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THE MATING STRATEGY OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE): III. INTERMALE AGGRESSION AND A COST-BENEFIT ANALYSIS

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ABSTRACT

Similarities between the mating strategy of the males of *Phidippus johnsoni* and models for optimal foraging are discussed. A predator encounters potential prey, each of which has an associated search time (S_i) and pursuit time (P_i) per net benefit. In principle, net benefit (benefits minus costs or risks) should be expressed in units of fitness. Males of *P. johnsoni* encounter females differing in location and maturity, each of which has an associated S_i and P_i. The numerators of P_i vary in the following order: adult female outside nest (ca. 2 min), adult inside nest (16 min), subadult inside nest (1 week). Denominators seem to follow the opposite trend. Considering fertility, sperm competition, cannibalism, predation, and male-male aggressive interactions, net benefit for males seems to be least if they pursue adult females outside nests, greater if they pursue adults inside nests, and greatest if they pursue subadults inside nests. The optimal type of female, the type with the smallest P_i, is probably a subadult inside her nest.

INTRODUCTION

There are certain similarities between the mating strategy of a salticid spider, *Phidippus johnsoni*, and models for the evolution of predatory strategies. In these models, a predator encounters different types of prey with which it may use different predatory tactics, and each type of prey requires differing search (S_i) and pursuit (P_i) times per unit net benefit. Males of *P. johnsoni* encounter different types of females which they pursue with distinctly different tactics: (1) adult females outside nests, type 1 courtship (pursuit time, P_o) (2) adult females inside nests, type 2 courtship (P_n) (3) subadult females inside nests, cohabitation (P_s). In an earlier paper, only the numerators of P_o, P_n, and P_s were considered (Jackson 1978a). The demoninators (net benefit) will be considered in this paper.

The benefit to the male from mating with a given female might be viewed as the number of progeny she will leave after copulation under conditions that are optimal for the male. Optimal conditions would include absence of other males that might copulate with the same female, etc. Using net instead of simple benefit as the denominator takes into account less than optimal conditions for the male.

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The benefit a male derives from a given copulation depends on the number of fertile eggs the female oviposits, the probability that she will not copulate with another male (fidelity), and the consequences of additional copulations if the female should mate again. Cost might be related to risks such as predation, cannibalism, and various types of physical interference. Data concerning these factors have been presented elsewhere (Jackson 1976a, b, 1980a). In this paper I will present data related to aggression, another potential factor affecting net benefit. This will be followed by a comparison of P_o, P_n, and P_s.

Aggression will be loosely defined as behavior directed toward causing physical harm to a conspecific individual (Hinde 1974). It is useful to exclude cannibalism from the definition in the present context.

Threat displays and ritualized fights were sometimes performed by all sex/age classes of *P. johnsoni*, but this type of behavior was most pronounced in adult males, occurring invariably when two males were placed together in the laboratory (Jackson 1977). If a male encounters another male that is courting or copulating with a female, the aggressive interaction which ensues either temporarily or permanently interrupts the first male's interaction with the female. I designed an experiment to compare the consequences of intermale interference when males pursued females inside and outside nests.

METHODS

Apparatus— Cages were the same as those used for recording cohabitation duration (Jackson 1978a) except that they had four instead of two entrances (Fig. 1). During maintenance, each entrance was plugged with a cork. During observations, plastic corridors were substituted for the corks in two of the entrances. Each corridor contained a narrow slit cut half-way through from the top. A stiff paper partition fit inside the slit, and it was shaped so as to fill the corridor and prevent passage by the spiders. During observations cages were connected by corridors to terraria, and each terrarium was filled with a meshwork of corrugated cardboard.

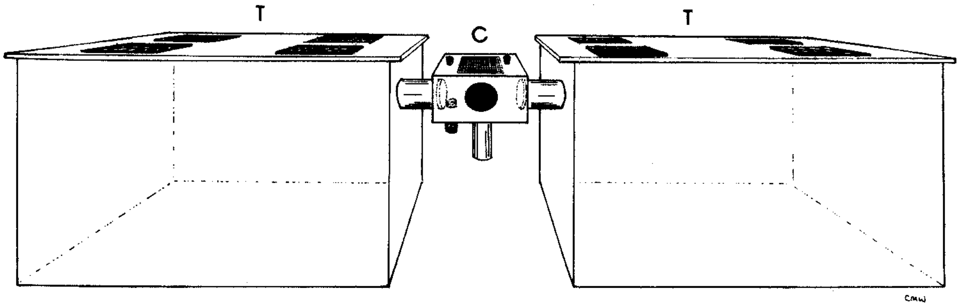

Fig. 1.—Apparatus for observing consequences of aggressive interactions (not to scale). C: Transparent plastic cage (10 x 10 x 6.5 cm) with 4 entrances (4.5-cm-diameter holes); 2 entrances plugged with corks (one shown: large blackened circle in front of diagram); 2 fitted with corridors (5-cm-long transparent tubes). Top of cage: two 1-cm-diameter holes plugged with corks (small black circles) and a 4.5-cm-diameter hole covered by metal screen for ventilation. Bottom of cage: glass vial containing sugar (food for flies) inserted through hole (1.5-cm-diameter, center of cage), moist cotton roll inserted through 1-cm-diameter hole (on left). T: Transparent plastic terrarium (56 x 53 x 30 cm). Lid (61 x 61 cm transparent plastic) with 4 holes covered by metal screen. Entrance on side accepts corridor from cage (top of entrance to lid: 5 cm). See text for details.

Table 1.–Consequences of intermale aggression in the presence of females. Each observation: one male (resident) courting or copulating with female when second male (intruder) begins interaction (intrusion). Females outside nests: Groups 1 and 2; inside: Groups 3 and 4. Intrusion while resident courted: Groups 1 and 3; copulated: Groups 2 and 4.

			MALE WITH WHICH FEMALE MATED AFTER INTRUSION		
Group	Female Inside Nest	Resident Already Copulating	Resident	Intruder	Neither
1	No	No	0	0	12
2	No	Yes	2	0	10
3	Yes	No	1	8	3
4	Yes	Yes	3	2	7

Procedure– Except for specific differences noted here, maintenance and testing procedures were as described previously (Jackson 1978a, 1980b). Females were maintained individually in the cages for 1 to 2 weeks previous to testing. Each built at least one nest, always partially fastened to one of the large corks in the entrances. To begin a test, two entrances were fitted with corridors. When a nest was required for the test, the pair of entrances was chosen so as not to damage the nest occupied by the female; when not required, all were destroyed before the corridors were connected.

Virgin females were assigned to 4 groups (Table 1). To begin a test, first one male ("resident") was introduced into the female's cage through one of the small cork holes at the top of the cage. A second male ("intruder") was introduced either while the first male copulated (Groups 2 and 4) or while he courted the virgin female (Groups 1 and 3). The female was either outside (Groups 1 and 2) or inside (Groups 3 and 4) the nest when the intruding male encountered the resident male-female pair. Using enamel paint, each male was marked with an identifying color combination (see Jackson 1979).

When the intruding male encountered the male-female pair, the partitions were removed from the corridors, providing the spiders with access to the terraria. Observation was continued until 15 min after the last interaction between any 2 of the spiders. The terraria provided space to which the spiders could escape from each other after interaction, and the corrugated cardboard increased surface area and provided shelters for hiding.

Statistical tests are from Sokal and Rohlf (1969). Data are given as means ± S.D.

RESULTS

When encountering another male that was courting a female, the intruding male began by courting the female (female outside nest, 4 cases; inside, 7) or by threatening the male (outside, 8; inside 5). Usually the resident males reciprocated almost immediately when the pair was outside the nest with threat displays. With the female inside her nest, the two males generally alternated between interacting with each other and courting the female from opposite ends of the nest.

The initial responses of males encountering mating pairs was to court. Sixteen (11 outside, 5 inside) mounted the mating pairs and walked, tapped, scraped, and stroked (postmount courtship; Jackson 1977) on both the female and the male; and in eight cases (5, outside; 3, inside) the males embraced and pushed each other while standing on the female.

Almost all females that were outside their nests (Groups 1 and 2) decamped and entered one of the terraria while the two males interacted. The exceptions were two cases in which the intruder mounted and the males embraced and pushed, after which the intruder decamped; and the resident male renewed copulation without having dismounted.

Considering cases in which intruding males encountered courting male-female pairs (Groups 1 and 3), copulation more frequently followed male-male interactions when females were initially inside rather than outside nests ($\chi^2 = 11.368$, $P < 0.001$). (When the male-female pairs were already copulating before the intrusions, these frequencies were not significantly different.)

When nests were present, all copulations except one transpired inside nests. The exception was a female in Group 4 that departed her nest after the intrusion. She remained in the cage and mated outside her nest with the intruder after the aggressive encounter between the males ended.

A distinct winner and loser could be distinguished after each male-male interaction. The loser decamped and did not interact further (45 males),or he was killed and eaten by the winner (3 males). After decamping losing males entered one of the terraria. Sometimes the winner entered a terrarium also, but this was always at least 1 min after the loser. If the female was still in the cage after the loser decamped, the winner always courted. Sometimes 2 or even 3 spiders would enter the same terrarium before the observation period ended, but no interactions took place once inside.

The males that won interactions were larger than the losers (body length of winner minus that of loser: 1.4 ± 0.63 mm; range: 1-3 mm, in 39 cases, smaller only once (difference in body lengths, 1 mm) and the same size in 8 cases ($G = 42.657$, $P < 0.005$).

Four male-male interactions were observed in the context of cohabitation with subadult females. In each case the resident male had been cohabiting with a subadult for 2 to 8 days before the intruding male was introduced into the cage. The resident male departed the nest and threat displays were exchanged in each case. Eventually, one male decamped (resident, 3 cases; intruder, 1); and the other male remained with the nest and cohabited with the subadult female.

OBSERVATIONS IN NATURE

1. A male was standing on a rock, the ground was covered by grass, and the tops of the rocks were above the level of the grass. When another male walked onto a different rock ca. 50 cm away, the first male watched the second walking and turning on the rock and occasionally facing the first male, but only briefly. After ca. 30 sec, the second male stood facing the first for several seconds, whereupon the first male displayed. Immediately the second male also displayed. A few seconds later, the first male ceased displaying, departed his rock, and walked more or less directly toward the rock on which the second male waited. Meanwhile, the second male ceased displaying and resumed walking and turning. After ca. 15 sec, the first male walked onto the rock with the second male, the two males displayed; and after ca. 30 sec, the second male departed from the rock. Several minutes later, I lost sight of him over 2 m away. The winning male walked onto the side of the rock and groomed. A few minutes later, he walked onto the ground and I lost sight of him between the two rocks. There were no nests under the rocks, and no females were seen in the vicinity.

2. A pair of males was exchanging threat displays while standing ca. 3 cm apart on a piece of wood when I discovered them. After briefly embracing and pushing, one male departed; and I lost sight of him more than 1 m away. I inadvertently disturbed the other male, and he ran under the wood. When I overturned the wood ca. 30 min later, I found not only the male, but ca. 30 cm away I found a female inside a nest. This observation suggested that the type of interference envisaged in the laboratory occurs in nature.

DISCUSSION

Aggression.—Evidently interference by an intruding male is likely to lead to more serious consequences for the resident male if it occurs during courtship with a female outside her nest. As with pursuit time, copulation duration, and receptivity (Jackson 1978a, 1980b), this difference is probably related to the female's reluctance to depart her nest. With the female inside her nest, the male is subject to the risk of a prevented copulation due to an intruding male driving him away; but if he wins the aggressive interaction, his chances of subsequently initiating copulation are probably good. In contrast, when the female is outside her nest, interference by an intruding male is likely to prevent copulation, regardless of whether he can drive the intruder away.

Only virgin females were used in this study, and different estimates for these probabilities might be expected if other types of females had been used. For example, maternal females might have been more reluctant to depart their nests. More data are needed, especially for male-male interactions in the context of cohabitation. However, as long as the probabilities estimated here were even roughly accurate, it would seem that the consequences of male interference tend to be more serious to the resident male when the female is outside rather than inside her nest. Unless the frequency of intermale interference is substantially greater with females inside nests, pursuit of females outside nests probably entails greater costs related to this factor; females inside nests, lesser costs

Crane (1949) reported that males of salticids interacted aggressively more readily and intensively when females were present than when they were absent This seems likely in the case of *P. johnsoni* also. In three of the 24 male-male interactions with females present outside nests, one of the males was killed by the other. In another case a male was injured but not killed. However, only one male was killed and none simply injured in the 60 male-male interactions outside nests in the absence of females (Jackson 1977).

The presence of females is not necessary for male-male aggression, raising questions about functions of this behavior (Crane 1949). There is no evidence that males maintain territories in a traditional sense, but each male seems to defend a mobile personal space around himself that he strives to keep free of other males. A male with a larger personal space might be less likely to suffer from interference by other males when the opportunity to court and mate arises. However, one might envisage spacing out by simple avoidance behavior. Why do males threaten and fight? Perhaps there are optimal areas for sexual searching which males are hesitant to depart. Also if males have systematic searching routines of some type, these are likely to be disrupted by departure from the area. Whatever the precise cause, if there is an advantage in being the male that remains rather than departs, there would be selection favoring males that interact aggressively and win encounters.

Pursuit Time per Net Benefit.—Estimating P_o, P_n, and P_s is a highly difficult operation. The numerators (time) can be estimated relatively easily; but the denominators (net benefit) need to be expressed in units of fitness, a much more difficult quantity to measure. The most serious difficulty is that conditions operating in nature need to be evaluated, and this information is not readily available Quantitative estimates of net benefit will not be attempted here. Instead, an attempt will be made to rank types of females according to decreasing pursuit time per net benefit.

Factors related to benefit (Jackson 1980b) will be considered first. Some females failed to oviposit fertile eggs after copulation, but the probability of this happening was greater after shorter copulations. Following the very lengthy copulations associated with cohabitation, all females in the laboratory oviposited fertile eggs. However, given that the female oviposited fertile eggs at all, there was no relationship between the number she oviposited and the duration of the preceding copulation. Sperm competition can diminish the number of progeny that a male leaves by a given female since inseminated females sometimes copulated with additional males; and when this happened, partial or complete sperm displacement sometimes occurred. After longer copulations, females were less prone to copulate with additional males. Benefit for the male seems to increase with copulation duration, and copulation duration varies with the type of female in a manner such that subadult female inside nest (cohabitation), adult inside nest, and adult outside nest is the order of decreasing benefit.

Expression of the various types of risks to which males are subject (predation, cannibalism, etc.) might be accomplished by using estimates of the probabilities of each type of risk as a weighting factor. Considering cannibalism, for example, a first approximation might be to multiply the male's expected progeny from the female in question by $1 - C$, where C is the probability that she will kill him before copulation. The sum of the male's expected progeny from females that he is likely to encounter in the future should be multiplied by $1 - C$ also. These two quantities should be added next to the male's expected progeny from all females with which he has previously mated.

Various ways in which nests might protect spiders from predators have been discussed elsewhere (Jackson 1976a); and the risks to the male seem greater when courting females outside their nests. Observations of Mathew (1940) and Edmunds (1978) suggest that this factor is especially important in salticids that associate with ants.

Cannibalism is a special type of predation that probably occurs only infrequently in *P. johnsoni*, but the differences in frequencies are such that males pursuing adult females outside nests are probably in the greatest danger (Jackson 1980a). Risks related to interference by other males are probably greater for males pursuing females outside rather than inside nests.

Although various events such as avalanches and large mammals walking past might disrupt interactions between spiders, this type of interference seemed to be too infrequent to be very significant. The longest pursuit time recorded for this species was a 14-day cohabitation (Jackson 1978a). When rocks and pieces of wood were painted and checked monthly in the field for 4 months in succession, it was estimated that the chances of a nest site being overturned during a 14-day period was ca. 1 or 2 in 1000 (Jackson 1976b).

The apparent order of increasing benefit, decreasing risks (cost), and consequently increasing net benefit for the males is as follows: adult females outside nests, adult females inside nests, and subadult females inside nests. Since the numerators, pursuit time, follow the same trend, the ranking of P_o, P_n, and P_s is difficult.

Pursuit times associated with subadult females inside nests (ca. 1 week) are greater than pursuit times associated with adult females outside nests (ca. 2 min) by a factor of ca. 5000 (see Jackson 1978a). Perhaps the numerator of P_i should be viewed as handling time (the sum of courtship, cohabitation, and copulation durations) instead of simply pursuit time. Adding 14 min for copulation outside nests and 14 hr for copulation after cohabitation, the numerators still differ by a factor of ca. 500.

These estimates are somewhat misleading because all hours of the day and night are not equivalent for males with respect to searching. For example, *P. johnsoni* males remain inside nests at night even if not cohabiting (Jackson 1979). Since the alternative of searching during this period is not available, perhaps the time involved should be subtracted from the measurement of pursuit time. As another example, if the male cohabits during inclement weather, searching would have been prevented or hindered anyway. Apparently, a realistic model should weigh pursuit time according to how much is subtracted from potential search time. However, even after weighting of this type has been taken into account, pursuit times probably still differ by two or three orders of magnitude.

In order for P_s (pursuit time per unit net benefit for males pursuing subadult females) to be less than P_o (adult, outside nest), differences in net benefit would have to be greater than the difference in weighted pursuit time. Considering sperm competition and infertile matings, a difference of an order of magnitude or more seems probable for the number of progeny the male will leave in the two situations; and even greater differences in the magnitude of predation risks might occur. Adult females inside nests seem intermediate with respect to each factor.

A tentative conclusion will be proposed. The trend in net benefit counters the trend in pursuit (or handling) time, and pursuit times per net benefit increase in the following order: P_s (cohabitation with subadult female), P_n (courtship of adult female inside her nest), P_o (courtship of adult female outside her nest).

In the mating strategy of *P. johnsoni*, there are three types of females pursued by males, one of which should have the smallest or optimal P_i. If the optimal type of female is "subadult inside nest," why do males also pursue the two suboptimal types? Also, males do not pursue every type of female that they encounter. For example, males of the sparassid spider *Isopeda immanis* are reported (Clyne 1971, Coleman 1938) to remain with subadult females outside their nests and mate when they mature. In other words, males of *I. immanis* apparently pursue subadult females outside nests, a type of female not pursued by males of *P. johnsoni*. The most that occurs when an adult male of *P. johnsoni* encounters a subadult female outside her nest is a brief display followed by a speedy departure (Jackson 1977).

The general question that arises is analogous to one concerning the optimal diet of a predator. There are various types of females that males of a species will encounter. What set of these do they pursue? As in optimal foraging theory (MacArthur 1972, Pyke *et al.* 1977), we begin by ranking types of females, higher rank corresponding to smaller P_i. Beginning with the type of female with highest rank, additional ones are added to the set ("pursued females") in decreasing rank order (increasing order of P_i). This is continued so long as benefit divided by handling times with each addition is greater than would be the case without the addition. The optimal set of pursued females is one for which the next addition reverses the inequality. For *P. johnsoni* adding subadult females outside nests may reverse the inequality because net benefit is very small due to high risks of predation, interference by other males, and physical disturbances that cause males to lose visual contact with subadults amongst the vegetation and rocks in the habitats of the spiders.

A surprising property of optimal foraging theory is that whether or not a type of prey (type of female) is pursued is independent of the abundance of that type of prey (female). The important factor is the absolute abundance of the types of higher rank. Following this line of thought, pursuit of subadult females inside nests is predicted even if this type of female is rare in a population. However, if the density of subadult and/or adult females inside nests is very high in a population, pursuit of adult females outside nests might not occur. Populations with differing densitites and phenology have been studied (Jackson 1978b), but males from all of these pursued each of the three types of females. However, there were interpopulational differences in courtship persistence by males pursuing adult females outside nests, and optimal foraging theory has been discussed in reference to this (Jackson 1980c).

Concepts of optimality have generated insights concerning predation that would not have arisen so readily from more traditional viewpoints. Pyke *et al.* (1977) expressed optimism concerning the future of this relatively new approach in the study of predation. Similar approaches have been initiated in the study of mating behavior (Parker 1974), and similar optimism seems warranted.

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