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## THE NATURAL SELECTION OF SEXUAL CANNIBALISM

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Cannibalism, or intraspecific predation, is widespread in the animal kingdom, occurring occasionally in many terrestrial herbivores but more often in generalist predatory species (Fox 1975*a*). Such predation may take the form of siblings eating one another, mothers feeding on young, or individuals killing nonrelatives that encroach on their space (Polis 1981). In many cases of cannibalism, factors such as stress, population density, or the availability of an alternative food source may significantly affect rates of intraspecific predation.

In sexual cannibalism, the subject of this study, a female kills and feeds upon her mate during or following copulation. Sexual cannibalism has been observed in at least 30 species, including members of all orders of arachnids and three orders of insects (Polis 1981). In many of these species numerous incidences of sexual cannibalism in natural as well as captive populations suggest that the phenomenon is not just a result of crowded or stressful situations.

In some populations cannibalism can be a major source of mortality (e.g., Edgar 1969; Hallander 1970; Polis and Farley 1979*b*). Even in species in which cannibalism is generally rare, it may have a significant impact on population size or density if it occurs at specific stages in the life cycle (Mertz 1969) or at particular seasons (Fox 1975*b*). Depending upon food levels, sibling cannibalism may be advantageous as a food-cache strategy or may serve to reduce competition (Duelli 1981; Polis 1981). As we show in this paper, however, life history characteristics which affect the occurrence of sexual cannibalism are not the same as those most strongly affecting other forms of cannibalism.

Only a few studies have attempted to account for the evolution of cannibalism. Under many specific circumstances nutritional benefits and competitive effects convey a selective advantage to cannibals (Polis 1981). Eickwort (1973) calculated that only a small increase in survival or decrease in time to maturity as a result of egg cannibalism of siblings will maintain the trait in a population. In general, however, literature concerning cannibalistic behavior does not focus on its selective advantages but rather concentrates on ecological phenomena which presumably act to reduce cannibalism, e.g., habitat separation of different instars (Edgar 1969) or staggered emergence and dispersal of siblings (Eisenberg and Hurd 1977).

Cannibalism of mates is often cited in the popular literature, but in fact has

received little in-depth or quantitative study. Even detailed observations of black widow spiders by Kaston (1970) and of captive mantids by Roeder (1935, 1962) did not give rates of sexual cannibalism but simply suggested conditions under which it might occur more often. Only a few recent field studies have attempted to estimate rates of sexual cannibalism and its role in the species biology (Jackson 1980*a*; Polis and Farley 1979*a*). This paper represents the first explicit treatment of theoretical aspects of sexual cannibalism, although the phenomenon has been cited in previous theoretical papers on parental investment (Thornhill 1976) and mating strategies (Parker 1979). Such studies of paternal investment strategies suggest that a male should permit himself to be eaten only if he increases his inclusive fitness more in that manner than by surviving to inseminate other females.

Here we present a model that describes the life history conditions under which sexual cannibalism would be selected and compare model predictions with life history information for several arthropod species. The two most important factors that determine whether sexual cannibalism is an advantageous male strategy are: the expected number of matings during a male's lifetime and the proportional increase in the male's offspring if sexual cannibalism occurs. Because of the lack of data on male reproductive success in the literature reviewed we do not test the model quantitatively, although for several species it would be possible to design experiments to do this. A descriptive analysis of the information available concerning several species does suggest, however, that the observed incidence of sexual cannibalism is consistent with the predictions of the model. That is, sexual cannibalism is seldom observed except for species in which males can expect few potential matings and cannibalism is likely to increase the number of offspring resulting from a mating.

#### A MODEL FOR THE EVOLUTION OF SEXUAL CANNIBALISM

Here, and more explicitly in the Appendix, we develop a model to calculate the conditions under which the fitness  $w_{NC}$  of a male in a population with no cannibalism is less than the fitness  $w_C$  of a male in an otherwise identical population in which males can be eaten by their mates following insemination. We assume there is no parental care by the male after mating. For this model, we define the following parameters:

- $P$  = the average number of offspring produced after a particular mating when the male is not cannibalized.
- $P + A$  = the average number of offspring produced after a particular mating when the male is cannibalized by the female.
- $C$  = the probability that a male will be cannibalized after any particular mating.
- $E_{NC}$  = the expected number of matings in a male's lifetime when no sexual cannibalism occurs.
- $E_C$  = the expected number of matings in a male's lifetime in a population which is otherwise identical but in which sexual cannibalism may occur.

In a noncannibalistic population, the expected offspring would be  $w_{NC} = E_{NC}P$ . In a cannibalistic population, however, it is possible for a male to survive his matings without being cannibalized, or he can be eaten after one of his matings. The expected number of offspring  $w_C$  is calculated by summing the expected number of offspring resulting from successive matings but adjusting this number to account for the possibility that the male did not survive previous matings (see Appendix).

If sexual cannibalism is to have a selective advantage, then  $w_C > w_{NC}$ . In terms of the variables defined above, this inequality becomes (from eq. [A10]):

$$A/P > \frac{1}{C} \left( \frac{E_{NC}}{E_C} - 1 \right). \quad (1)$$

This inequality holds even if death between matings can occur from causes other than sexual cannibalism.

For any particular real species, it is difficult to estimate the parameters  $C$ ,  $A/P$ ,  $E_C$ , and  $E_{NC}$  from data in the literature. Nevertheless, the above expression shows explicitly the additional offspring  $A$  that must be produced in order for sexual cannibalism to be beneficial to a male. For simplicity here we will assume that death of the male can occur only by sexual cannibalism, and thus  $E_{NC}$  will be the maximum possible number of matings that can occur in a male's lifetime. In this special case, equation (1) becomes (see eq. [A12]):

$$A/P > \frac{E_{NC}}{1 - (1 - C)^{E_{NC}}} - 1/C. \quad (2)$$

Note that if males can only mate once ( $E_{NC} = 1$ ), the term on the right becomes 0, and thus any value of  $A/P$  greater than 0 would convey a selective advantage to sexual cannibalism. On the other hand, if males can mate many times and  $E_{NC}$  becomes extremely large, then the term  $(1 - C)^{E_{NC}}$  approaches 0. Under these conditions,  $A/P$  must be very large; in fact, it must be greater than  $(E_{NC} - 1)/2$  in order for sexual cannibalism to be advantageous.

For a particular species, we can represent equation (2) graphically to illustrate the situation (fig. 1). For example, suppose that in species  $X$  the value of  $A/P$  is about 2.5 and the likelihood of sexual cannibalism at each mating is 0.5. If males of this species can mate four or fewer times, we see in figure 1 that sexual cannibalism is a beneficial strategy, since the plotted point  $X$  falls above the  $E_{NC} = 4$  line. However, the plotted point falls below the acceptable range as determined by equation (2) if  $E_{NC}$  is 5 or greater. Thus sexual cannibalism will be disadvantageous for males if they can expect to mate more than four times.

#### INTERPRETATIONS OF THE MODEL

##### *Predictions and Limitations*

This model predicts that sexual cannibalism would be expected to evolve in species with high  $A/P$  or low  $E_{NC}$ ; i.e., either when cannibalism of the male after mating results in a significantly higher proportion  $A/P$  of offspring than otherwise

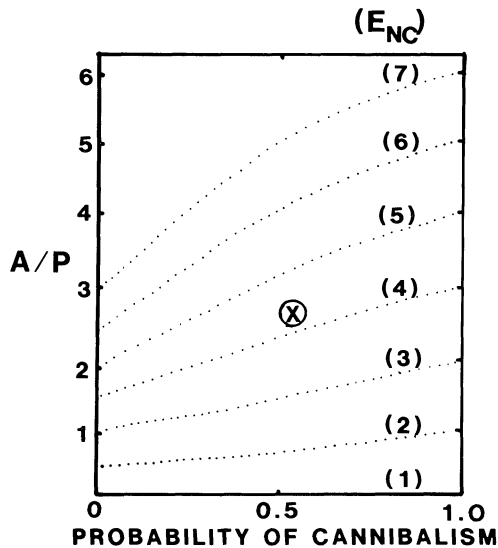


FIG. 1.—Graph of equation (2) in text, showing the relationship of  $A/P$  to  $C$  for different values of  $E_{NC}$ ; i.e., the relationship of the proportion of additional offspring produced as a result of sexual cannibalism to the rate of sexual cannibalism in the species, computed for different values of the maximum number of matings expected for a male of that species (see text for definitions). For the hypothetical species (X), since  $C = 0.5$  and  $A/P = 2.5$ , the expected number of matings below which sexual cannibalism would be advantageous is  $E_{NC} = 4$ .

would occur, or, alternatively, when a male's maximum possible number of matings  $E_{NC}$  is small. Any paternal investment that will significantly increase  $A/P$ , i.e., an investment that will increase the additional number or viability of the male's offspring per mating, would confer a selective advantage. This advantage would be outweighed by the loss of potential offspring produced by subsequent matings if the expected number of matings were sufficiently large. Although the model is quite general, it does predict certain specific situations in which sexual cannibalism is expected to occur. For example, sexual cannibalism is always favored when  $E_{NC}$  is 1, as long as females obtain any nutritional benefit and produce additional offspring. It is also favored whenever  $A/P$  becomes sufficiently large, which may occur, for example, when  $P$  approaches zero. The limited observations available suggest that the component of the model which is most predictive of the occurrence of sexual cannibalism is the potential number  $E_{NC}$  of male matings. From the available data there is no clear indication that sexual cannibalism is more common in species with high  $A/P$ .

#### *Application to Selected Arthropod Species*

The primary limitation of the model is the lack of available data for estimating the parameters. For instance, no convincing experimental studies have established that a male's nutritional contribution to the female actually increases his

fitness (Walker 1980). Existing measures are insufficient for testing the appropriateness of the model quantitatively. For example, new data on a particular species that changed the estimate of its  $E_{NC}$  from 2 to 4 could reverse the model's prediction as to whether sexual cannibalism will convey a selective advantage to males (fig. 1). Even though it is not possible to test the model quantitatively for particular species at this time, we can make a qualitative evaluation of successful male strategies for a number of species under various conditions. In this section we apply the model to five arthropod taxa. From natural history observations on each, we determine whether model conditions might be met for the natural selection of sexual cannibalism.

Sexual cannibalism is common in black widow spiders of the genus *Latrodectus* (Araneae: Theridiidae), although it does not occur invariably (Kaston 1970; Ross and Smith 1979). Often in *Latrodectus hesperus* the male lingers at the female's web for several days after copulation and eventually is eaten (K. G. Ross, personal observations). The small size of the male relative to his mate (often less than 2% of her mass) as well as the large size of the egg mass suggest that  $A/P$  would be small. Frequencies of male matings are not known, but observations are consistent with a low  $E_{NC}$  (table 1). During mating the tip of the embolus on the male's palp breaks off and remains in the genitalia of the female. This phenomenon occurs in several spider species (Levi 1974), and the broken tip may serve as a mating plug. A broken palp presumably cannot be used again for copulation, but a male could copulate with his second palp, either with the same or another female. Black widow males utilize both palpi in only one third of observed matings (Kaston 1970). Other observations also suggest a low number of matings for black widow males. The probability that the small male can abandon his web and successfully locate and inseminate many receptive females appears low. More than one male is commonly observed on the web of a single female, and mature males wait on the webs of large immature females for them to molt to adulthood (D'Amour et al. 1936; Ross and Smith 1979). Because the expected number of matings for male black widows is small, sexual cannibalism can convey a selective advantage.

Because of the variety of behavioral patterns in different species of jumping spiders (Salticidae), we cannot generalize whether sexual cannibalism would be an advantageous male strategy. In the jumping spider *Phidippus audax* (Araneae: Salticidae) newly molted adult females feed voraciously, and the timing of oviposition is dependent on food supply (Givens 1978). The mass of the male is about half that of the female and about twice that of the eggcase, and the male's mass is about 2–8 times the daily consumption of the female. From these data we estimate  $A/P$  in *Phidippus* spiders would be higher than that for black widows. Although cannibalism is not usually reported in captive or natural populations of jumping spiders, a careful study of *P. johnsoni* by Jackson (1980a) reported that a female killed and fed on a male in 1% of the mating interactions (involving 2% of the females). Male jumping spiders are known to mate more than once, and Jackson (1978) observed one male *P. johnsoni* to mate with two different females in an hour. At times males spend up to a week returning to the retreat of a single female or locate subadult females about to molt and remain with them until they can

TABLE I  
OBSERVATIONS OF SEXUAL CANNIBALISM RELATIVE TO MODEL PARAMETERS

Taxa	Cannibalism of Adults in Nature?	Sexual Cannibalism in Nature?	$E_{NC}^*$	$A/P^*$
<i>Latrodectus</i> species (black widows) . . . . .	yes <sup>a</sup>	yes <sup>a</sup>	low	low
<i>Paruroctonus mesaensis</i> (scorpion) . . . . .	yes <sup>b</sup>	yes <sup>b</sup>	low	high
Mantidae (praying mantids) . . . . .	yes <sup>c</sup>	yes <sup>c</sup>	low	high
<i>Phidippus johnsoni</i> (jumping spider) . . . . .	yes <sup>d</sup>	rare <sup>d</sup>	high	high
Lycosidae (wolf spiders) . . . . .	yes <sup>e</sup>	no <sup>e</sup>	high	high

\*  $E_{NC}$  (expected number of male matings with no cannibalism, see text) and  $A/P$  (proportional increase in offspring resulting from cannibalism of the male, see text) are estimates by the authors based on personal observations and the natural history literature.

SOURCES.—a, Kaston 1970, Ross and Smith 1979; b, Polis and Farley 1979a, 1979b; c, Gurney 1950, Edmunds 1972, Ross 1982; d, Jackson 1980b; e, Edgar 1969, Hagstrum 1970, Hallander 1970.

mate. Such long attendance times of a male to a single female would limit the number of matings. Cannibalism may be one selective factor in the mating behavior of *P. johnsoni* (Jackson 1980a).

In adult female wolf spiders (Araneae: Lycosidae) high feeding rates speed the onset of reproduction and increase both the size and number of eggs (Edgar 1971; Kessler 1973). Females require 10%–20% of their body weight of food per day before they can begin laying, and for many species the male is about half the mass of the female and up to 1.5 times the mass of the eggcase (Hagstrum 1970; Edgar 1971; Breymeyer and Jozwik 1975). Cannibalism is extremely common in wolf spiders (up to 20% of the diet in *Pardosa lugubris*, Edgar 1969; Hallander 1970), but sexual cannibalism is not cited. In a laboratory study of copulation in *Lycosa rabida* there was no mate cannibalism. In fact, the end of the copulatory sequence was characterized by a cheliceral pinch from the male, which seemed to inactivate the female and insure her mate's escape (Rovner 1972). No field data on the number of times a male mates are available in the literature, but male wolf spiders in captivity are known to mate numerous times and do not spend much time in attending the female. We estimate that although these species have potentially high  $A/P$  values, the number of male matings is high enough to make sexual cannibalism a disadvantageous male strategy.

In the desert scorpion *Paruroctonus mesaensis* (Scorpiones: Vaejovidae) cannibalism is common and may be an important population regulation mechanism (Polis and Farley 1979a, 1979b). Conspecific animals comprise 9% of the diet, and 17% of all cases of cannibalism involved adult females eating adult males. However, rates of sexual cannibalism, per se, were not determined. The effect of food limitation on egg production has not been measured, but females are known to resorb their embryos during food shortage, and emergence of the young may be

timed with resource availability to gravid females. Both sexes of *P. mesaensis* can mate in the breeding season of their second year. However, while females may breed another 3 or 4 yr, over 75% of the males die before their third season. We estimate the expected number of matings is low, presuming that in males mortality is high and mating frequency is also constrained by spermatophore production. According to our model, sexual cannibalism is likely to convey a selective advantage to male scorpions.

Like black widows, praying mantid females (Dictyoptera: Mantidae) are known for consuming their mates. In this group the males often escape cannibalism unless they are confined with the female (Roeder 1935; Gurney 1950). In many cases, however, the female attacks the male during mating, and the male's copulatory movements continue, in fact at a higher rate, when he is decapitated (Roeder 1962). Males are nearly as large as the female and are much bigger than the prey she normally takes. Raised in crowded conditions, female mantids grow more slowly and produce fewer offspring (Hurd et al. 1978). Field data suggest that mantid females are food limited and heavier females produce more offspring (Eisenberg et al. 1981). There are, however, no published measures of mantid eggcase productivity under different feeding regimes. The number of matings is poorly known for mantids, especially for the males, although both sexes of the common North American species can mate more than once (Gurney 1950). Of 20 male Chinese mantids (*Tenodera aridifolia sinensis*) monitored by Bartley (1982), three were observed with different mates over intervals of 2, 5, and 6 days. In at least one tropical species, *Acanthops falcata*, mating is restricted to the dawn hours (Robinson and Robinson 1979), and even with pheromonal cues it may be difficult for an animal as large and weak-flying as a male mantid to find many females without suffering predation. If the expected number of matings is indeed relatively low (table 1), then our model suggests that sexual cannibalism would be an advantageous strategy for mantids.

#### *Possible Experiments for Testing the Model*

It is possible to acquire quantitative measures of  $E_{NC}$  and  $A/P$  for these groups with a combination of appropriate laboratory studies and field manipulations. For example, supplementary feeding of the spider *Linyphia marginata* (= *Nereine radiata*, Araneae: Linyphiidae) was shown to increase fecundity (Turnbull 1962); in the same species, reproduction of females was demonstrated to be food limited in the field (Wise 1975). Similar experiments with cannibalistic species would lead to quantitative estimates of  $A$  and  $P$ . Both black widow spiders and praying mantids are groups for which males and females could be reared in laboratory or field enclosures on standardized diets. Initially, one would determine the effects of the timing, quantity, and components of diet on egg production in adult females. For example, animals could be reared on ad lib diets, diet levels simulating field conditions, or low food levels with pulses of ad lib feeding at various times in the life cycle. Such studies would make it possible to estimate the effect on egg production of additional biomass at particular times in the female's



lifetime. These results could be compared to those from females reared in the lab and allowed to consume their mates at various intervals before oviposition.

The frequency of mate cannibalism in natural populations can be estimated from intensive observations of marked individuals. Species in which females are relatively sedentary, such as some web spiders, would be easier to investigate since they could be monitored by an observer routinely at intervals, or continuously with a video recording system. Because black widow spiders and other urban species inhabit garages and outbuildings, these structures are naturalistic field enclosures in which to monitor number of matings and rates of cannibalism. In a parallel study, one could check the effectiveness of monitoring matings in such natural enclosures by sterilizing (via irradiation) all males initially found and marked in the enclosure.

In a more comprehensive study, measurements of this kind for different species might help to elucidate the factors leading to sexual cannibalism. For instance, field estimates of  $E_C$ ,  $E_{NC}$ ,  $A$ , and  $P$  for the black widow *Latrodectus hesperus* in southwestern North America could be compared to estimates of  $E_{NC}$ ,  $A$ , and  $P$  for the taxonomically and ecologically similar *Achaearanea tepidariorum* from the Northeast, for which cannibalism has not been reported.

#### DISCUSSION

##### *Life History Conditions Favoring Sexual Cannibalism*

Several life history characteristics are important in determining the parameter values of our model.  $A/P$  would be zero unless the male's biomass is indeed transferred to the eggs which will be fertilized by his sperm. As with other forms of paternal investment, there must be a high confidence of paternity (Thornhill 1976; Maynard Smith 1977; Parker 1979). Reproductive phenomena in the female such as sperm storage and delayed oviposition would insure that the investment goes to a male's own offspring, not to an egg complement fertilized by a competing male. In the arthropods in table 1 that show mate cannibalism, oviposition occurs at least 10 days after copulation (Roberts 1937; Jackson 1978; Polis and Farley 1979*b*). One mechanism for greater confidence of paternity is the copulation plug, and the broken tip of the palpal embolus in the male black widow may serve as such a device. A male may also increase the probability of paternity by prolonged attendance or defense of the female. Mechanisms such as sperm displacement and male-induced nonreceptivity also prevent investment without confidence of paternity. For many insects, the last male to mate with a female before oviposition sires most of those offspring (Walker 1980), although some first-male precedence has been found for spiders (Jackson 1980*b*; Austad 1982; Martyniuk and Jaenike 1982). In addition, prolonged copulation apparently makes females less likely to mate again in some jumping spiders (Jackson 1980*b*) and increases the time of female nonreceptivity to further matings in wolf spiders (Rovner 1972).

The maximum potential number of matings for a male,  $E_{NC}$ , is limited by a

number of factors, such as: (1) the length of a male's reproductive lifetime; (2) morphological factors (such as loss of palpal embolus tips in the black widow spider); (3) the time and effort a male invests in courting or defending a particular female; (4) the time and energy required for the male to produce a sperm complement (especially in the many arthropod species that produce spermatophores); and (5) the ability of males to locate other females.  $E_{NC}$  is potentially high for species which join in mating aggregations or leks (even though the actual number of matings per male may be highly skewed in the population). Also, in some species reproductively active animals become more habitat specific or utilize pheromones for long-distance advertising and rely less on chance encounter. In such species cannibalism would be less likely because a male's  $E_{NC}$  is not so restricted by his ability to locate a female.

The adult sex ratio of a species may also determine whether sexual cannibalism is advantageous, especially if mating synchrony was high. Males of a species in which females have higher mortality or mate only once would be more likely to have a low  $E_{NC}$ , because the male has a low chance of locating receptive females (Parker 1979). Thus males may benefit by investing more in the offspring from a single mating. In field observations on the jumping spider *Phidippus johnsoni* sexual cannibalism (although observed rarely) was most common in the study population in which males encountered females least frequently (Jackson 1980a, 1980c, personal communication). Mate cannibalism may also be associated with reproductive competition among females, although we have not included this possibility in our model. When males are rare and when resources for rearing young are limited, natural selection could favor females who eat their mates following insemination, because removal of the males would decrease the probability that competing females would encounter a male (Polis 1981).

In highly seasonal breeders, both a limited  $E_{NC}$  and the potential of a comparatively high  $A/P$  during food shortages would increase the possibility of selection for sexual cannibalism. In many of the species in which mates are cannibalized, the females produce packets of eggs well after the end of the breeding season or after the males have died. One fertilization provides enough sperm for several egg masses. Thus sexual cannibalism might be expected more often in species living in highly seasonal environments than in long-lived or tropical species. Indeed, Maynard Smith (1977) calculated that in species with well-defined breeding seasons a viable female strategy is to delay mating until it is advantageous for the male to stay with her and donate the necessary parental investment. For the species discussed here, such investment might include sexual cannibalism.

Finally, if a species generation time is short compared to its mating life span, some situations favoring sexual cannibalism are not covered by our model. In our model we calculate a male's effectiveness simply by determining the expected number of offspring he will have in a lifetime. Clearly offspring produced earlier in his lifespan may contribute a male's genetic material to the gene pool faster than offspring produced later. In some circumstances the extra offspring resulting from cannibalism of the male might carry more of his genetic material than the male himself carries. With the possible exception of the desert scorpion example above, however, we are unaware of species with the capability for sexual can-

nibalism in which males generally survive to compete with their offspring. Ecological situations selecting for a syndrome of earlier maturity, larger broods, and shorter lifespans (Stearns 1976) would also favor a higher early reproductive investment by the male in the form of sexual cannibalism.

### *Why Sexual Cannibalism is So Rare*

Although other forms of cannibalism are widespread in many different groups of animals, the incidence of sexual cannibalism appears much more restricted. We could find documented cases only among the Insecta and Arachnida, and in fact there are very few examples. Even in species capable of intraspecific predation (Fox 1975*a*; Polis 1981), mate cannibalism generally does not occur.

The same parameters of the model which outline the conditions favoring the selection of sexual cannibalism also explain why it is absent in most species. In most vertebrates the capacity for repeated matings counters the natural selection of sexual cannibalism. Most birds and mammals can mate several times within a breeding season and continue to breed for several seasons. In addition, other forms of extended paternal care would negate the advantage of sexual cannibalism. In animals which have external fertilization there is no mechanism for the male's biomass to become part of his offspring, even if he does mate only once. For example, many fish are cannibalistic, but sexual cannibalism is not advantageous to the male because most species spawn externally. In many species of insects, females store sperm but are not predatory and are physically incapable of capturing their mates. In all of these groups, with high  $E_{NC}$  or low  $A/P$ , any observations of sexual cannibalism must be explained by unusual circumstances. All these considerations suggest sexual cannibalism would be selected in animals which are predatory, have sperm storage, and whose males are short lived or otherwise limited to one or two matings.

### SUMMARY

Sexual cannibalism, in which a male is eaten by his mate following copulation, is expected to convey a selective advantage to the male under certain conditions. As shown quantitatively in our model the phenomenon is expected when (1) a male can mate only a few times in his lifetime and (2) the cannibalism significantly increases the number and/or viability of eggs fertilized by his own sperm. The expected number of male matings appears to be the more important of these two conditions. The few available observations of sexual cannibalism in several species of arthropods agree qualitatively with the predictions of our model. The same parameters of the model also explain why sexual cannibalism is generally rare among vertebrates. Phenomena selecting for sexual cannibalism appear more closely related to paternal investment strategies than to ecological factors associated with other forms of cannibalism. Because few field studies of invertebrates have followed the mating history of marked males, we cannot test our model quantitatively with existing data. We suggest specific field observations which would provide quantitative estimates of the expected number of male matings. In

addition we describe possible laboratory experiments which would give more precise measurements of the increase in fecundity of the cannibalized male.

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#### APPENDIX

Here we derive equations (1) and (2) used in the model for the selection of sexual cannibalism. Our model evaluates the expected number of offspring produced by males of a given population in their lifetime. In addition to the parameters  $P$ ,  $P + A$ ,  $C$ ,  $E_{NC}$ , and  $E_C$  defined in the second section of the text, we define:

- $D$  = probability that a male will die after mating by causes other than mate cannibalism.  
 $S$  = probability that a male will survive between matings. Note that  $S$  depends on  $C$  and  $D$ , i.e.,  $S = 1 - C - D$ .  
 $N$  = maximum possible number of matings that a male can have in a lifetime if he is not cannibalized and if he does not die from other causes after mating.

We wish to calculate the number of offspring  $w_C$  expected by a male of a population with sexually cannibalistic females, and compare  $w_C$  to the number of offspring  $w_{NC}$  expected by a male of a similar population with noncannibalistic females. For simplicity we shall assume here that  $C$ ,  $D$ ,  $A$ , and  $P$  are constants independent of the age or experience of the male, and that the number of potential matings  $N$  is the same for all males in the species. We calculate  $w_C$  by summing the expected number of offspring for males that die after the  $k$ th mating, i.e.,

$$w_C = \sum_{k=1}^N (A + kP)S^{k-1}C + \sum_{k=1}^N kPS^{k-1}D + NPS^N. \quad (\text{A1})$$

The  $k$ th element in the first sum is the number of offspring produced by the male cannibalized on the  $k$ th mating. Each such male produces  $A + kP$  offspring. Only a fraction ( $S^{k-1}C$ ) of all males are in this category, i.e., they survive their first  $k - 1$  matings and then are cannibalized on the  $k$ th mating. In the second sum, we count offspring from males who survive their first  $k$  matings and then die from causes other than cannibalism. Clearly the fraction of males in this category is ( $S^{k-1}D$ ) and each produces a total of  $kP$  offspring. Finally the last sum on the right in equation (A1) accounts for the fraction  $S^N$  of males who survive all  $N$  matings without being cannibalized.

To simplify equation (A1) it is convenient to make use of two properties of sums of fractions. In particular, if  $S$  is any number with  $|S| < 1$ , then

$$\sum_{k=1}^N S^{k-1} = \frac{1 - S^N}{1 - S} \quad (\text{A2})$$

and

$$\sum_{k=1}^N kS^{k-1}(1 - S) = \frac{1 - S^N}{1 - S} - NS^N. \quad (\text{A3})$$

Reorganizing terms in equation (A1), we get

$$w_C = CA \sum_{k=1}^N S^{k-1} + P \sum_{k=1}^N kS^{k-1}(C + D) + NPS^N.$$

However, since  $C + D = 1 - S$ , we can simplify the second term using equation (A3), and the first term using equation (A2), and we find that

$$w_C = CA \left( \frac{1 - S^N}{1 - S} \right) + P \left( \frac{1 - S^N}{1 - S} - NS^N + NS^N \right)$$

$$w_C = (CA + P) \left( \frac{1 - S^N}{1 - S} \right). \tag{A4}$$

For an identical species with no sexual cannibalism  $A = 0$  and  $C = 0$ , and so the expected number of offspring  $w_{NC}$  is

$$w_{NC} = P \left( \frac{1 - S_0^N}{1 - S_0} \right) = P \left[ \frac{1 - (1 - D)^N}{D} \right]. \tag{A5}$$

To avoid confusion with equation (A4) we have added a subscript 0 to the survival  $S$ , i.e.,  $S_0 = 1 - D$ . In the special case where there is no death between matings from causes other than sexual cannibalism ( $D \rightarrow 0$ ), then the expression simplifies to:

$$w_{NC} = NP. \tag{A6}$$

Equations (A4) and (A5) are somewhat cumbersome, but they can be put much more simply if they are expressed in terms of the expected number of matings  $E_{NC}$  or  $E_C$  in a male's lifetime. Clearly, if males have a chance  $S$  of surviving each mating, and if we only consider males who mate at least once, the expected number  $E$  will be just (see eq. [A2]):

$$E_C = \sum_{k=1}^N S^{k-1} = \frac{1 - S^N}{1 - S} \quad \text{and} \quad E_{NC} = \frac{1 - S_0^N}{1 - S_0}. \tag{A7}$$

Note that if there can be no cannibalism and no death due to other causes then the maximum number of matings equals the expected number from the no-cannibalism strategy, i.e.,  $E_{NC} = N$ .

Thus by substituting these into equation (A4) and equation (A5) we have expressions for the expected number of offspring in terms of the expected number of matings, namely

$$w_C = (CA + P)E_C \tag{A8}$$

and

$$w_{NC} = PE_{NC}. \tag{A9}$$

These expressions are true for any  $N$ , even when we allow  $N$  to become arbitrarily large.

Under what conditions will males produce more offspring if they permit sexual cannibalism? From equation (A8) and equation (A9),  $w_C > w_{NC}$  implies that

$$(CA + P)E_C > PE_{NC}$$

or

$$\frac{CA}{P} > \frac{E_{NC}}{E_C} - 1. \tag{A10}$$

For the special cases when death between matings is caused only by sexual cannibalism, then  $D = 0$  and  $C = 1 - S$ . Substituting into  $w_C > w_{NC}$  from equation (A4) and equation (A6) the inequality simplifies to:

$$A/P > \frac{N}{1 - S^N} - \frac{1}{1 - S}. \tag{A11}$$

In this special case since  $N = E_{NC}$  and  $S = 1 - C$ , equation (A11) can also be written as:

$$A/P > \frac{E_{NC}}{1 - (1 - C)^{E_{NC}}} - 1/C. \tag{A12}$$

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