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CANNIBALISM WITHIN MATING PAIRS OF THE PARASITIC ISOPOD, *ICHTHYOXENUS FUSHANENSIS*

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ABSTRACT

Two types of sexual cannibalism, differing in the sex of the victim, were found among heterosexual pairs of the parasitic isopod *Ichthyoxenus fushanensis* Tsai and Dai, 1999, residing in the body cavity of the freshwater fish *Varicorhinus bacbatulus* (Pellegrin, 1908). In one type, categorized as sexual cannibalism, the male was consumed by the female before or after mating. In the other, reversed type, the female was eaten by her mate during or after breeding. Both types of cannibalism occurred during the breeding season from April to November, with female-on-male cannibalism occurring earlier on, and the reversed type later. Both types of cannibalism occurred in pairs inhabiting smaller hosts (<10 cm in body length), which suggests that resource limitation is an important factor triggering the cannibalism. Cannibalism may lead to rapid growth or sex change of the cannibal. The availability of free-living mancas during the breeding season enables a mating pair to be re-formed after cannibalism has occurred. Both types of cannibalism occurred in mating pairs with a low size ratio (below 1.6, female to male), and both resulted in a greater discrepancy between female and male sizes in the re-formed pairs. This increase in size ratio between paired individuals may ultimately lead to an increase in clutch size. Because an individual of *I. fushanensis* undergoes protandrous sex change, the cannibalistic behavior could not have evolved in response to selection on either the male or female sexuality. Rather, both types of cannibalism may be regarded as the result of competition between paired individuals, which appears to be a by-product in the evolution of a reproductive strategy rather than a consequence of sexual selection.

Cannibalism, or intraspecific predation, is a behavioral trait found in a variety of animals (Fox, 1975; Polis, 1981; Buskirk *et al.*, 1984; Leonardsson, 1991; Elgar and Crespi, 1992; Warburg, 1994). It occurs in various forms, such as cannibalism between young (siblicide), between adults (in particular, sexual cannibalism), or between adults and young (infanticide and matriphagy) (Kim and Horel, 1998). Factors such as stress, population density, or the availability of an alternative food source may significantly affect rates of cannibalism (Polis, 1981; Buskirk *et al.*, 1984). Cannibalism may also play an important role in shaping the size distribution of individuals, the recruitment pattern, and the population size and age structure of many species (e.g., Fox, 1975; Hines *et al.*, 1987; Leonardsson, 1991; Hurd *et al.*, 1994; Moksnes *et al.*, 1997; Sparrevik, 1999). Cannibalism may directly confer nutritional fitness benefits in the form of increased survival, developmental rate, and fecundity (Polis, 1981). It follows that when cannibalism confers such benefits, the propensity for cannibalism should be greater when food availability is low.

Sexual cannibalism, as defined by Elgar (1992), is the consumption of a male by a female at some stage of courtship or copulation or immediately thereafter. It occurs in many spiders and scorpions, opisthobranch molluscs, amphipods, copepods, and three orders of insects (Polis, 1981; Buskirk *et al.*, 1984; Elgar, 1992; Arnqvist and Henriksson, 1997). The term "sexual cannibalism" can be misleading because it masks important differences between "economic" and "sacrificial" cannibalism (Peretti *et al.*, 1999). Selection for economic cannibalism is based on what is optimal for females (Newman and Elgar, 1991), and this can explain precopulatory cannibalism in spiders. Obviously, it is never optimal for a male to be eaten by a female before sperm transfer, so such cannibalism reflects greater female power in the "conflict of interest" (Peretti *et al.*, 1999). On the other hand, selection for sacrificial cannibalism has been shown to have two paternity advantages: cannibalized males fertilize more eggs than do noncannibalized males, and females are less likely to remate following consumption of their first mate (Andrade, 1996). Sexual cannibalism may thus evolve via two routes. First, from a female's point of view, if the risks involved in cannibalizing males are slight, and males are sufficiently common, then any particular male may have more value as a meal than as a mate. Second, if a male is unlikely to survive to mate with another female, and by self-sacrifice he increases the fitness of his offspring (through greater provisioning, for example), cannibalism may be favored (Buskirk *et al.*, 1984; Andrade, 1996). The costs and benefits with respect to male and female fitness have been examined both theoretically and empirically (Buskirk *et al.*, 1984; Newman and Elgar, 1991; Arnqvist and Henriksson, 1997), but there is still some dispute as to who benefits from sexual cannibalism (Johns and Maxwell, 1997).

A flesh-burrowing protandrous parasite, *Ichthyoxenus fushanensis* Tsai and Dai, 1999 (Isopoda: Crustacea), was found residing in the body cavity of a freshwater fish, *Varicorhinus bacbatulus* (Pellegrin, 1908) (Cypriniidae: Barbinae) (Tsai and Dai, 1999). The isopods, often in heterosexual pairs, live in a membranous sac of the host fish adjacent to the pectoral fin that opens through an orifice directly to the outer environment, providing a channel for gas exchange, excretion of waste, and manca release. Free-living mancas are released from April to November. The mancas search for a host immediately after being released, and those failing to find a host die within a week (Tsai and Dai, 1999). Once a manca enters a host, it loses its swimming ability completely and shortly becomes a male. Because of the low transmission rate, selection favors large and productive females to compensate for the mass mortality of mancas (Tsai *et al.*, 1999). Most of the unpaired individuals are males, and the onset of sex-change possibly occurs immediately after the second manca enters the same host (Tsai *et al.*, 1999). Because of the constraints of available space or resources provided by the host, there exists a body size trade-off between the paired female and male. The clutch size not only depends directly on the female size at reproduction, but is also indirectly associated with the body sizes of her mate and the host (Tsai *et al.*, 2001). Selection favors the more productive combination of a larger female and a smaller male; however, how such a productive mating system can be achieved remains unanswered. Here, we describe two types of sexual cannibalism in the protandrous isopod *I. fushanensis* and provide evidence to address questions of how cannibalistic behavior influences the performance of the mating system.

MATERIALS AND METHODS

Infected *Varicorhinus bacbatulus* were collected biweekly from Spring, 1998, to Summer, 2000, in upstream sections of Nanshih Stream, a fast-running stream located in a mountainous area of northern Taiwan. The fish infected by *Ichthyoxenus fushanensis* were distinguished by the existence of an orifice near the pectoral fin. All infected fish were brought to the laboratory alive.

Each infected fish was cultured separately in a 35 × 45-cm aquarium with a biofilter and air supply. *Ichthyoxenus fushanensis* in the hosts contained embryos at different developmental stages that could not be examined from the exterior of the host fish. After the first manca was released from the orifice, the host fish was dissected, individual isopods were removed from the membranous sac, and the body lengths of both hosts and parents were measured in millimeters. A water jet was used to remove mancas from the brood pouch of the female, and the mancas were counted to represent clutch size. After one week, those fish that did not release mancas were also dissected and examined.

After dissection, the contents of the membranous sacs of each infected fish were carefully examined. Pairs with one individual observed in the act of eating its mate or with incomplete fresh remains and a live isopod of the opposite sex were recognized as positive cases of cannibalism. In some cases, this could be discerned without dissection, especially when the male was the victim, because the male is always located near the opening of the orifice. In other cases, the gut contents of the intact isopods was examined under a dissecting microscope, and the presence of chitinous cuticle in their guts confirmed the occurrence of cannibalism.

The sex of the cannibal or the victim was confirmed by checking the reproductive organs or other sexually dimorphic characteristics (Tsai and Dai, 1999). Depending on the integrity of the remains, body parts of the victims were measured (e.g., body width, telson length, or head width). The body size of the victim was estimated by a linear regression model of each part of the body *versus* body length, based on measurements obtained from intact animals.

In order to determine whether cannibalism occurred before or after copulation, the brooding of a single female was monitored. After the fragments of a male victim had been removed carefully from the orifice, a female isopod that had been cannibalizing her mate was cultured with six host fish separately in a tank without a new mate for three months. Mancas eventually released by the female indicated that the cannibalistic behavior had occurred during or after copulation.

RESULTS

Twenty-nine cases of cannibalism were found in paired *Ichthyoxenus fushanensis* (Fig. 1). These instances could be classified into two types based on the sex of the cannibals. In 12 cases, females preyed on males; this was recognized as sexual cannibalism. The other 17 cases represented a reversed type of sexual

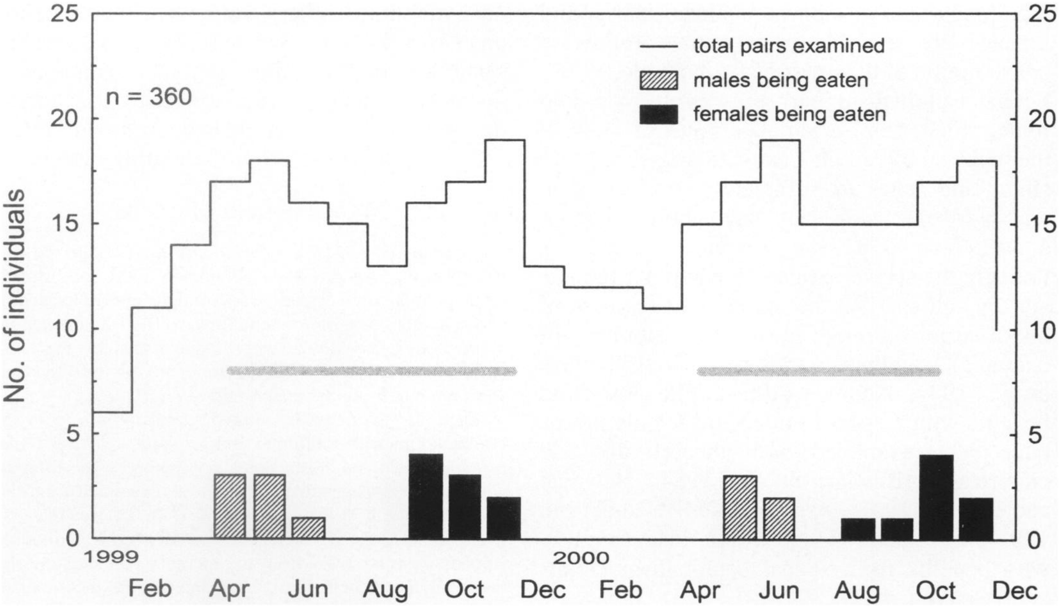

Fig. 1. Occurrence of cannibalistic events involving the parasitic isopod *Ichthyoxenus fushanensis* living in its host fish, *Varicorhinus bacbatulus*, from January 1999 to December 2000. The horizontal bars indicate the breeding season, during which free-living mancas were released.

cannibalism, in which females were consumed by males. In these latter cases, the remnants of the female were found to contain a few living mancas or empty oostegites, indicating that the cannibalism had occurred during or after the release of mancas. In addition, a few cases consisting of a brooding female and a small immature individual were found; we interpreted such cases as indications that the original mate of the female had been replaced.

In six of the 12 cases of sexual cannibalism, the hosts were cultured separately after the remains of the consumed males had been carefully removed from the orifices. During the following three months, only four females released mancas, indicating that cannibalism may have occurred before, during, or after copulation which is consistent with the definition of sexual cannibalism (Elgar and Crespi, 1992).

Both types of cannibalism of *Ichthyoxenus fushanensis* took place during the breeding season from April to November, when free-living mancas were available (Fig. 1). Female-on-male cannibalism mainly occurred in the early part of the breeding season, and male-on-female cannibalism occurred later (Fig. 1). In addition, all cases of cannibalism among pairs of *I. fushanensis* occurred in host fish shorter than 10 cm in standard length (Fig. 2), and when the body size ratio of the paired female and male parasites was below 1.6 (Table 1). When a new manca entered the membranous sac, the size ratio of the new pair might be considerably greater than before the cannibalism (Table 1).

In natural pairs, the body size of the female was always larger than that of her mate. However, body size distributions of the two sexes overlapped (Fig. 3). During the breeding season, females were often 1.6 times or more larger than the males paired with them (Fig. 4). The distribution of size ratios (female to male) of 87 brooding pairs showed one major peak at 2.5 (Fig. 4). This indicates that cannibalism may result in a rapid shift in size ratio of the mating pairs.

The size ratio of the paired female and male at reproduction displayed a significant positive relationship with clutch size (Table 2a); the size ratio was, however, positively related to host body size ($r = 0.706$, $P < 0.001$; Table 2a) and female size ($r = 0.865$, $P < 0.001$), and clutch size was also closely related to female size at reproduction ($r = 0.987$, $P < 0.001$; Table 2a). Thus, the relationship between size ratio and clutch size might be masked by these dependent variables (host size and female size). In order to obtain the actual relationship between the size ratio of paired sexes and clutch size, the multiple regression models were used. In a multiple regression model, the partial correlation coefficient is applied to measure the

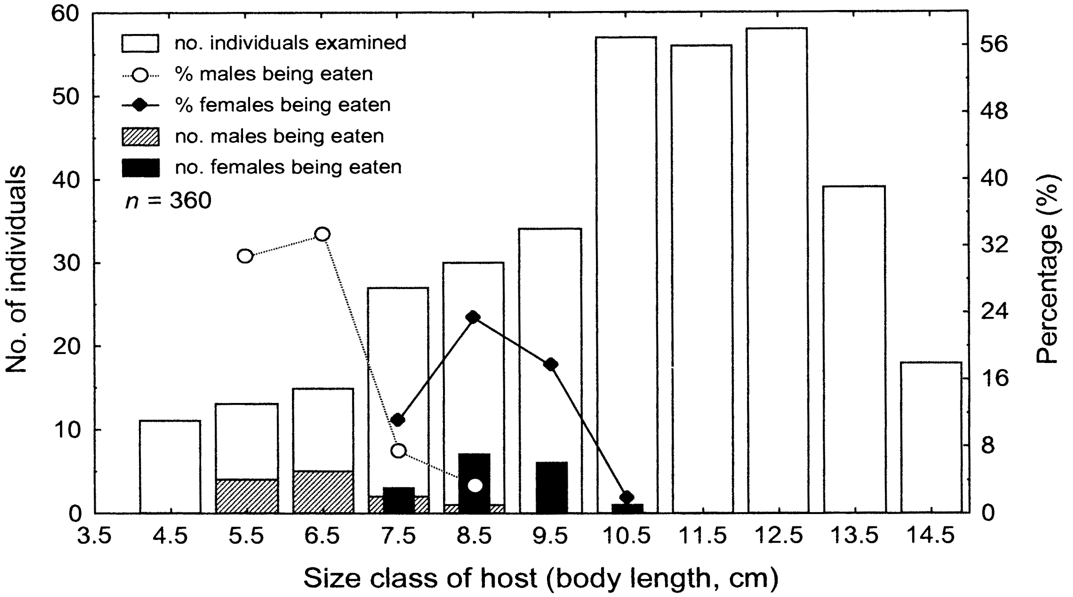

Fig. 2. Relationship between frequency and percentage of the two types of cannibalism in the parasitic isopod *Ichthyoxenus fushanensis* and body size of its host fish, *Varicorhinus bacbatulus*.

correlation between any pair of variables when other specified variables have been held constant (Sokal and Rohlf, 1995). When the effect of host size was removed, both the absolute and relative clutch sizes remained significantly related to the size ratio of the paired female to male (Table 2b; Fig. 5). This indicates that mating pairs with larger size ratios are a more productive combination, and that the size ratio may, either directly or indirectly, influence the number of mancas being released.

DISCUSSION

Sexual Cannibalism

Based on the sex of the victims, two types of cannibalism among heterosexual pairs of the parasitic isopod *Ichthyoxenus fushanensis* were found. One could be considered a classic example of sexual cannibalism in which the male is consumed by the female during or following copulation (Elgar, 1992). The other was a reversed type in which the female was eaten by the male during or after breeding. The several pairs of isopods consisting of a sexually immature juvenile and a brooding female, or a juvenile and a molting male were possibly at transitional stages after cannibalism. Because the whole process of cannibalism may be finished within 24 hours (Tsai, M.-L., unpublished data) and our samples only represent snapshot evidence, the frequencies of both types of cannibalism are possibly much higher than we have observed.

Cannibalism in many species involves larger individuals preying on smaller individuals, or same-sized individuals preying on each other (Polis, 1981; Warburg, 1994). Because the female of *I. fushanensis* is always larger than the paired male, predation on males by females is likely the result of a size advantage. On the other hand, male-on-female cannibalism may be the outcome of two possible situations: the female dies spontaneously after breeding and afterwards her body becomes a source of food

Table 1. Average body size (body length; mm) of both sexes of mating pairs of *Ichthyoxenus fushanensis* when cannibalism occurred, and estimates of the size ratio (female/male) before and after cannibalism.

	Body size		Size ratio	
Type of cannibalism	Female	Male	Before cannibalism	After cannibalism[b]
Female-on-male (n = 6)	10.6 ± 2.4	9.3 ± 1.1[a]	1.14 ± 0.18	3.03
Male-on-female (n = 17)	14.6 ± 4.5[a]	10.2 ± 2.0	1.43 ± 0.40	2.90

[a] Estimated by a regression of body length vs. other characteristics.
[b] Based on the average body size (3.5 ± 0.3 mm; n = 103) of free-living mancas.

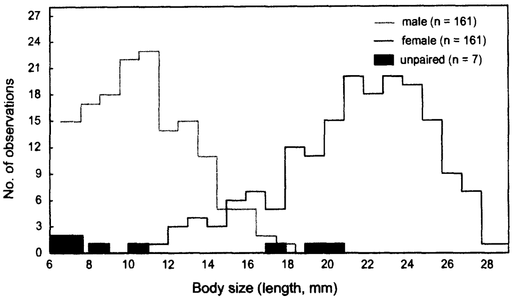

Fig. 3. Body size distributions of unpaired males and paired females and males of *Ichthyoxenus fushanensis* living in their host fish, *Varicorhinus bacbatulus*.

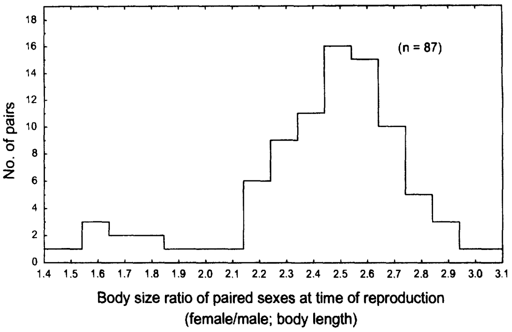

Fig. 4. Distribution of size ratios (body length ratio of a paired female and its mate) of mating pairs at time of reproduction in *Ichthyoxenus fushanensis*.

for her mate; or, at a certain age or stage, the male ceases to be tolerant towards his mate and treats her as prey. The brooding female of *I. fushanensis* always lies upside down inside the membranous sac and is less capable of moving than the male (Tsai and Dai, 1999). The male lies in a belly-to-belly position directly above the female, which may provide an opportunity to cannibalize the female, especially when she is in vulnerable conditions that accompany her ecdysis or breeding (Sparrevik, 1999).

Both types of cannibalism occurred during the breeding season and in those pairs whose host body length was less than 10 cm. The small host size implies that the resources provided by the host are limited, and thus, the victim could be a valuable resource for the cannibal. Such resource limitation is thought to increase cannibalism in many predatory arthropods (Polis, 1981; Leonardsson, 1991; Sparrevik and Leonardsson, 1998). Cannibalism can thus be viewed as an outcome of competition between a heterosexual pair. By preying on a smaller male, the female obtains additional energy resources and goes on to reproduce more times. In addition, by consuming his/her mate, the isopod on a marginal host ensures its own survival by ensuring the survival of the host.

Both types of cannibalism took place only in mating pairs with relatively similar body size (size ratio below 1.6). Additionally, female-on-male cannibalism occurred during the early stages of the breeding season, whereas the reversed type occurred later. This seasonal shift of two types of cannibalism is likely the outcome of intraspecific competition between protandrous individuals. The female is preying on smaller male early in the season before he gets too big to be an effective competitor. While later in the season, the male becomes larger and is more capable of preying on the female; he may consume the female when she is in vulnerable conditions. Cannibalism is then followed by sex change from male to female and the availability of free-living mancas during the breeding season ensures the re-establishment of a new mating pair after cannibalism.

Table 2. Simple and partial correlation coefficients (r) of host size, paired female size, and paired male size associated with clutch size (number of mancas) and size ratio of paired *Ichthyoxenus fushanensis* living in its host fish, *Varicorhinus bacbatulus* ($n = 161$).

	r (with clutch size)	P	r (with size ratio)	P
(a) Simple correlation				
Host size	0.811	<0.001	0.706	<0.001
Paired female size	0.987	<0.001	0.786	<0.001
Paired male size	0.493	<0.001	−0.872	<0.001
Size ratio (female/male; body length)	0.481	<0.001		
(b) Partial correlation (the effect of host size removed)				
Relative size ratio* vs. Clutch size[a]	0.874	<0.001		
Relative size ratio* vs. Relative clutch size[b]	0.419	<0.001		

* The residual part that unexplained by host size.
[a] Number of offspring being released per brood.
[b] Residual part that unexplained by female size.

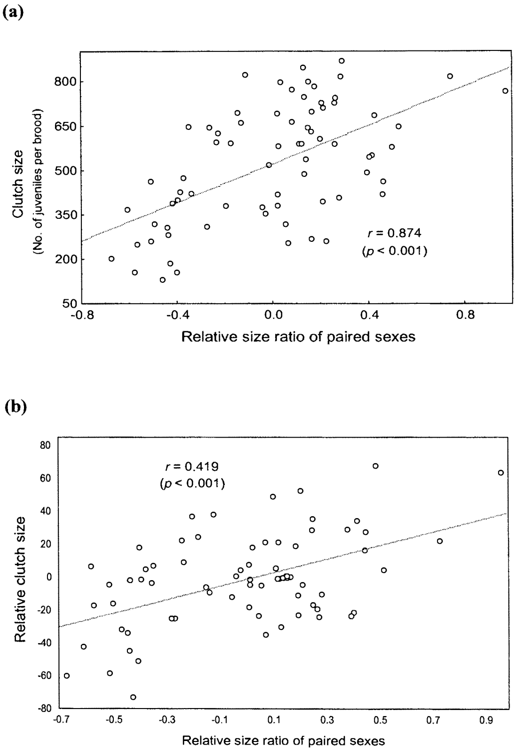

Fig. 5. Correlations of (a) absolute clutch size and (b) relative clutch size (with the effect of female size removed in a multiple regression model) with the relative size ratio of mating pairs (female/male) of the parasitic isopod *Ichthyoxenus fushanensis*.

Cannibalism and the Size Ratio of a Mating Pair

Body size affects survivorship, reproductive output, and individual fitness of many organisms and is among the most important determinants of organismal function (Honek, 1993; Claessen *et al.*, 2000; Twombly and Tisch, 2000). In many arthropods, body size of a female is generally associated with her fecundity (e.g., Wickman and Karlsson, 1989; Honek, 1993; Poulin, 1995; Tsai *et al.*, 1999, 2001). Patterns of sexual dimorphism in gonochoric organisms have been explained in terms of the consequences of body size for both reproductive output and survivorship, both of which may differ for males and females (Elgar and Fahey, 1995). For example, females of many insects and spiders are larger than males, perhaps because fecundity increases with body size in females. Alternatively, selection may favor protandry, resulting in a shorter developmental time and hence a smaller size of males (Tsai *et al.*, 1999).

For *I. fushanensis*, the size ratio between a mating pair may directly influence the number of offspring (Tsai *et al.*, 1999). Because of the low transmission rate of mancas, selection may favor a more productive female to compensate for the mass loss of mancas. Additionally, because of limitations of available resources from a host, there is a body size trade-off between a paired female and male (Tsai *et al.*, 2001). A more productive combination is a mating pair with a larger size ratio. The overlap of size distribution of the two sexes in nature and the large size ratio between paired females and males suggest that such sexual size dimorphism may be due to other factors besides protandrous sex change. Sexual cannibalism has been shown to significantly increase female body mass and fecundity in spiders and mantids (Birkhead *et al.*, 1988; Elgar and Nash, 1988; Elgar and Fahey, 1995). Both types of cannibalism result in a mating pair with a relatively larger female and a smaller new mate; thus, both types provide an effective way to increase the size ratio, which would then result in more offspring. In this way, the two types of intersexual cannibalism in *I. fushanensis* may significantly influence the performance of the mating system.

The Origin of Cannibalistic Behavior

The protandrous species *I. fushanensis* may provide a different way of viewing the evolution of sexual cannibalism, apart from the usual debate of "who benefits" (Johns and Maxwell, 1997). The consumption of a male may have the immediate benefit of allowing a larger female to produce more offspring, but the male loses the possibility to be a productive female in the future. If a larger female dies soon after releasing mancas—i.e., she can expect no future mating success—then the female has nothing to lose by being cannibalized, and the benefits of cannibalism could outweigh the costs. In this protandrous isopod, either sex may have the possibility to become a victim in nature. The cannibalistic behavior would not have evolved in response to selection on either the male or female stage. Both types of cannibalism in *I. fushanensis* may be regarded as the result of competition between paired individuals and may represent a special case of "economic cannibalism." It is possibly a by-product of the evolution of a reproductive strategy rather the consequence of sexual selection.

In conclusion, cannibalism is likely part of the biological repertoire of *I. fushanensis*. The occurrence of cannibalism in this species appears to be regulated by the size ratio of a mated pair and by host size. Both types of cannibalism of *I. fushanensis* appear to be the outcome of complex interactions between the paired female and male. These interactions may not only act on the development of cannibalistic behavior itself but also on the corresponding endogenous states. Cannibalism is not an artifact but is rather an important phenomenon that might play a significant role in maintaining the population.

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