually be recaptured are still searching). Relative to null models, very few males successfully reach a web after searching for more than 5 days.

examine whether stabilizing selection operates on male size during mate searching. The mean leg size of the recaptured males was 0.50 ± 0.01 mm, which was not significantly different from the null distribution (0.49 mm, $P = 0.19$, Figure 2). There was also no difference in the variance in male size between released and recaptured males (Bartlett's test; $F = 1.08$, $df = 1$, $P = 0.30$). Therefore, size was not a predictor of mate-searching success, and there is no evidence for directional or stabilizing selection.

We performed the same subsampling technique to determine whether male condition had an influence on mate-searching

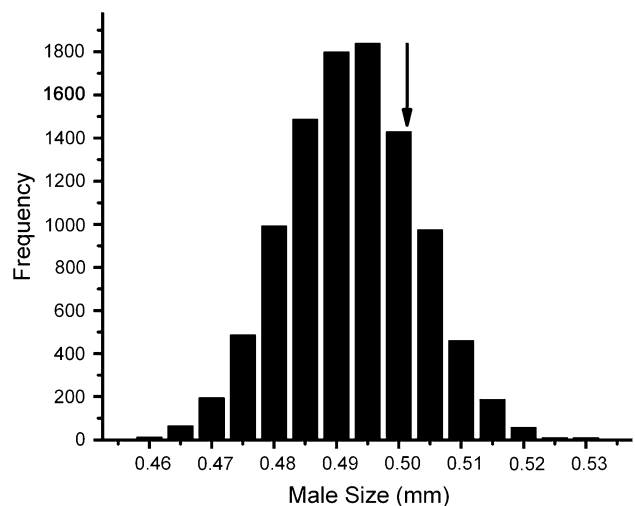


Figure 2

The null distribution of male size generated by randomly subsampling 34 individuals from the original population ($N = 100$) 10 000 times. The arrow is the observed mean (0.50 mm) of the recaptured individuals, which is not significantly different from that expected by chance ($P = 0.19$).

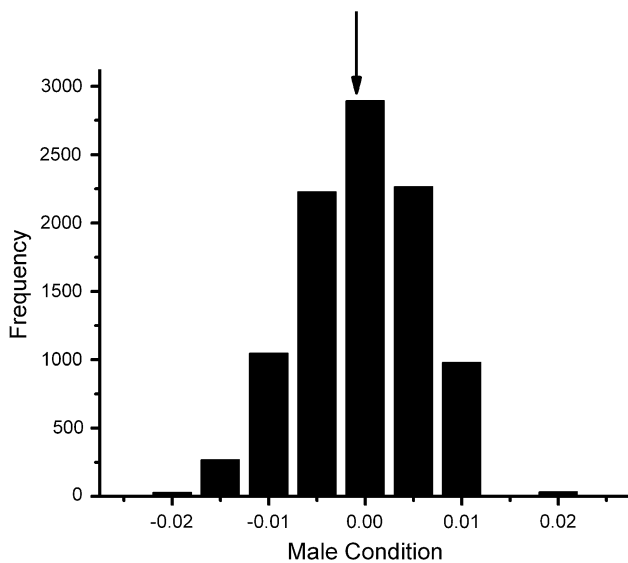


Figure 3
The null distribution of male condition generated by randomly subsampling 15 individuals from the second experimental population ($N = 48$) 10 000 times. The arrow is the observed mean (-0.34) of the recaptured individuals, which is not significantly different from that expected by chance ($P = 0.74$).

success. In this case, we randomly subsampled 15 males from the 48 released in the second experiment 10 000 times to create a null distribution. In this analysis, males in better condition before release were not more likely to be recaptured with a female (recaptured mean = 0.0028 ± 0.0067 ; null distribution mean = 0.0003 , $P = 0.54$, Figure 3). Moreover, 14 of the 15 males recaptured in experiment 2 were heavier after recapture than prior to release (release = 17.41 ± 0.26 mg, recapture = 18.68 ± 0.26 mg; paired t -test = 4.83 , $df = 14$, $P < 0.0003$).

Male mate choice experiment

At the end of our field-enclosure trials, we collected a total of 35 adult females and 21 penultimate females from the enclosures. The deviation from the original number of adult and penultimate females was due to 4 of the original penultimate females either dying or being killed by neighboring females, whereas 5 other penultimate females moulted to maturity overnight before males were released. No interfemale aggression was observed during the trials. A total of 51 of the 60 (85%) males released were collected from female's webs. One other male was located on the wall of the enclosure. It is unlikely that males mated with females in the 6 h allotted for the mate choice experiment because males cohabit with females for long periods of time and do not attempt to mate with females until females are distracted with a prey item (Elgar and Fahey 1996; Schneider and Elgar 2001; Elgar et al. 2003), and no prey items were found in females' webs. Furthermore, it was unlikely that males were cannibalized as females store all food caught (Griffiths et al. 2003), and we did not find any wrapped bodies of males in females' webs. Thus, males that were not recovered were likely those that failed to find a female. This suggests that, even in the enclosure, there was a moderate mate-searching failure rate (15%).

Of the females that attracted males, the mean number of males per female's web was 1.7 (range 1–8, Figure 4). Female instar or weight were not predictors of whether a female attracted at least one male (Table 1). Because previous work

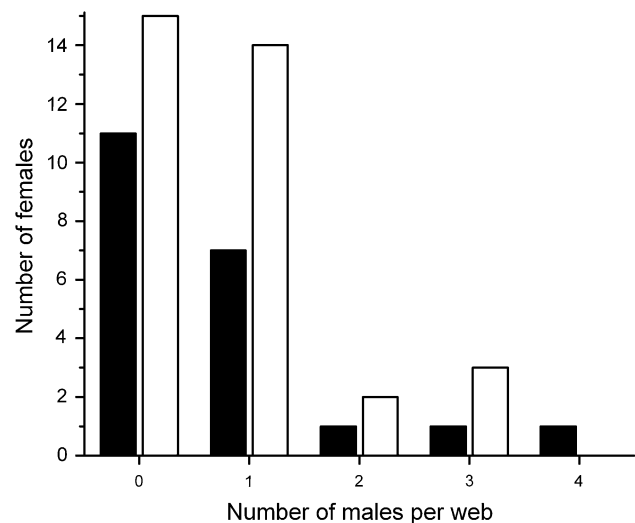


Figure 4
The number of males attracted to the webs of adult (white) and penultimate (black) females in a field-enclosure release experiment.

found that a male's weight influenced the female males chose (Elgar et al. 2003), we used 2 separate nominal logistic analyses to examine whether successful males made their choice 1) based on their own size and/or weight (with condition calculated as a covariate, Garcia-Berthou 2001) and also 2) based on size and/or condition calculated by residuals (see Methods). Our results show that heavier better condition males preferred penultimate females over adults (condition of males choosing penultimate: 0.0010 ± 0.0007 , and adult: -0.0004 ± 0.0005 females; Table 2). However, unlike in the mark-recapture experiment, males could not have increased their condition through kleptoparasitism because there were no prey items found in any of the females' webs.

DISCUSSION

We found no phenotypic correlates of male mate-searching success in *N. plumipes* because neither condition nor leg size predicted success at finding a potential mate. Furthermore, there was no evidence for directional or stabilizing selection for male size. There are 3 other studies that have examined phenotypic correlates of male mate-searching success in highly dimorphic spiders. The first 2 (Vollrath 1980; Andrade 2003) also used mark and recapture techniques to follow individual males and found no phenotypic predictors of mate-searching success. The third study (Foellmer and Fairbairn 2005b) compared the phenotypes of males found on female's webs (successful mate searchers) to recently matured males found on their own webs (before mate searching began).

Table 1
Nominal logistic analysis demonstrating that whether a female attracted at least one male did not depend on female instar and/or weight

Source	df	Likelihood ratio chi square	<i>P</i>
Female instar	1	0.432	0.51
Female weight	1	0.067	0.80
Instar \times weight	1	0.727	0.39

Table 2

Results of 2 separate nominal logistic analyses examining whether A) male size, weight, and condition (calculated as a covariate) and B) male size and condition (calculated by residuals) influence choice of available females. In both analyses, heavier and better condition males preferred penultimate females

	Source	df	Likelihood ratio chi square	P
A	Male size	1	2.66	0.10
	Male weight	1	6.09	0.01
	Size × weight (condition)	1	5.38	0.02
B	Male size	1	2.90	0.09
	Male condition	1	5.47	0.019
	Size × condition	1	2.65	0.10

Although they found that successful males were larger, this result was limited to a single population in one of 2 years. These results, together with our study, suggest only limited evidence that male size may be under selection during mate searching, and this may be true only under certain environmental conditions. In this species, size is more likely determined by stronger selection pressures such as smaller size for scramble competition and larger size for direct competition (e.g., Kasumovic and Andrade 2006).

We also provide the first evidence that successful males may be in better condition after recapture than before release. Because web-building spiders are thought to refrain from feeding while searching (Foelix 1982), this difference is most likely due to kleptoparasitism on the female's web or perhaps nectar feeding during mate search (Pollard et al. 1995). Although condition will undoubtedly be important during mate search, especially, in species that do not feed as they search, it may be sufficient for males to achieve some threshold condition that makes it physiologically possible to survive the necessary period of mate searching (Proctor 1992). Males may then be able to supplement their energy reserves that have been used during searching with resources found on a female's web. This may explain why examinations of condition in other mate-searching web-building spiders have never showed significant effects (e.g., Andrade 2003; Foellmer and Fairbairn 2005b).

The most striking result of our experiment is the low male survival rate despite the fact that males are searching in dense web aggregations (Elgar 1989). Such aggregations are thought to decrease mortality rates because the costs of sampling should be lower. Despite these aggregations, a total of 76% of males perished during mate search. We believe our recapture rates accurately represent male survival rates in the field. Once males mature, they apparently focus on mate searching. In our mate choice experiment, no males built their own capture webs instead of seeking females. This means that males that were not found on a female's web at our site were either dead (as we conclude), were still searching, or had emigrated from the site. First, it is unlikely that males were still searching within the site at the end of our experiment as recapture rates of males were high initially, but we found no marked males in the last 14 days of our sampling period (Figure 1). Second, emigration rates are apparently low because no males were located on the smallest island in the first release study, and none were found outside the island of their release in the second experiment. Our survival estimate is in agreement with previous studies on other species with extreme sexual-size dimorphism (*L. hasselti*: 80–93% mortality, Andrade 2003; *N. clavipes*: 88% mortality, Vollrath 1980) and suggests that there are several size and condition-independent factors influencing mortality.

Because survivorship decreases as the time spent searching increases (this study; Kotiaho et al. 1999), one of the most important features influencing male survival is mate-searching time. This could be for 2 reasons. First, actively searching males are more conspicuous (Sakaluk and Belwood 1984) and increase their probability of encountering predators as time progresses (Gwynne 1987; Magnhagen 1991) than individuals stationary on their webs. Second, this could also be due to senescence or due to depleted energy reserves in species with short-lived males (e.g., Andrade 2003; Bonduriansky and Brassil 2005). Therefore, any variables that increase the time required to successfully find a mate are likely to decrease male survival during mate searching.

One strategy that is likely to increase search times, and thus mortality rate, is male choosiness. *Nephila plumipes* males typically only get a single opportunity to mate (Schneider and Elgar 2001) and are therefore predicted to be choosy (Bonduriansky 2001). By increasing choosiness, males decrease the probability of choosing inappropriate females but potentially increase the risk of predation and depletion of energy reserves because they may be searching for longer periods. Other studies examining attractive pheromones in spiders show that males can successfully find penultimate females (Andrade and Kasumovic 2005). We show here that although males do not prefer females of a particular instar, a male's choice of female was based on male weight and condition (this study, Elgar et al. 2003), preferring penultimate instar females over adults when they are heavier. This pattern might also arise if males that cohabit with juveniles are more likely to be successful at kleptoparasitism or if males in poor condition fight more vigorously to exclude rivals from webs of adults. These explanations are unlikely because 1) there were very few prey species in the enclosure, and none were found wrapped in or below females' webs. There was similarly no evidence of cannibalism. 2) Males of this species engage in very little combat (Elgar and Fahey 1996), and no intermale aggressive interactions were observed in this study, even in webs with multiple cohabitants. As a result, males are often forgoing females on nearby webs and traveling further than necessary (8 m in this study) to reach preferred females.

Males are predicted to be choosy in this species if the benefit gained by being choosy is greater than the increased mortality risk. Males that settle with penultimate females will be required to cohabit for longer periods of time and may require greater resources to do so. However, by settling with penultimate females, males can ensure their mate first which may lead to a greater proportion of paternity (Elgar et al. 2003). Males in poorer condition may benefit by settling with adult females because this would allow them an opportunity to mate more quickly (e.g., Elgar et al. 2003), decreasing their risk of starvation. Further studies of male mate choice and female attributes are required to help determine the factors influencing male choice. Despite being choosy with respect to female phenotype and instar, males are not leaving females' webs regardless of the presence of conspecifics both in the field and the enclosure experiment.

Other factors that may influence male searching times are likely to be associated with female density and environmental conditions. Decreases in female density should result in increased search times as should environmental conditions that decrease detectability of females. Because many male spiders use pheromones to locate potential mates (Searcy et al. 1999; Papke et al. 2001; Gaskett et al. 2004; Kasumovic and Andrade 2004; Andrade and Kasumovic 2005; but see Anderson and Morse 2001), conditions that decrease the spread of pheromones will force males to search for longer than if pheromone gradients are clearly detectable (Bell and Cardé 1984). These conditions could include unfavorable wind speeds

or low temperatures because this not only leads to poorer airborne dispersion of pheromones (Bell and Cardé 1984) but also results in slower movement by males (Foelix 1982).

Our study, along with others (Vollrath 1980; Andrade 2003), suggests that male survival during mate search is very low in some web-building spiders and that phenotypic correlates have a weaker effect on success than do extrinsic factors. High mortality rates during mate searching have been previously proposed to 1) lead to decreased precopulatory competition between conspecifics leading to the evolution of the extreme sexual-size dimorphism (Vollrath and Parker 1992; Prenter et al. 1998; Prenter et al. 1999) and 2) cause a female-biased sex ratio and thus decrease the risk of sperm competition and the likelihood of investment in paternity-protection mechanisms (e.g., Fromhage et al. 2005). However, here we found that, despite high mortality rates, the presence of rivals on a female's web did not seem to discourage settlement by newly arriving males, and multiple males commonly cohabit with females. A male-biased sex ratio on individual female's webs can occur if there is an overall male-biased sex ratio after mate searching or if a proportion of females do not attract males due to their location and, therefore, remain unmated (as in our field enclosure). Thus, high mortality rates will not necessarily relax selection on male traits for combat or sperm competition because the local operational sex ratio can still be male-biased (e.g., Foellmer and Fairbairn 2005a). Our study shows how male choosiness can have significant effects on the dynamics of systems with risky mate searching (e.g., Bonduriansky 2001; Foellmer and Fairbairn 2005a; Fromhage et al. 2005) and highlights the difficulty in establishing the direction of causality when examining links between mate search mortality and male mating strategies.

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