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Bad tenants: female sheet-web spiders, *Cambridgea foliata* (Araneae: Desidae), lose feeding opportunities when cohabiting with males

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Abstract. In web-building spiders, females are often too widely distributed across the landscape for males to monopolize more than one mate. Consequently, males seek females one at a time and may cohabit with females in their webs. Pre-copulatory cohabitation is most common in araneomorphs, which suggests that the first male to mate with a female will have a greater share of paternity than any subsequent mates (first sperm precedence). However, pairs of adult New Zealand sheet-web spiders (*Cambridgea foliata* (L. Koch, 1872); Desidae) cohabit for longer than required to achieve copulation. This is counter-intuitive as it suggests that males defend females they have already copulated with, in lieu of seeking additional mating opportunities. To investigate the costs and benefits of extended cohabitation on male and female *C. foliata,* we conducted surveys of webs of solitary and paired males and females. We found that solitary spiders of both sexes consistently position themselves in the center of their webs but that when in pairs, females are displaced from the webs by males and will frequently leave the web altogether. Males in pairs would respond to vibrations simulating prey, while females would not respond. This strongly suggests that extended cohabitation should be costly for females. By contrast, for males, cohabitation is a valuable foraging strategy which, combined with the advantages of mate-guarding, may compensate for any lost mating opportunities due to foregoing searching for further mates.

Keywords: Mate-guarding, sperm competition, behavior, spider, New Zealand

Males regularly compete to ensure both mating success and the likelihood that their sperm will be used by females to fertilize their eggs (Parker 1970). This competition can manifest in a variety of ways, including defense of mates or resources, and scramble competition. In the former, males compete through agonistic contests or displays to defend spatially clustered females or resources important to females (Emlen & Oring 1977; Thornhill & Alcock 1983). In the latter, if females are widely distributed or are only available for a limited time, defense is not economical so males scramble to mate with as many females as possible. This seems to be a relatively common mating system among spiders (e.g., desert spiders, *Stegodyphus lineatus* (Latreille, 1817), (Berger-Tal & Lubin 2011); redback spiders, *Latrodectus hasselti* Thorell, 1870 (Kasumovic & Andrade 2009); bowl and doily spiders, *Frontinella pyramitela* (Walckenaer, 1841) (Austad 1984); golden orb spiders, *Nephila plumipes* (Latreille, 1804) (Kasumovic et al. 2007)).

However, while it is advantageous for male spiders to mate multiply over their life time, brief periods of cohabitation, a form of mate-guarding, are not uncommon. In spiders, mate-guarding males will share nesting chambers (e.g., jumping spider *Bavia aericeps* Simon, 1877) or webs (e.g., *Inola subtilis* Davies, 1982), or remain on secondary structures of the females' webs (e.g., *Araneus anatipes* (Keyserling, 1887) reviewed in Jackson 1986). Male spiders predominantly cohabit with subadult females with records for 161 species in which adult male araneomorphs cohabit with conspecific juvenile females (Jackson 1986). In these cases, males often mature earlier than females, find a female one or two molts from maturity and remain with her until she matures.

This predominance of males cohabiting with subadult females is logical, provided that the first male to mate with a female receives some advantage over subsequent males. If that male alone mates with the female and she oviposits shortly after or becomes unreceptive, then he will secure 100% paternity for her clutch. However, while cohabitation with subadults is more common, post-copulatory cohabitation with adults does occur, even at the cost of additional mating opportunities (Parker 1974). Alcock (1994) identifies several alternative hypotheses to explain the evolution of prolonged male-female associations following copulation. Mate-guarding may prevent females from accepting additional copulations (Thornhill 1984) or favoring the ejaculates of subsequent males (Eberhard 1991). In species that exhibit "last sperm precedence" in which subsequent mates receive a greater share of paternity, it is valuable for males to guard their mates (Austad 1984) in some cases until oviposition (e.g., cellar spiders, *Pholcus phalangioides* (Fuesslin, 1775), Schaefer & Uhl 2003) or until females enter a refractory period during which they are unreceptive to further mating (e.g., marbled cellar spiders, *Holocnemus pluchei* (Scopoli, 1763), Calbacho-Rosa et al. 2010).

Males may also associate for longer in order to mate multiply and increase their share of paternity (Simmons 2001). For example, male leaf-curling spiders (*Phonognatha graeffei* (Keyserling, 1865)) improve fertilization success through multiple, prolonged copulations and for this reason cohabit with adult females for several days (Fahey & Elgar 1997). While only a short period of pre-copulatory cohabitation may be needed to ensure a single copulation, longer periods of cohabitation may maximize fertilization success for the male.

Nevertheless, cohabitation should be costly to males as they forgo seeking additional mates (Birkhead & Moller 1992; Fryer et al 1999; Harts & Kokko 2013). However, these "costs" assume not only that there are a large number of receptive females available elsewhere but also that, if they should locate additional mates, males would not meet any resistance from other guarding males (Harts & Kokko 2013). Furthermore, remaining in a female's web may provide additional benefits not directly related to reproduction, such as safety. Austad (1984) remarks that post-copulatory mate-guarding should only be advantageous if moving between webs, and finding a newly molted female is risky. This risk of travelling has been demonstrated in several spider species in which less than a quarter of males observed in a female's web are likely to be found again in the web of another female (e.g., golden orb web spider, *Nephila clavipes* (Linnaeus, 1767), Christenson & Goist 1979; bowl and doily spider, *Frontinella pyramitela*, Austad 1984; redback spider *Latrodectus hasselti,* Andrade 2003). Predation by other invertebrates is likely to be greatest source of mortality (Andrade 2003). Consequently, it can be advantageous for males to maximize their reproductive output with a resident female before rather than risk searching for another.

Cohabitation may also provide males with greater feeding opportunities. Suter & Walberer (1989) found that male bowl and doily spiders (*Frontinella pyramitela*) feed on prey caught in female's webs and suggest that this could be why cohabitation can go on for several days, far longer than is necessary for only courtship and copulation. They suggest that this may compel the female to eventually expel her tenant. Furthermore, Erez et al. (2005) demonstrated clear benefits of cohabitation for males at the expense of resident female desert spiders, *Stegodyphus lineatus*. When they provided food to webs containing cohabiting pairs, the males gained in condition while females did not. In species that depend on capture webs to feed, foraging in a resident female's web is an ideal way for a male to prepare for searching for his next mate (Austad 1983). Apart from these studies, there are no other examples that we are aware of which test whether males gain feeding benefits while cohabiting on female webs.

Cambridgea foliata (L. Koch, 1872) (Desidae) are arboreal spiders distributed throughout the North Island of New Zealand. They are nocturnal and build three-dimensional sheet-webs in native forest which males and females can be seen sharing. The webs consist of a non-sticky, thick horizontal mainsheet anchored from below, with many knock-down threads above the mainsheet. The spiders run along the underside of the mainsheet. The rear of the web tapers into a silken tunnel or "retreat" which may extend under the bark of trees or into vacated burrows; the spider resides in the retreat during the day. During the summer, males mature in their natal webs before leaving to wander in search of female webs. Once a male finds a female's web, he may cohabit with her. McCambridge (2017) found that *C. foliata* will cohabit for between one day to about 14 days, with a small number of males cohabiting with subadult females for more than 20 days. Based on the author's data and our own observations, we expect that one to two days is the most common duration for cohabitation. During this time, the cohabiting male defends the female's web by engaging in ritualized fights with intruding males (pers. obs). When males fight in a female's web, we have often observed the resident female departing the mainsheet and sitting either on one of the anchoring threads or off the web entirely. This suggests that one male's presence in females' webs, or a succession of cohabiting males, may entail some foraging cost to females. However, we have not observed any instances of sexual cannibalism or fighting between males and females, which are similar in size.

Courtship and mating behaviors have not been observed in this species. However, as most spiders take only a few minutes to copulate (Fahey & Elgar 1997), it is reasonable, barring the use of mating plugs or genital mutilation (reviewed in Huber 2005), to expect that cohabiting pairs have the opportunity to mate more than once. Males often cohabit with juvenile females— which is consistent with the predictions of Austad (1984) for cases of first sperm precedence—but males have also been observed cohabiting with adults. As *C. foliata* are entelegyne spiders with "conduit" or "one-way" type copulatory ducts, we may expect them to exhibit first sperm precedence. However invertebrate copulatory and fertilization duct morphology is highly variable, which can generate significant variation in the strength of first or last sperm precedence (Uhl 2000). For this reason, we do not assume whether this species exhibits first or last sperm precedence.

Given that male *C. foliata* cohabit with females for longer than required for a single copulation, in the present study we aim to assess the impact of males cohabiting with females by (1) comparing positions of male and female spiders on their webs when alone and when cohabiting, and (2) comparing responses of males and females to simulated prey. If we assume that the probability of prey landing is approximately equal at all points on the mainsheet, then the center of the mainsheet (which we call the "hub") should be the optimal location for the spider to sit, as it is approximately equidistant to all edges of the web and to the retreat where these spiders hide if disturbed. For this reason, we predict males and females will most commonly position themselves in the hub when alone. When in pairs, we expect that both sexes will spend less time in the hub compared to when alone but that males will spend more time in the hub than females, as the mainsheet serves as the arena on which males fight each other. Due to males and females sharing the web when in pairs, we expect that both will be less likely to approach a simulated prey item compared to when alone. Another objective is to describe courtship interactions on females' webs, which have not been described before and may be useful for understanding mate-guarding in this species.

METHODS

Courtship observations.—In addition to making observations of male-female interactions in the field, we collected juvenile *C. foliata* for a lab population which included females with a known reproductive history. Each spider was housed in a 30 × 30 × 60.1 cm mesh enclosure. A wooden retreat was attached to the upper rear corner of the enclosure. We modelled these on wētā enclosures devised by Bowie et al. (2006). They consist of a (45 × 45 × 150 mm) block of untreated wood with a furrow (18 × 18 mm) cut two-thirds the length of the block, which was placed against the mesh wall. A black polyethylene flap was attached to the outside of the cage, covering the retreat. We fed the spiders every two days on a mixture of meal worms (*Tenebrio moliter*), blow flies (*Lucilia sericata*) and locusts (*Locusta migratoria*). Spiders were misted with water three times a day.

By the time females reached maturation their webs were dense enough to support multiple spiders. To observe courtship interactions, we introduced a random unmated male to a random female's web and recorded subsequent behaviors for up to 3 hours.

Cohabitation surveying.—We surveyed *C. foliata* webs at night in Matuku Forest and Bird reserve in West Auckland (36° 51′ 48.3″S 174° 28′ 47.7″E). We observed webs on either side of the walking track across the 2015/2016 and 2016/2017 summer seasons. We could ensure that we did not observe the same individuals across the separate seasons as in 2015/2016 the spiders were subsequently collected for other research. Meanwhile in the 2016/2017 season, we ensured that we did not repeat observations of the same spiders by not visiting the same trees. We do not have data on the reproductive history of observed males and females.

When we found an adult spider in a web, we made a note of sex, location in the web and whether the spider was solitary or in a pair. The "locations" we included were: "retreat," meaning at the opening of the retreat or on the mainsheet immediately outside the retreat; "hub," referring to the approximate center of the mainsheet; "web," referring to all remaining parts of the mainsheet; and "off," indicating that the spider was either on the knock-down threads, on the guying threads or just off the mainsheet on the substrate within 10 cm of the web.

To examine whether spiders changed how they responded to a prey stimulus when in a pair compared to when alone, we provided an artificial stimulus simulating prey movement in the web. All surveys were conducted between 1 and 3 hours after sunset. In order to standardize the stimuli, we used a Wittner tuning fork with a pitch A440 (440 Hz). We had previously observed that *C. foliata* females consistently approach a vibrating tuning fork when it is touched to the mainsheet of the web, and will attempt to bite it before realizing that it is not a prey item. In the current study, we would strike the tuning fork and touch the tip lightly approximately 20 cm from spider's location. This controlled for differences in web size, which varied considerably (mean area = 3169.48 cm^2, SD = 1220.63).

We recorded whether the spider(s) approached, moved away from or did not respond to the stimulus. As most individuals either responded within 5 seconds of the stimulus being applied or did not respond for more than 30s or with additional applications of the stimulus, we did not record latency.

We surveyed the webs of 62 solitary females, 34 solitary males and 47 adult pairs. We collected response data for 35 solitary females, 22 solitary males and 23 pairs. When analyzing spider locations and responses, we excluded 11/62 of the webs with solitary females, 3/34 webs with solitary males and 5/47 webs with pairs because spiders were feeding. We kept these data separate to our other location data as a prey item falling into the web would draw one or both spiders away from their original location and therefore would not be representative of the "preferred" location.

Statistics.—We conducted a χ^2 test for homogeneity of variance on contingency tables for female locations depending on whether they were alone or in a pair. When tabulating responses to the stimulus, our expected count values for our contingency tables violated the assumptions for a χ^2 test of homogeneity. In the vast majority of responses, the spider either approached or did not respond; very few moved away from the stimulus. Thus, we pooled negative responses and no response together. The resulting contingency table for whether females approached the stimulus (with binary responses of yes or no) did not violate the assumptions for a χ^2 test.

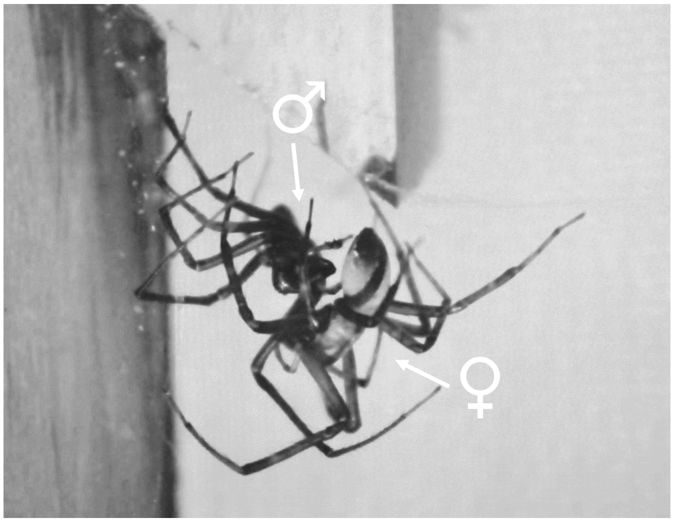

Figure 1.—Male and female *Cambridgea foliata* in copulatory posture.

We calculated odds ratios for the probability that females would take up certain positions when in pairs compared to when alone, and for the probability that they would approach a stimulus as opposed to move away or not respond. We conducted these same tests for males. All analyses were conducted in R version 3.2.0. (R core team 2015).

RESULTS

Courtship.—We observed 10 instances of courtship by the male. Of these observations, 6 males entered a copulatory posture. When males first enter webs occupied by females, they may shake the web using their whole body. The female orients towards him and, soon after, approaches him. She touches him with her forelegs and then may retreat a short distance in the direction of the retreat. The male may continue to interact with the female or move past her and enter the retreat. The interactions we observed lasted for an average of 93.8s (SD = 168.3s). In one case, a male courted a female for 615s.

Often at the entrance of the retreat, the male shakes the web and dorso-ventrally flexes his abdomen. If the female approaches, he will drum on the web with his first and second pairs of legs. The female may angle her cephalothorax away from the web allowing the male to approach and place one palp over her epigyne (Fig. 1). The pairs which we observed remained in this copulatory posture for 382.8s (SD = 212.5). While the male's palp was placed over her epigyne at all times, the male's palp was never charged with sperm, meaning that sperm transfer could not have been occurring. Males also only ever used one palp. When the male moved out of this posture, he would either remain on the web a short distance from the female or return to the retreat.

Cohabitation.—We observed males cohabiting with both adult and subadult females and, in one case, we found an adult male sharing a web with a subadult male. We never observed

Table 1.—Positions of female *C. foliata* on webs.

Location	Solitary	Pair	Total
Hub	28	8	36
Retreat	4	13	17
Web	19	5	24
Off	0	16	16
Total	51	42	93

Table 2.—Positions of male *C. foliata* on webs

Location	Solitary	Pair	Total
Hub	16	20	36
Retreat	5	12	17
Web	10	10	20
Off	0	0	0
Total	31	42	73

copulation. When surveying for solitary males, we sometimes found individuals on webs produced by heterospecifics (e.g., *Badumna* sp. Thorell, 1890).

In addition to sharing webs during the night, males and females can frequently be found sharing retreats during the day. As adult males wander, we expect that these webs and retreats belong to the female. We observed that in the morning when the pair return to the retreat, the male will usually enter the retreat first with the female following (pers. obs.). Similarly, if the pair are disturbed during the night, the male will enter the retreat first regardless of whether he or the female is closer to it.

Beyond occasional observations from other research of marked males appearing in different females' webs over sequential nights, we do not have data to show how many females a *C. foliata* male may encounter in his lifetime. However, McCambridge (2017, pers. comm.) marked and recaptured 3/26 adult male *Cambridgea plagiata* Forster & Wilton, 1973 after 29, 43 and 49 days. While we cannot extrapolate these findings to the survival rate of males in general, these males should have encountered at least two females' webs.

Preference for location.—When alone, males and females demonstrated very similar preferences for different locations in the web. Solitary females were most often found in the hub of the web or near the retreat (Tables 1, 2). Similarly, solitary males were most often found in the hub or at the retreat (Fig. 2). Indeed, the hub was the most frequented location for spiders alone in the web, regardless of sex. The second most common location for the spiders was off center from the hub but more than 10cm from the edge of the web. When we observed spiders feeding (both in pairs and alone), they were similarly found in or near the hub.

Male distribution did not change significantly when in a pair compared to when alone (χ^2= 1.708, df = 2, $P = 0.426$). Males in pairs were still most often found at the hub, although they were more likely to be found at the retreat compared to solitary males (odds ratio, OR = 1.77). By contrast, we found that females in pairs placed themselves differently on the web compared to lone females (χ^2= 40.109, df = 2, $P < 0.0001$). Females in pairs were less likely to be in the hub or elsewhere on the mainsheet (OR = 0.346, 0.320 respectively). They were 3.95 times more likely to be at the retreat. However, the largest share of females in pairs (38.1%) were found off the web entirely. They were sometimes found on the knock down threads, but most frequently on the guying threads. They were never seen off the web when alone, making it impossible to calculate a meaningful odds ratio.

Responses to stimulus.—When alone, the majority of males and females approached a vibratory stimulus (Fig. 3, Tables 3, 4). However, while solitary females almost always approached, males sometimes moved away or did not respond. For cohabiting females, we found significant evidence that the presence of a male in the web affected the likelihood of approaching a stimulus (χ^2 = 42.437, df = 1, $P = <0.0001$). Females in pairs were 31.96 times more likely not to respond or to move away from the vibratory stimulus, with 20/23 females in pairs not responding to the stimulus at all compared to only 1/35 of solitary females. Of the 20 paired females which did not respond, 10/20 were on the mainsheet (retreat, mainsheet or hub) while 10/20 were off the web (guying threads, knockdown threads, off entirely). This suggests that

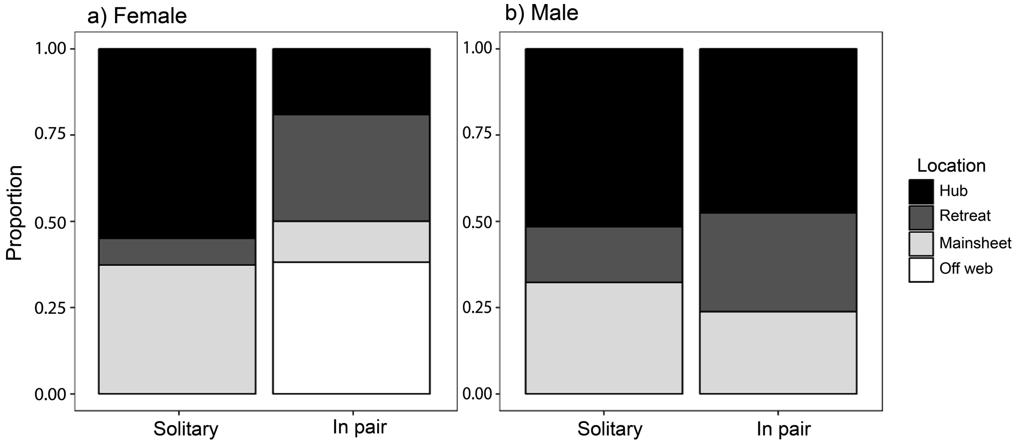

Figure 2.—Proportion of webs in which (a) females and (b) males were found in the hub, retreat, mainsheet (web) or off the web depending on whether the spider was alone or in a pair.

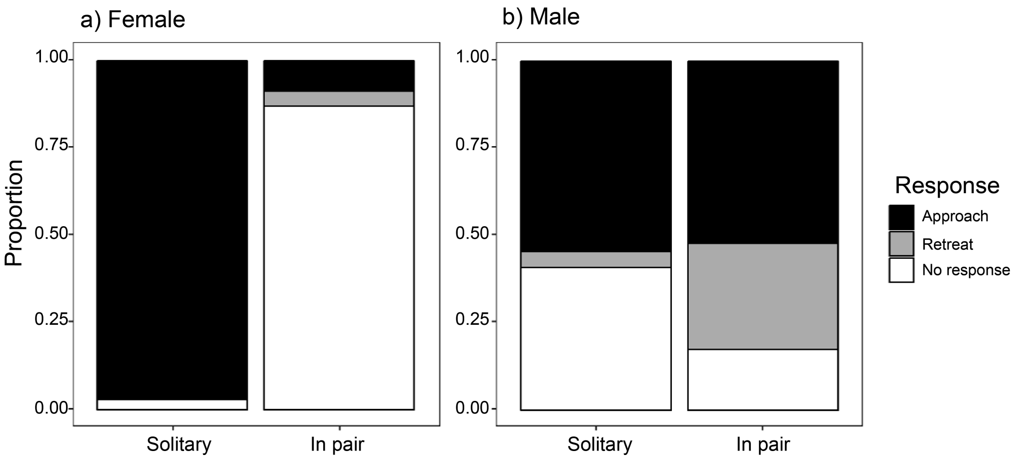

Figure 3.—Proportion of webs in which (a) females and (b) males approached, moved away from or did not respond to the artificial prey stimulus depending on whether they were alone or in a pair.

even females who are still in contact with the main web (and able to feel the vibration) did not respond to the stimulus.

There was also no evidence that males were more likely to approach a stimulus when sharing a web compared to when alone (OR $= 0.957$; $\chi^2 = 0$, df $= 1$, $P = 1$).

Feeding behavior.—We observed 19 instances of spiders feeding. In total, spiders were most often observed feeding in the hub closely followed by elsewhere on the mainsheet (Table 5). We observed one solitary female feeding on the knockdown threads. Within the cohabiting pairs we observed, we only saw males feeding.

DISCUSSION

While *C. foliata* of both sexes most frequently placed themselves in the hub of their web and approached prey when alone, male and female behavior diverged significantly when cohabiting. When in a pair, males were still found most frequently in the hub and still approached a stimulus mimicking prey. By contrast, females were often off the web entirely and almost never approached our stimulus. Cumulatively, this suggests that cohabitation is disadvantageous for females but advantageous for males.

The *C. foliata* mating system is best described as "prolonged searching polygyny" (Herberstein et al. 2017). It is advantageous for males to find unmated females rapidly and males depart webs in search of other webs. However, at each female's web, males may invest significant time into cohabiting. The hub of the web is equidistant from all edges of the sheet and the retreat, suggesting that it is probably the location which minimizes distance to both prey and to safety. It is unsurprising, then, that we predominantly found solitary females and males in the hub of the web.

However, while males in pairs largely continued to place themselves in the hub when cohabiting, a large proportion of females in pairs were found off the mainsheet entirely. In this way, it is unsurprising that so few females responded to vibrational signals given that they were less likely to detect the vibrations or be in a position to rapidly take prey. However, even females that remained on the mainsheet in the presence of a male were less likely to approach the stimulus compared to when alone. In this way, females that cohabit with males for an extended period or with a series of males almost certainly forgo most, if not all, foraging opportunities. Given that when we observed pairs, we only saw males feeding, it is reasonable to expect that if cohabitation were prolonged, male condition would improve at the expense of female condition, as has been found in desert spiders (*Stegodyphus lineatus*; Erez et al. 2005).

An extended period of cohabitation would also be particularly advantageous for males if travelling between females' webs were risky (Austad 1984). In other spider species, there is a high mortality rate for males travelling in search of females, most likely as a result of predation (e.g., Christenson & Goist 1979; Andrade 2003; Berger-Tal & Lubin 2011). It would be worth investigating whether this is also true for *C. foliata*.

At least, the value of webs as a source of food is apparent in how males take advantage of abandoned webs which, naturally, provide no reproductive opportunities. We sometimes observed males in webs previously inhabited by females who had disappeared after storms. We even observed one male living on a web built by a house spider (*Badumna* sp.) suggesting that males can be truly opportunistic about finding refuges while roaming. We expect that the majority of solitary males we found were inhabiting webs built by spiders other

Table 3.—Female responses to simulated prey.

Response	Solitary	Pair	Total
Approach	34	2	36
Move away	0	1	1
No response	1	20	21
	35	23	58

Table 4.—Male responses to simulated prey.

Response	Solitary	Pair	Total
Approach	12	12	24
Move away	1	7	8
No response	9	4	13
	22	23	45

Table 5.—Number of spiders observed feeding in different web localities.

	Solitary		Paired		
Location	Male	Female	Male	Female	Total
Web	2	4	1	0	7
Hub	1	5	2	0	8
Retreat	0	1	2	0	3
Off	0	1	0	0	1

than themselves, given that the adult males we kept in the lab did not build webs. This cumulatively suggests that the most important advantages of cohabiting may be directed towards male survival.

Our primary limitation to fully understanding the benefits of cohabiting is that we do not yet know how often cohabiting pairs copulate. While we observed males placing only one palp over the female's epigyne during courtship, our males never charged their palps with sperm prior to this and we never observed copulation in the cohabiting pairs we found in the field. Based on our behavioral observations, we expect that courtship and copulation should occur at least once more, after the male has charged his palps with sperm, if not on the web during the night then in the retreat during the day. If a single copulation does not ensure paternity then guarding is essential to ensure male fertilization success which would make sperm competition the primary benefit of guarding rather than safety and/or foraging opportunities.

Furthermore, as we do not know the sperm precedence patterns for this species, it is difficult to estimate to what extent cohabitation reduces sperm competition. It is possible that if females re-mate, subsequent males may gain a proportion of paternity, making mate-guarding an adaptive strategy. *Cambridge foliata* are entelegyne spiders, generally thought to have first sperm priority, which should lessen the value of post-copulatory cohabitation (Austad 1984). However, it has been demonstrated in other entelegyne spiders that the second male may gain between a 5% share of paternity (*Frontinella pyramitela*; Austad 1982) to near parity (46% in *Nephila plumipes*; Schneider & Elgar 2001) or even the majority (66% in *Nephila edulis*; Schneider et al. 2000). Regardless, even if re-mating by the female merely reduces the first male's share of paternity, a male will benefit from mate-guarding, particularly if there are additional benefits to remaining with the same mate.

Extended cohabitation with adult females is a relatively uncommon form of mate- guarding in spiders, and cohabitation beyond the time required for copulation seems particularly uncommon. Furthermore, in New Zealand sheet-web spiders, cohabitation seems particularly costly to the female, who frequently leaves the mainsheet of her web when in pairs and most likely loses foraging opportunities as a consequence. By contrast, cohabitation has the potential to be highly beneficial for males. First, it helps males to control mating by allowing multiple copulations and preventing re-mating by the female. Second, it provides males with feeding opportunities and likely keeps males safe from heterospecific predators which they may meet when searching. Determining when copulation occurs, how frequently it occurs and how sperm competition manifests when females mate multiply is critical to understanding the value of cohabitation in comparison to searching for additional mating opportunities in this species. However, male and female behavior on webs when in pairs compared to when alone provides an explanation as to why males frequently cohabit following copulation rather than continue searching for additional mates.

LITERATURE CITED

Alcock, J. 1994. Postinsemination associations between males and females in insects: The mate-guarding hypothesis. Annual Review of Entomology 39:1–21.

Andrade, M.C.B. 2003. Risky mate search and male self-sacrifice in redback spiders. Behavioral Ecology 14:531–538. Online at https://doi.org/10.1093/beheco/arg015

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

Austad, S.N. 1983. A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). Animal Behaviour 31:59–73.

Austad, S.N. 1984. Evolution of sperm priority patterns in spiders. Pp. 223–249. *In* Sperm Competition and the Evolution of Animal Mating Systems (R.L. Smith, ed.). Academic Press, London.

Berger-Tal, R. & Y. Lubin. 2011. High male mate search costs and a female-biased sex ratio shape the male mating strategy in a desert spider. Animal Behaviour 82:853–859.

Birkhead, T.R. & A.P. Möller. 1992. Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press, London.

Bowie, M.H., S. Hodge, J.C. Banks & C.J. Vink. 2006. An appraisal of simple tree-mounted shelters for non-lethal monitoring of weta (Orthoptera: Anostostomatidae and Rhaphidophoridae) in New Zealand nature reserves. Journal of Insect Conservation 10:261–268.

Calbacho-Rosa, L., A. Córdoba-Aguilar & A.V. Peretti. 2010. Occurrence and duration of post-copulatory mate guarding in a spider with last sperm precedence. Behaviour 147:1267–1283.

Christenson, T.E. & K.C. Goist. 1979. Costs and benefits of male-male competition in the orb weaving spider, *Nephila clavipes*. Behavioral Ecology and Sociobiology 5:87–92.

Eberhard, W.G. 1991. Copulatory courtship and cryptic female choice in insects. Biological Reviews 66:1–31.

Emlen, S.T. & L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Erez, T., J.M. Schneider & Y. Lubin. 2005. Is male cohabitation costly for females of the spider *Stegodyphus lineatus* (Eresidae)? Ethology 111:693–704.

Fahey, B. F. & M.A. Elgar. 1997. Sexual cohabitation as mate-guarding in the leaf-curling spider *Phonognatha graeffei keyserling* (Araneoidea, Araneae). Behavioral Ecology and Sociobiology 40:127–133.

Fryer, T., C. Cannings & G.T. Vickers. 1999. Sperm competition. II. Post copulatory guarding. Journal of Theoretical Biology 197:343–360.

Harts, A.M.F. & H. Kokko. 2013. Understanding promiscuity: when is seeking additional mates better than guarding an already found one? Evolution 67: 2838–2848.

Herberstein, M.E., C.J. Painting & G.I. Holwell. 2017. Scramble competition polygyny in terrestrial arthropods. Advances in the Study of Behavior 49:237–295.

Huber, B.A. 2005. Sexual selection research on spiders: Progress and biases. Biological Reviews of the Cambridge Philosophical Society 80:363–385.

Jackson, R.R. 1986. Cohabitation of males and juvenile females: a prevalent mating tactic of spiders. Journal of Natural History 20:1193–1210.

Kasumovic, M.M. & M.C.B. Andrade. 2009. A change in competitive context reverses sexual selection on male size. Journal of Evolutionary Biology 22:324–333.

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

McCambridge, J.E. 2017. Male contest dynamics in New Zealand sheetweb spiders (*Cambridge plagiata*) (Master's thesis, The University of Auckland). Retrieved from http://hdl.handle.net/2292/34087

Parker, G.A. 1970. Sperm competition and its evolutionary consequences in the insects. Biological Reviews 45:525–567.

Parker, G.A. 1974. Courtship persistence and female-guarding as male time investment strategies. Behaviour 48:157–183.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online at http://www.R-project.org/

Schaefer, D. & G. Uhl. 2003. Male competition over access to females in a spider with last-male sperm precedence. Ethology 109:385–400.

Schneider, J.M. & 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.

Schneider, J.M., M.E. Herberstein, F.C. De Crespigny, S. Ramamurthy & M.A. Elgar. 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. Journal of Evolutionary Biology 13:939–946.

Simmons, L.W. 2001. Sperm Competition and its Evolutionary Consequences in the Insects. Princeton University Press, Princeton, N.J.

Suter, R.B. & L. Walberer. 1989. Enigmatic cohabitation in bowl and doily spiders, *Frontinella pyramitela* (Araneae, Linyphiidae). Animal Behaviour 37:402–409.

Thornhill, R. 1984. Alternative hypotheses for traits believed to have evolved by sperm competition. Pp. 371–426. *In* Sperm Competition and the Evolution of Animal Mating Systems. (R.L. Smith, ed.). Academic Press, London.

Thornhill, R. & J. Alcock. 1983. The Evolution of Insect Mating Systems. Harvard University Press, Cambridge, Massachusetts.

Uhl, G. 2000. Female genital morphology and sperm priority patterns in spiders (Araneae). Pp. 145–156. *In* Proceedings of the 19th European Colloquium of Arachnology, Aarhus, Denmark.

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