

Cannibalism as a factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae)

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Summary

Males of the salticid spider *Phidippus johnsoni* (Peckham & Peckham) encounter females differing in location (inside or outside nests) and maturity (adult or subadult) and use different tactics to pursue each type of female. In the laboratory, predation by adult females upon courting males was more frequent with adult females outside rather than inside nests, and it never occurred when males cohabited with subadult females and mated with them when they matured. These data were consistent with the hypothesis that reduced risk of cannibalism has been a factor in the evolution of nest-related mating tactics in this species. However, the rarity of observations of cannibalism in the laboratory and in nature suggested that other factors have been more important, despite the great importance traditionally placed on cannibalism in discussions of mating in spiders. Starving females for 25-31 days did not greatly increase the frequency of cannibalism.

Introduction

In discussions of the courtship and mating of spiders, cannibalism (defined as intraspecific predation) has repeatedly been given major importance, either explicitly or implicitly (reviewed in Jackson, 1979a). One of the most important questions concerning spiders is whether the major function of male courtship behaviour in this group is reduction of the probability that females will prey upon males. How frequently cannibalism occurs is a related but distinct question. The popular myth that female spiders usually devour the males either during courtship or

after copulation has been disputed repeatedly (e.g. Bristowe, 1958; Kaston, 1948; Nielsen, 1932; Savory, 1928; Turnbull, 1973). However, exactly how important cannibalism by females is in the mating behaviour of spiders remains unclear; and the answer probably varies considerably from species to species (e.g. see Gerhardt & Kaestner, 1937; Peckham & Peckham, 1889). Data are clearly needed concerning these issues. In this paper I will present data concerning the incidence of cannibalism in a common salticid from North America, *Phidippus johnsoni* (Peckham & Peckham); and a particular hypothesis will be considered.

Male *P. johnsoni* encounter females differing in location (inside or outside nests) and maturity (adult or subadult) and use different tactics to pursue each type of female (Jackson, 1977).

- (1) If the female is an adult outside her nest, the male performs vision-dependent displays (type 1 courtship) consisting of gesturing movements with his forelegs, dancing, etc.
- (2) If the female is an adult inside her nest, the male performs type 2 courtship, consisting of various tugging, probing and vibrating movements made on the silk of the nest and not dependent on vision.
- (3) If the female is a subadult inside her nest, the male performs type 2 courtship; then he spins a second chamber on the female's nest and cohabits until she moults (matures).

A "subadult" is defined as a spider that will mature at its next moult. Unless qualified, "male" and "female" refer to mature spiders.

Nests (retreats) consist of sheets of silk enclosing a hollow interior, usually with two doors. A door is an elastic opening through which the spider enters and departs. Generally, spiders remain inside their nests during periods of inactivity, such as at night, and at times of moulting and oviposition; and after type 2 courtship, copulation takes place inside the nests.

In this paper I will discuss data concerning the relative importance of cannibalism as a selection pressure acting on the mating strategy of males of *P. johnsoni*. Also, I will consider the question of whether males are subject to greater risks of cannibalism when courting females outside rather than inside their nests. This hypothesis seemed reasonable since the predatory behaviour of salticids is evidently

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directed entirely by visual stimuli (Drees, 1952; Forster, 1977), nests are generally built in rather dark locations (Jackson, 1979b), and salticids usually leave their nests at times when they are most prone to be predatory (Plett, 1962).

Cannibalism was observed only three times in nature (Jackson, 1978a). Since in each case I failed to see the predatory attack, I cannot say whether mating and/or courtship preceded the act of cannibalism. This distinction is important. Cases in which the female attacks a male before courtship represent a component of his risks during searching. This type of cannibalism would not seem to present a selection pressure especially different from other types of predation that might befall a searching male. On the other hand, attacks by the female while the male courts are qualitatively different because they constitute risks emanating from the object being pursued; and they might constitute a selection pressure influencing whether, how, and for how long a given type of female will be pursued.

Further data were collected during studies in the laboratory (Jackson, 1978b, c, 1980a). The following were excluded from Table 1: interactions during which there was vegetation present, those taking place under red light (Jackson, 1977), and those during which the females were already feeding on either flies or conspecific males killed during earlier interactions. Cannibalism did not occur in any of these, however. It is noteworthy that feeding did not prevent copulation, since 12 of 32 females accepted males while eating flies and 2 of 11 accepted males while feeding on males they had killed earlier.

P. johnsoni were maintained in the laboratory with continual access to food (Jackson, 1974), but spiders in nature may tend to be less well fed (Anderson, 1974; Miyashita, 1968). This suggested the hypothesis that hunger in the laboratory might be reduced to a point at which differences in the frequencies of cannibalism might not be distinct when comparing interactions in which nests were present with those in which they were absent. In an effort to elevate the frequency of cannibalism, 35 randomly selected post-reproductive females (ones that had ceased to oviposit fertile eggs) were kept without food for 25 to 31 days. Afterwards, each was presented with courting males.

Results

Frequencies with which cannibalism occurred

Data in rows 1-3 of Table 1 will be considered first. Females killed and fed upon males in fewer than 1% of the 1834 interactions. Females killed males during a smaller percentage of interactions inside (0.56%) compared with outside (1.08%) nests and not at all during cohabitation. Most cases of females injuring males without killing them occurred outside nests. Also, there was a decreasing percentage of individual females involved.

There were 14 cannibalistic females, one of which killed a male while occupying a nest and another when she was outside. Eleven killed a single male each, ten outside nests and one inside. Another two females each killed two males while outside their nests. Each case of injury without death involved a different female from those that killed males. Each female that killed or injured a male was also involved in other interactions, both inside and outside nests, during which death or injury of the male did not occur.

One starved female killed one male while outside her nest (1.75% of the interactions). A different female killed one male while she was inside her nest (1.33% of the interactions) (Table 1, rows 4-5).

Predation by females upon males was not the only form of cannibalism that occurred. Two males killed and fed upon females during interactions involving courtship outside nests (Table 1). Also, there were instances of cannibalism during other types of interactions: male-subadult, subadult inside nest (1 of 183 interactions); male-male, outside nest (1 of 60 interactions; Jackson, 1978b); male-male, outside nests, with females present (3 of 24 interactions; Jackson, 1980b).

Description of cannibalism

Several cases of cannibalism occurred during embracing, a common element of behaviour when individuals of *P. johnsoni* interact (Jackson, 1978b). Embracing spiders stand face-to-face with their forelegs extended 90° to the side and touching. Their faces may touch also. In each case when cannibalism occurred, one spider pushed the other backwards, positioned its chelicerae over the other individual's

carapace or the basal portion of a leg, and inserted its fangs. All cases of injury without death occurred during embracing when one spider grasped a leg I of the other with its fangs, but the grasped spider pulled free and ran away with its leg bleeding.

Male-female pairs, females outside nests

In six cases, when the displaying male turned away from the female and began to depart, he was leaped upon and killed. In another six cases, when the male walked past an inactive female, she turned towards him. The male immediately turned towards the female and began an erected-legs display; but the female quickly leaped and killed him. Another four males were killed during embracing, and one male killed a female during embracing. In another case, embracing occurred, after which the female suddenly turned 180° and began to run. The male instantly leaped and killed her.

Male-female pairs, females inside nests

In one case, the female departed from the nest after the male began nest-specific courtship, and an

interaction ensued involving courtship displays typical of outside nests. Eventually, the male turned away from the female and began to depart, but the female leaped and killed him. Thus, although this was a case of cannibalism involving a female initially inside her nest, the female was actually outside her nest when the predation occurred. Another two males were killed during embracing at the doors of the nests. Each female was partially inside the nest; the males were outside. It was of interest that in one of these cases, the male was continuing courtship after having mated with the female shortly before. In contrast, copulation did not take place in any other cases of cannibalism involving male-female pairs. The single case of injury without death with a female inside her nest happened during an embrace, with the spiders at the nest door (female partially inside nest, male outside).

Male-male and male-subadult pairs

Each case of cannibalism of one male upon another adult male occurred during embracing. Another male killed a subadult male that he encountered in a nest without embracing.

Type of Interaction	No. of interactions				No. of spiders				
	F Killed M	F Injured M	M Killed F	N	Killed M	Females Injured M	N	Males Killed F	N
Female outside nest	15	2	1	1390	13	2	266	1	210
Female inside nest	2	1	0	359	2	1	143	0	137
Cohabitation	0	0	0	85	0	0	85	0	85
Starved female outside nest	1	0	1	57	1	0	19	1	19
Starved female inside nest	1	0	0	75	1	0	23	0	21

Table 1: Observations of cannibalism during male-female interactions in the laboratory. Injured: Death did not occur. F: Female. M: Male. N: Number of interactions or number of spiders. Each spider involved in variable numbers of interactions. See text for details.

Discussion

Statistical tests on these data are of dubious value since the numbers of interactions involving different individual females varied. Also, some females were observed only outside nests, some only inside nests, and some both inside and outside nests. However, the data seem consistent with the hypothesis that females outside nests are more prone toward cannibalism than ones inside nests.

Although three males were killed after encountering females initially inside nests, the female was either completely or partially outside her nest at the moment when cannibalism actually took place. The illumination in the laboratory was much greater at the spiders' nests than would have been the case in the field, and this laboratory artifact may have obscured differences in the probability of cannibalism when females were inside instead of outside nests. It is noteworthy that there were no cases of injury or cannibalism during the twelve courtships and matings with females inside nests observed under red light.

Starvation did not greatly increase the frequency of cannibalism. Considering the fasting abilities of many spiders (Anderson, 1974; Savory, 1928), perhaps one month's fast did not have a substantial effect on predatory thresholds. Also, starvation might have had greater effects if females had been of some other reproductive state. For example, mated females before their first oviposition normally feed voraciously, and these might prove better subjects for experiments related to cannibalism.

The rarity of cannibalism in this study of *P. johnsoni* emphasises the need for caution when invoking the cannibalism reduction hypothesis for the ultimate causation of mating strategies in spiders. In various spiders in addition to *P. johnsoni*, males cohabit with subadult females and mate when they mature. Speculations concerning the functions of this behaviour have generally emphasised reduction of the male's risks of being killed by the female (Bristowe, 1941; Forster & Forster, 1973; Montgomery, 1908; Nielsen, 1932), and in some cases the female has been described as "helpless" when she mates after cohabitation. This portrayal warrants closer scrutiny. Although it might be appropriate for some species, it is questionable for *P. johnsoni*. Usually an hour or more elapses between the end of moulting and the

beginning of copulation in this species, and sometimes the female resists the male's efforts for a considerable time after he enters her chamber. When three females were removed from their nests about one hour after moulting and placed in the presence of courting males, they effectively resisted attempts by the males to copulate, indicating that females are not completely helpless after moulting. The possibility remains that a recently moulted female is weaker in some way which renders her less capable of injuring the male, but I am not aware of evidence related to this for any of the species reported to cohabit. In the case of *P. johnsoni*, my impression is that males are somewhat safer from the risk of cannibalism if they cohabit rather than pursue mature females, but the temptation to view the newly moulted female as helpless may exaggerate this difference and distract our attention from other factors.

The mating strategy of *P. johnsoni* seems to be the product of a number of different selection pressures, one of which may be cannibalism. However, this factor should not be overemphasised. Other factors which may be of greater relative importance include sperm competition, inter-male interference, and predators other than conspecific females (Jackson, 1976, 1980a, b).

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