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Polyandrous females discriminate against previous mates

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ABSTRACT **In most animal species, particularly those in which females engage in polyandry, mate choice is a sequential process in which a female must choose to mate or not to mate with each male encountered. Although a number of theoretical and empirical investigations have examined the effects of sequential mate choice on the operation of sexual selection, how females respond to solicitation by previous mates has received little attention. Here, we report the results of a study carried out on the polyandrous pseudoscorpion, *Cordylochernes scorpioides*, that assessed the sexual receptivity of once-mated females presented after a lapse of 1.5 hr or 48 hr with either their first mate or a different male. Females exhibited a high level of receptivity to new males, irrespective of intermating interval. By contrast, time between matings exerted a strong effect on female receptivity to previous mates. After a lapse of 48 hr, females did not differ significantly in their receptivity toward previous mates and different males, whereas at 1.5 hr after first mating, females were almost invariably unreceptive to males from whom they had previously accepted sperm. This result could not be attributed to male size or mating experience or to male sexual receptivity. Indeed, males were as willing to transfer sperm to a previous mate as they were to a new female. This difference between males and females in their propensity to remate with the same individual may reflect a conflict between the sexes, with males seeking to minimize postcopulatory sexual selection and females actively keeping open the opportunity for sperm competition and female choice of sperm by discriminating against previous mates.**

Theoretical models of sexual selection have traditionally assumed that females can maximize their reproductive success through precopulatory choice of the single best or most attractive male (1–4). However, this view of female mating behavior may be limited in its generality (5–7). Certainly, mate choice by females has been demonstrated in many species (reviewed in ref. 8), with choice based on assessment of male phenotypic characteristics such as body size, color, intensity of display, and complexity of song. However, in many other species, females do not appear to discriminate between males at the precopulatory stage (9–11). Moreover, there is now a considerable body of molecular data demonstrating that females across a wide array of taxa commonly mate with several males (reviewed in refs. 12–14). Although polyandry can sometimes be explained within the framework of promiscuous males and essentially choosy females (15, 16), in other cases, females appear to mate multiply as an active strategy for acquiring sperm from several males (11, 17, 18).

Although theoretical and empirical research on sexual selection has tended to focus on situations in which females can simultaneously evaluate a range of male phenotypes, in most species, females are likely to encounter potential mates in a sequential fashion (19–21). Under such conditions, a female must assess the current male against either an internal standard or her memory of males previously encountered (19, 20). Sequential mate choice is thus an iterative decision-making process in which a female must repeatedly choose whether to mate or not to mate. As Gabor and Halliday (21) have pointed out, the sequential model of female mate choice is likely to be particularly important in species in which females mate with more than one male.

In this paper, we report the results of a study that investigated sequential female choice in the polyandrous, neotropical pseudoscorpion, *Cordylochernes scorpioides*. Previous research has shown that *C. scorpioides* females typically refuse to accept more than one spermatophore during a mating event, but become receptive again if courted subsequently by a different male (11). Because males and females in nature do not remain together after mating, this tactic of staggering sperm collection across matings seemed sufficient to explain the high level of mixed paternity detected in the broods of field-inseminated females (22). Here, we demonstrate that polyandry in *C. scorpioides* is, in fact, a far more active strategy. In sequential-choice tests with a short (1.5 hr) lapse between matings, females recognized and rejected previous mates but accepted sperm from different males.

MATERIALS AND METHODS

Virgin males and females for this study were the laboratory-reared offspring of 54 female pseudoscorpions collected between December 1996 and December 1997 in the Republic of Panama from large populations inhabiting 10 decaying *Ficus* trees in the former Canal Zone and surrounding areas. After nymphs hatched from females' brood sacs, they were reared and maintained in individual vials, as described elsewhere (23). An additional 13 virgin individuals were obtained from laboratory rearing of field-collected immatures.

This study involved two experiments differing in the time lapse between consecutive matings. In the first experiment (Experiment 1), males and females were randomly assigned to one of two treatments, a "same-male" treatment (SM) in which females ($n = 26$) were each mated to a male and, 1.5 hr later, were given the opportunity to remate with the same male or a "different-male" treatment (DM) in which females ($n = 26$) were each mated to a male (male A) and, 1.5 hr later, were given the opportunity to mate with a second male (male B). The second experiment (Experiment 2), again with 26 replications for each treatment, was identical to the first, except that the time lapse between matings was increased to 48 hr. To equalize male mating experience and refractory period in the SM and DM treatments, replications in the DM treatment

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Abbreviations: DM, different male; SM, same male; TCL, total chela length; HD, chela hand depth; TD, tibia depth; FD, femur depth; CL, cephalothorax length; CW, cephalothorax width; PC1PALP, pedipalp composite measure; PC1CEPH, composite cephalothorax measure.

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were carried out in pairs and, for each pair, males were switched between the two replications for the second mating. For example, male A in replication 1 was used as male B in replication 2 and male A in replication 2 was used as male B in replication 1. Each replication was initiated by placing a virgin female with a virgin male in a 28-mm diameter mating arena. Interactions were videotaped with a Super VHS camcorder for 40 min under red fiber-optics illumination. Following this first mating opportunity, males and females were returned to their individual vials for 1.5 hr (Experiment 1) or 48 hr (Experiment 2). The second mating opportunity was carried out and videotaped, as above, with females being presented with either the same male as previously or a different male, depending on the experimental treatment.

The videotape of each mating was then transcribed to determine the number of spermatophores deposited and the number of sperm packets successfully transferred by the male to the female. In these pseudoscorpions, sperm transfer is indirect via a spermatophore deposited on the substrate. The spermatophore consists of a stalk, a ball of fluid, and at the apex of the stalk, a complex, folded, tubular packet containing the sperm (24). Mating involves a well defined sequence of behaviors in which the male grasps the female while he constructs and deposits a spermatophore. After spermatophore deposition, the male maneuvers the female into a position in which the sperm packet directly contacts her gonopore. High-magnification video analysis (×50) has revealed that successful attachment of the sperm packet to the gonopore only occurs when complete spermatophores are deposited (stalk + ball of fluid + sperm packet) and is associated with a pronounced abdominal flexure by the female (23). This flexure presses the sperm packet down onto the ball of fluid, causing a long, hooked tube to evert from the packet into the female's genital aperture, followed by evacuation of sperm into her reproductive tract. In a typical mating event, the male produces his first spermatophore within 6 min of encountering a female. A lapse of approximately 15 min is then required between successive spermatophore depositions, during which the male attempts to maintain his hold on the female.

This indirect method of sperm transfer makes female cooperation essential for successful insemination (11). Unreceptive females engage in one of several behaviors to block sperm transfer. In some cases, females aggressively resist males and terminate mating by breaking free from the male's grasp before he initiates construction of a spermatophore. Alternatively, females occasionally refuse to remain stationary during spermatophore deposition, forcing the male to move and lose contact with the still incomplete spermatophore. Finally, in the majority of cases, females cooperate with males throughout the entire period of spermatophore construction and deposition, only to resist being pulled forward over the sperm packet (11).

The combination of external spermatophore deposition and diagnostic female behavior provides a unique, noninvasive window on mating event characteristics such as the number of spermatophores accepted and rejected by a female. To obtain the 26 replications per treatment in each of these two experiments ($n = 104$ females total), we videotaped matings for 135 females, 31 of which had to be excluded from the analysis because (*i*) the female was clearly unreceptive in her first mating ($n = 2$), (*ii*) it was not possible to score spermatophore production and/or female receptivity unambiguously ($n = 14$), or (*iii*) the female was receptive (that is, allowed herself to be pulled over the spermatophore), but the male produced only defective spermatophores ($n = 15$). Spermatophores were scored as defective either because no spermatophore was visible when the videotape of the mating was transcribed or because an incomplete spermatophore (lacking either the ball of fluid or the sperm packet) was found attached to the mating-arena substrate immediately after the mating event had been terminated.

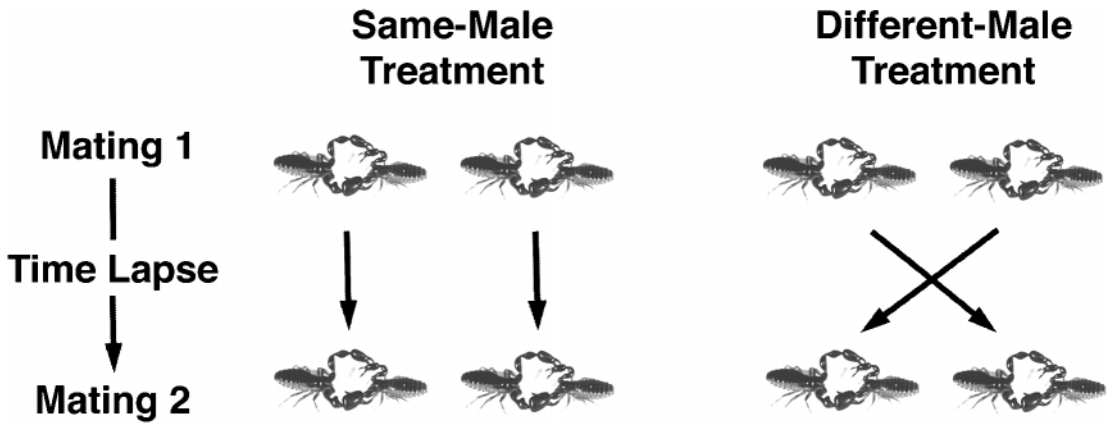
In this sexually dimorphic pseudoscorpion, male size has been found to be positively correlated with fighting ability and male reproductive success during dispersal (ref. 22, and see below). To investigate the effect of male size on the sexual receptivity of females at second mating, we used National Institutes of Health IMAGE (version 1.58) to compute linear measurements of six pedipalp and cephalothorax traits that are all fixed in size at the terminal molt to the adult stage: total chela length (TCL), chela hand depth (HD), tibia depth (TD), femur depth (FD), cephalothorax length (CL), and cephalothorax width (CW) (22) from high-magnification (approximately ×30) video images of live pseudoscorpions held flat under a glass slide with the right pedipalp fully extended. By using principal component analysis of these six morphological traits, we calculated composite size measures of the pedipalps (PC1PALP) and cephalothorax (PC1CEPH) for each male (22).

Because the numbers of sperm packets accepted by females in their first mating (one or two packets) and second mating (zero or one packet) were binomially rather than normally distributed, the maximum-likelihood option in the SAS categorical data modeling procedure, CATMOD (25), was used in statistical analyses.

RESULTS

In Experiment 1 (1.5-hr intermating interval), females typically accepted only a single sperm packet in their first mating, and the two treatments did not differ significantly in the mean number of sperm packets accepted (mean ± SEM: SM = 1.23 ± 0.08, DM = 1.12 ± 0.06; SAS CATMOD: $\chi^2 = 1.17$, $P = 0.276$). By contrast, there was a highly significant difference between treatments in the females' second mating, with females accepting sperm packets in only 4 of the 26 SM replications, compared with 18 of the 26 DM replications (Fisher's exact test: $P = 0.0002$; see Fig. 1). As a consequence, mean number of sperm packets transferred to a female in the second mating was significantly lower in the SM treatment than in the DM treatment (SAS CATMOD: $\chi^2 = 12.75$, $P = 0.0004$). The low rate of sperm transfer that occurred in the second matings of the SM treatment could not be attributed to lack of sexual stimulation of males presented with their previous mates. In 19 of the 22 replications in which no sperm transfer occurred (Fig. 2), the male deposited a spermatophore, but the female refused to be pulled over it. In the remaining three cases, the males attempted to initiate copulation but were thwarted by the aggressive behavior of the females.

In Experiment 2 (48-hr intermating interval), females again typically accepted only a single sperm packet in their first mating (Fig. 1), with no difference between treatments in mean number of sperm packets accepted (SM = 1.04 ± 0.04, DM = 1.04 ± 0.04; SAS CATMOD: $\chi^2 = 0.00$, $P = 1.0000$). In contrast to Experiment 1, we found no effect of treatment on female sexual receptivity after the 48-hr interval between matings. In their second mating, females accepted a sperm packet in 14 of the 26 SM replications, compared with 18 of the 26 DM replications (Fisher's exact test: $P = 0.393$; see Fig. 1). As a consequence, mean number of sperm packets transferred to a female in the second mating did not differ significantly between the two treatments (SAS CATMOD: $\chi^2 = 1.29$, $P = 0.2567$). In those replications in which no sperm packets were accepted in the second mating, absence of sperm transfer again could not be attributed to a lack of male sexual stimulation. In all 8 of the DM replications and 10 of the 12 SM replications in which no sperm transfer occurred (Fig. 2), the male deposited a spermatophore but the female refused to be pulled over it. In the remaining 2 cases, the female aggressively resisted the male's attempt to initiate copulation.



Time lapse	Proportion of females accepting sperm in 2nd mating	
1.5 h	4 of 26	18 of 26
48 h	14 of 26	18 of 26

FIG. 1. Design and results of two experiments in which the sexual receptivity of females given the opportunity to remate with the same male was compared with that of females presented with a different male. The two experiments differed only in the time lapse between matings (1.5 hr versus 48 hr).

When first spermatophores produced in first matings of the two experiments were scored as either normal or defective, we found a significant difference in patterns of female receptivity to the second spermatophore produced (Fisher's exact test, $P \ll 0.0001$). In only 10 of the 73 cases (14%) in which the male produced a normal first spermatophore did the female accept his second spermatophore. By contrast, in 14 of the 15 cases (93%) in which the male produced a defective first spermatophore, the female allowed herself to be pulled over the second spermatophore deposited by that male.

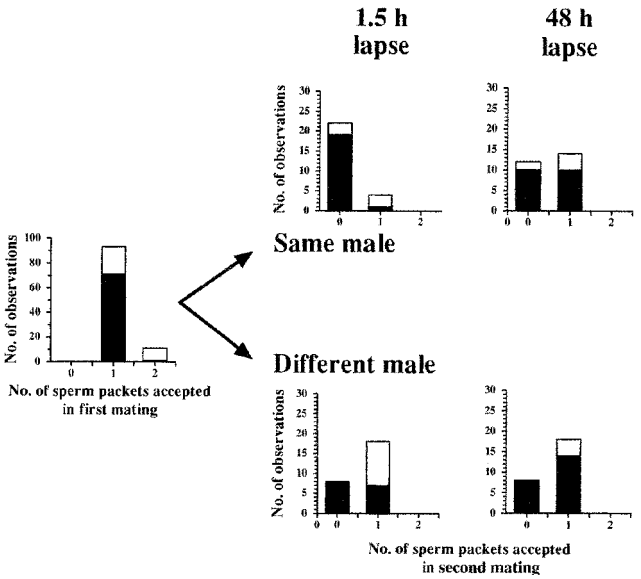


FIG. 2. Frequency distribution of the number of spermatophores accepted by females in their first mating (*Left*) and second mating (*Right*). For the females' first mating, data from both experiments (1.5-hr and 48-hr intermating interval) and mating treatments (SM and DM) were pooled. For the females' second mating, results were partitioned by intermating interval and mating treatment. Filled areas in the bars indicate the number of matings in which the male deposited an additional spermatophore that was rejected by the female.

As expected from the random assignment of individuals to treatments, males did not differ significantly between treatments for any of the six morphological traits measured (Experiment 1: TCL, $t = 0.103$, $P = 0.9184$; HD, $t = 0.104$, $P = 0.9177$; TD, $t = 0.021$, $P = 0.9833$; FD, $t = 0.280$, $P = 0.7809$; CL, $t = 0.298$, $P = 0.7672$; CW, $t = 0.003$, $P = 0.9975$; Experiment 2: TCL, $t = 0.432$, $P = 0.6675$; HD, $t = 0.817$, $P = 0.4180$; TD, $t = 0.724$, $P = 0.4727$; FD, $t = 0.995$, $P = 0.3246$; CL, $t = 1.392$, $P = 0.1702$; CW, $t = 1.496$, $P = 0.1408$). Similarly, in neither experiment did males differ significantly between treatments in terms of their pedipalp and cephalothorax composite size measures (Experiment 1: PC1PALP, $t = 0.103$, $P = 0.9182$; PC1CEPH, $t = 0.158$, $P = 0.8751$; Experiment 2: PC1PALP, $t = 0.702$, $P = 0.4860$; PC1CEPH, $t = 1.527$, $P = 0.1331$). To determine whether male morphology influenced female receptivity at second mating, we carried out the CATMOD equivalent of an analysis of covariance for each male trait separately, with treatment type as the categorical variable. None of the six traits or the PC1CEPH or PC1PALP (Fig. 3) composite size scores had a significant effect on the number of sperm packets accepted in either Experiment 1 or Experiment 2 (Experiment 1: TCL, $\chi^2 = 0.68$, $P = 0.4105$; HD, $\chi^2 = 0.11$, $P = 0.7451$; TD, $\chi^2 = 0.31$, $P = 0.5805$; FD, $\chi^2 = 0.02$, $P = 0.8951$; CL, $\chi^2 = 0.06$, $P = 0.8131$; CW, $\chi^2 = 0.44$, $P = 0.5054$; PC1PALP, $\chi^2 = 0.16$, $P = 0.6857$; PC1CEPH, $\chi^2 = 0.25$, $P = 0.6199$; Experiment 2: TCL, $\chi^2 = 2.02$, $P = 0.1553$; HD, $\chi^2 = 1.77$, $P = 0.1833$; TD, $\chi^2 = 2.03$, $P = 0.1547$; FD, $\chi^2 = 0.86$, $P = 0.3543$; CL, $\chi^2 = 4.19$, $P = 0.0406$; CW, $\chi^2 = 0.26$, $P = 0.6132$; PC1PALP, $\chi^2 = 2.01$, $P = 0.1567$; PC1CEPH, $\chi^2 = 2.00$, $P = 0.1577$). When the significance level was adjusted for multiple comparisons by using the sequential Bonferroni method, the P value for CL in Experiment 2 was not significant (critical $P = 0.05/6 = 0.0083$).

DISCUSSION

This study provides evidence that female *C. scorpioides* recognize and discriminate against previous mates over short time intervals. Whereas 69% of females were sexually receptive when presented with a different male 1.5 hr after their first

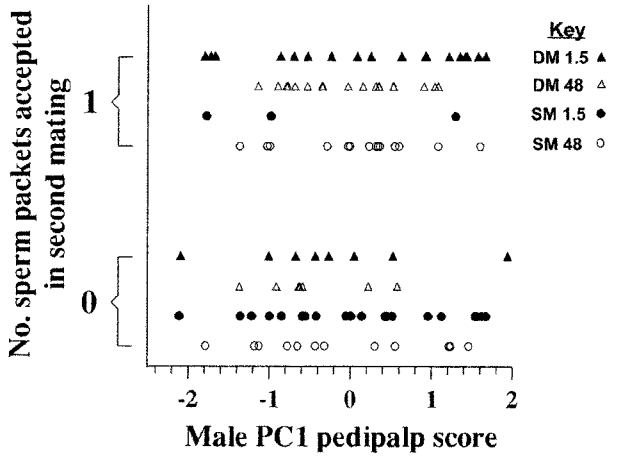


FIG. 3. Graph illustrating the absence of any relationship between the number of sperm packets transferred by a male to a female in her second mating (0 or 1) and a composite measure of the male's pedipalp size (PC1PALP). Data are categorized, as indicated in the key, by mating treatment (SM or DM) and intermating interval (1.5-hr or 48-hr).

mating, only 15% of females accepted a sperm packet when given the opportunity to remate with their first mate after this short intermating interval. This result could not be attributed to reduced libido toward previous mates on the part of males. In this experiment, in which we controlled for male size, mating experience, and refractory period, we found no between-treatment difference in males in their propensity to produce a spermatophore in their second mating. All males in the SM (and hence same-female) treatment attempted to initiate copulation in their second mating, and, in 23 of the 26 replications, reached the stage of depositing a spermatophore and trying to pull the female over it.

Female discrimination against previous mates largely disappeared when the interval between matings was increased to 48 hr, with 54% of females accepting a sperm packet in second matings of the SM treatment, compared with 69% in the DM treatment. Although the mechanism responsible for mate recognition remains to be investigated, perhaps the most parsimonious explanation, given this temporal breakdown in discrimination, is that females deposit a chemical cue on their mates that dissipates through time. Under natural conditions, such lability would not necessarily limit the utility of the chemical cue. Interestingly, unreceptive females typically allow males to proceed through the entire process of spermatophore construction and deposition before terminating the mating, thereby providing ample opportunity for renewal of a chemical cue. The alternative hypothesis that females are able to recognize distinctive features of individual males could also explain our findings, if pseudoscorpions possess a capacity for short-term but not long-term memory, as has been shown in mate choice studies on some birds (26) and fish (27).

Given the low probability of encountering previous mates within the large, decaying trees that serve as the primary habitat of *C. scorpioides*, it seems likely that the ability of females to recognize previous mates might have evolved as a consequence of selection acting on females during dispersal. This neotropical pseudoscorpion gains access to the rich, but patchily distributed and ephemeral, habitats of decaying trees in the families Moraceae and Apocynaceae by hitchhiking under the elytra of the harlequin beetle, *Acrocinus longimanus* (22). This novel mode of dispersal has been exploited by males who fight to force off rivals to monopolize beetle abdomens as strategic sites for intercepting and inseminating dispersing females (22). After its "maiden flight," a beetle typically carries under its elytra a single, large male pseudoscorpion, defending a mating territory on its abdomen. Dispersing females are therefore likely to experience repeated mating attempts by individual males within the confines of the harlequin beetle's subelytral space.

Our morphometric analyses demonstrated that male size exerted no effect whatsoever on a female's decision to accept or not to accept sperm in her second mating. Of particular interest was the finding that females remained receptive to males that produced defective spermatophores on their first attempt. This suggests that a critical factor determining female sexual receptivity toward a male is whether she has previously received sperm from that male. Certainly, female tolerance in response to male sexual incompetence seems inconsistent with a traditional "good genes" model of sexual selection as the basis for female choice in this pseudoscorpion. Because neither male size nor our measure of male sexual performance exerted an influence on female receptivity, this study failed to detect any evidence of female mate choice based on phenotypic indicators of inherent male genetic quality. Instead, an active strategy of accumulating sperm from more than one male appears to be the driving force shaping female mating decisions in this pseudoscorpion. Previous research has demonstrated that *C. scorpioides* females accept only the first of two or more sperm packets deposited by a male during a single mating event (11). Here, the results of our sequential-choice tests show that the "one male/one sperm-packet" rule extends to re-encounters with the same male, at least over the short term. Why should females limit the amount of sperm they accept from a particular male in this way? Single-locus DNA profiling of this pseudoscorpion has demonstrated extremely high variability at minisatellite loci, with heterozygosities of 95% to 99% in field populations (22, 28). We suggest that, by discriminating against previous mates, these sperm-storing females effectively ensure that they acquire sperm that are genetically diverse, at least at the level of heterochromatin, before fertilizing their eggs and producing a brood.

The question of whether females are less likely to accept sperm from previous mates than from different males has not previously been addressed with carefully controlled experiments, and the generality of our findings therefore remains to be determined by similar studies on other species. Certainly, females do remate with previous mates in nature, and multiple copulations with one male are not limited to socially monogamous species. Females have been observed to remate with the same male in a number of arthropod species that display neither pair-bonding nor paternal care (29), and a variety of hypotheses have been proposed to explain why females should copulate repeatedly with one male (30). However, as our results demonstrate, discrimination against previous mates may be a short-term phenomenon, and thus not easily detectable. Indeed, the growing molecular evidence that females across a wide range of species produce mixed-paternity broods (14) and therefore engage in polyandry suggests that female discrimination against previous mates may be more common than is currently appreciated.

Given the potentially high costs of multiple mating (31, 32), why do females often engage in polyandry? Hypotheses to explain polyandry can be broadly classified as proposing either material or genetic benefits (33, 34). In *C. scorpioides,* previous research has demonstrated that females that mate with more than one male achieve higher reproductive success than females restricted to a single mate, largely because they suffer a much lower rate of embryo failure (11). This embryo failure cannot be attributed to inferior material benefits received from the male or to intrinsic male genetic quality but most likely results from genetic incompatibility between maternal and paternal genomes (11). Such genetic incompatibility is unlikely to be manifested at the phenotypic level; therefore, females cannot rely on conventional precopulatory mate choice to defend against this threat to their reproductive success. In

contrast, by accumulating a genetically diverse sperm supply, females that mate with more than one male shift the arena for sexual selection from the external environment to their own reproductive tract, where interactions at the molecular and cellular level may provide females with direct, postcopulatory mechanisms for assessing genetic incompatibility (7, 11). A variety of other genetic-benefit hypotheses have also been proposed to account for polyandry (5, 35–40). With the exception of the "offspring-diversity hypothesis" (35, 37), these explanations have in common an emphasis on the potential for postcopulatory processes to increase female fitness and hence to influence female mating strategies.

Just as sexual selection may be better understood as a process in which males compete not for females themselves but for access to females' gametes (13, 41), so too may sexual selection be viewed as a process in which females choose not males themselves but rather the sperm which will fertilize their eggs. Indeed, in viviparous species such as *C. scorpioides*, a female may exert choice even beyond fertilization to the selection of embryos possessing paternal genomes that best promote successful embryonic development within her reproductive tract. Seen from this perspective, postcopulatory sexual selection is a process in which the interests of males and females may be diametrically opposed. On the one hand, males can increase their reproductive success by minimizing the opportunity for postcopulatory sexual selection. A male may, for example, increase his access to a female's gametes by numerically overwhelming competitors' sperm through prolonged copulation or remating (42). This may explain why *C. scorpioides* males are as willing to transfer sperm to females they have already inseminated as they are to new females. By contrast, if sperm competition, female choice of sperm, and reallocation of maternal resources from defective to viable embryos can enhance female reproductive success, then females should promote postcopulatory sexual selection by engaging in polyandry and by discriminating against previous mates, opting instead to acquire sperm from different males.

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