



# Spontaneous abortion depresses female sexual receptivity in a viviparous arthropod

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The 'trading-up' hypothesis for polyandry, which posits that females copulate with additional males as a means of improving on the quality of their first mating partner, has been proposed as a general explanation for mixed paternity in socially monogamous birds. As a corollary of this hypothesis, abnormally low reproductive output with a first partner should act as a strong stimulus for females to accept sperm from a new male. To test this prediction in a naturally polyandrous, sperm-storing, viviparous species, we restricted female *Cordylocheres scorpioides* pseudoscorpions to mating with a single male and then gave them the opportunity to remate with a different male after their first brood of embryos either aborted spontaneously, was experimentally removed, or was successfully carried to term. With complete brood failure presumably providing the strongest possible cue to females of a poor-quality first mate, the trading-up hypothesis would predict that females that aborted their first brood should have been significantly more sexually receptive than females that had produced a successful first brood. Instead, they were significantly less receptive. Furthermore, none of the sexually unreceptive, spontaneously aborting females produced a successful second brood, indicating that *C. scorpioides* females that copulate with a single male may become locked into cycles of brood failure followed by sexual unreceptivity. Our findings suggest that the negative impact of abortion on female sexual receptivity may place physiological constraints on the ability of viviparous females to use polyandry as a facultative mating strategy for improving on a bad first mate.

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Females of many species mate with more than one male and may derive a variety of material benefits from engaging in such polyandrous behaviour (e.g. Gwynne 1984; Hoogland 1998; Ivy et al. 1999). Alternatively, the benefits to polyandry may be genetic (e.g. Tregenza & Wedell 1998). In socially monogamous birds, molecular genetic evidence of extrapair paternity has led to the hypothesis that polyandry is a facultative mating strategy that depends on the genetic quality of a female's 'social mate'. According to this 'trading-up' hypothesis, females may often engage in extrapair copulation with a superior male in order to compensate for a breeding partner of relatively poor quality (Wetton & Parkin 1991; Kempenaers et al. 1992; Hasselquist et al. 1996; Petrie & Kempenaers 1998). The trading-up hypothesis thus makes the clear prediction that the production of poor-quality offspring, abnormally low reproductive output, or complete reproductive failure with a first partner should stimulate females to copulate with a different male.

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In viviparous species, reproductive failure is manifested as spontaneous abortion, a common but poorly understood phenomenon (Hertig & Rock 1959; Hertig et al. 1959; Alberman 1988; Hill 1995; Valhé et al. 1999). Testing the trading-up hypothesis in viviparous females that store sperm and can therefore potentially 'mate for life' provides an excellent opportunity to investigate the causal relationship between abortion and polyandry. Has spontaneous abortion resulting from embryonic inviability driven the evolution of polyandry (Zeh & Zeh 1996, 1997; Newcomer et al. 1999), or has the evolution of polyandry made selective/differential abortion available to viviparous females as an adaptive strategy for maximizing the genetic quality of their offspring (Birkhead & Møller 1998; Møller 1998)? Unfortunately, investigating the causes and consequences of abortion is seriously hampered in most viviparous animals precisely because embryos develop within the female and the intrusive and/or technologically complex methods required to diagnose abortion render its study impracticable. By contrast, spontaneous abortion, particularly of entire broods, is easily diagnosed in pseudoscorpions. Females nourish developing embryos in a translucent, external brood sac

overlying the genital opening (Weygoldt 1969). This form of viviparity makes it possible to accurately assess gravidity and subsequent spontaneous abortion.

Here, we exploit the unique features of pseudoscorpion reproductive biology in a study designed to investigate the potential constraints on trading-up in a sperm-storing, viviparous species. In the harlequin beetle riding pseudoscorpion, *Cordylochernes scorpioides*, females can store sperm indefinitely (Newcomer et al. 1999) and acquiring sperm from more than one male prior to offspring production is an active mating strategy. Females recognize and discriminate against previous mates, preferring instead to accept sperm from different males (Zeh et al. 1998). If experimentally restricted to multiple inseminations by a single male, females suffer a significantly higher rate of spontaneous abortion compared with females accepting the same quantity of ejaculate from two different males (Newcomer et al. 1999). In the experiment reported here, all females were restricted to mating with a single male and were then given the opportunity to engage in polyandry after their first brood either aborted spontaneously, was experimentally removed, or was successfully carried to term. The pattern of sexual receptivity shown by these females was found to be the opposite of that predicted by the trading-up hypothesis, with both spontaneous and experimentally induced brood abortion acting to suppress rather than stimulate female sexual receptivity towards a different male. Taken together with previous findings, our results suggest that polyandry in *C. scorpioides* is a pre-emptive mating strategy for minimizing the impact of potentially costly abortions on female reproductive success.

### Biology of *Cordylochernes scorpioides*

Distributed throughout the rain forests of Central and South America (Beier 1948), *C. scorpioides* inhabits decaying trees in the families Moraceae and Apocynaceae. The pseudoscorpions gain access to these rich but patchily distributed and ephemeral habitats by hitchhiking under the elytra of the giant harlequin beetle, *Acrocinus longimanus* (Zeh & Zeh 1992). Because of this obligate association, pseudoscorpion colonization is restricted to the brief period when newly fallen or dying trees attract beetles for mating and oviposition (Zeh et al. 1992b). Populations in dead trees remain marooned for several generations until beetle larvae complete development and the pseudoscorpions can climb on board new adult harlequins to disperse en masse. This novel mode of dispersal has been exploited by males that fight to monopolize beetle abdomens as strategic sites for intercepting and inseminating dispersing females (Zeh & Zeh 1992). DNA profiling has demonstrated a strong, positive correlation between male size and reproductive success during the pseudoscorpion's dispersal phase on beetles (Zeh et al. 1997). However, this intense selection is undermined by polyandry and sperm storage by females. After dispersal, the majority of females produce mixed-paternity broods sired by up to four males (Zeh et al. 1997). Evidence suggests that many of these offspring are sired by males that females had mated with before boarding beetles to

disperse. Polyandry and prolonged sperm storage may therefore enable smaller males to circumvent the bottleneck of dispersal-generated sexual selection and thereby transmit their genes to future tree populations.

As invertebrates that are both polyandrous and viviparous, these pseudoscorpions possess a suite of reproductive and behavioural traits that makes them highly amenable to investigation of the proximate mechanisms and evolutionary causes of polyandry in the context of viviparity. 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 (Weygoldt 1969). Mating involves a well-defined sequence of behaviours in which the male grasps the female while he constructs and deposits a spermatophore. After spermatophore deposition, the male manoeuvres the female into a position where the sperm packet directly contacts her gonopore. Successful attachment of the sperm packet to the gonopore is associated with a pronounced abdominal flexure by the female (Zeh & Zeh 1994). 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.

This indirect method of sperm transfer makes female cooperation essential for successful insemination (Zeh 1997). Females typically accept only the first of two or more sperm packets deposited by a male during a single mating event (Zeh 1997; Zeh et al. 1998). Unreceptive females engage in one of several behaviours to block sperm transfer. In some cases, females aggressively resist the male 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, the female cooperates with the male throughout the entire period of spermatophore construction and deposition, only to resist being pulled forward over the sperm packet (Zeh 1997). The combination of external spermatophore deposition and diagnostic female behaviour provides a unique, noninvasive window on mating event characteristics, such as the number of spermatophores accepted and rejected by a female.

In pseudoscorpions, egg membranes rupture early in development and individual embryos use a specialized mouth precursor (the pumping organ) to actively draw nutritive fluid, consisting of phospholipids, proteins and polysaccharides, from the mother's reproductive tract (Weygoldt 1969). Embryos develop in a translucent brood sac overlying the female's genital aperture and development can be easily monitored with minimal disturbance to mother or embryos. This 'external-womb' form of viviparity circumvents the technical difficulties of diagnosing spontaneous abortion in other viviparous species such as mammals. After becoming gravid, *C. scorpioides* females use frass and silken threads to construct a brood nest. Embryos require approximately 14 days to complete

**Table 1.** Level of sexual receptivity in females 24 h after they aborted their first brood (aborted-first-brood females), successfully gave birth to nymphs (successful-first-brood females), or had their brood sacs experimentally removed (experimental-removal females)

Female category	Number of sexually receptive females	Number of sexually unreceptive females
Aborted-first-brood females	7	14
Successful-first-brood females	20	3
Experimental-removal females	6	14

Fisher's exact test:  $N=64$ ,  $P=0.00005$ .

development, and birth occurs when the embryos rupture the brood sac and emerge as protonymphs (see Weygoldt 1969). After birth, nymphs remain in the nest for approximately 2 days until they are fully sclerotized (Zeh 1997).

## METHODS

Virgin males and females for this study were the laboratory-reared offspring of 31 field-inseminated females collected in December 1996 from large populations inhabiting three decaying *Ficus* trees in the former Canal Zone of the Republic of Panama. Previous research involving both multilocus and single-locus DNA profiling has demonstrated that such tree populations are founded by highly genetically diverse breeding groups of unrelated individuals (Zeh et al. 1992a, 1994, 1997). Levels of heterozygosity within large tree populations do not differ significantly from heterozygosity estimates based on random samples of individuals collected from multiple trees (Zeh et al. 1994, 1997; D.W. Zeh, unpublished data).

After birth, nymphs were reared individually, as described elsewhere (Zeh & Zeh 1994). On attaining sexual maturity, we allowed virgin females ( $N=228$ ) from each of these families to mate with a single, virgin male. To avoid possible confounding effects of inbreeding depression, no matings were carried out between full siblings or half-siblings. With this exception, we paired males and females randomly. It was necessary to carry out a large number of single-male matings to obtain a statistically sufficient number of cases of spontaneous brood abortion for the aborted-first-brood category of females in this experiment. After mating, we maintained females individually in transparent, plastic vials containing naturally produced *Ficus* frass, and fed them 8–10 late-instar *Tribolium confusum* larvae per week. We monitored female reproductive status every 3–4 days until brood sac production, and then once per day thereafter. Since females generally construct their brood nests on the walls of their vials and embryonic development within the brood sac is readily visible with the naked eye, it was possible to monitor females and embryos with minimal disturbance. A female was categorized as having suffered spontaneous abortion of her entire brood if her brood sac detached prematurely from her abdomen and no protonymphs were born. For females whose first brood was successful, we removed protonymphs from the brood nest immediately after birth and counted them.

To evaluate the effect of reproductive outcome with first mating partner on the propensity of females to accept sperm from a second male, approximately 24 h after either first-brood spontaneous abortion or the birth of the first brood of nymphs, we allowed aborted-first-brood females ( $N=21$ ) and a random sample of successful-first-brood females ( $N=23$ ) the opportunity to remate with a new male. For each of the two first-brood categories, we initiated replications by placing the female with a randomly chosen, nonsibling male in a 28-mm diameter mating arena. We videotaped interactions using a Super VHS camcorder for 30 min under red, fibre-optics illumination. We then transcribed the videotape of each mating to determine the number of spermatophores deposited and the number of sperm packets successfully transferred by the male to the female. We assessed the influence of first-brood abortion and postabortion sexual receptivity on subsequent female reproductive success by monitoring aborted-first-brood females for 35 days following their remating opportunity, as described above.

To investigate whether abortion per se influences female sexual receptivity rather than some unknown correlate of abortion, such as poor female condition, we carried out a manipulative experiment in which we randomly selected gestating females ( $N=20$ ) carrying late-stage embryos (8–11 days after brood sac production) for brood sac removal ('experimental-removal' females). In this pseudoscorpion, a fine tube connects the embryos developing within the external brood sac to the mother's reproductive tract. Gestation can be experimentally terminated with minimal disturbance to the female by gently lifting the brood sac from the female's abdomen, thereby severing the connecting tube. Twenty-four hours after brood sac removal, we gave each female the opportunity to remate, as described above. We then transcribed videotapes of the matings to assess female sexual receptivity.

## RESULTS

Level of sexual receptivity in the successful-first-brood category was very high, with 20 of the 23 females (87%) accepting a sperm packet 24 h after giving birth to nymphs (Table 1). Interestingly, of the three females that were sexually unreceptive, two had given birth to very few nymphs (six and eight nymphs). These broods sizes were more than one standard deviation below the mean number of nymphs born to females in the successful-first-brood category ( $\bar{X} \pm SD = 39 \pm 25$ ,  $N=23$ ). By contrast,

level of sexual receptivity in the aborted-first-brood category of females was low, with only seven of the 21 females (33%) accepting a sperm packet (Table 1). This difference was highly significant (Fisher's exact test:  $N=44$ ,  $P=0.0005$ ). The low rate of sperm transfer to the aborted-first-brood females could not be attributed to lack of sexual stimulation in males. The mean number of spermatophores deposited by males placed with aborted-first-brood females ( $\bar{X} \pm SE=1.76 \pm 0.19$ ) did not differ significantly from that deposited by males placed with successful-first-brood females ( $1.83 \pm 0.15$ , Mann-Whitney  $U$  test:  $U=239$ ,  $N_1=21$ ,  $N_2=23$ ,  $P=0.949$ ). Furthermore, in 12 of the 14 replications of the aborted-first-brood female category in which no sperm transfer occurred, the male deposited at least one spermatophore, but the female refused to be pulled over it. In the remaining two replications, the males attempted to initiate copulation but were thwarted by the aggressive behaviour of the females.

In the 35 days following the remating opportunity, one of the 14 sexually unreceptive females in the aborted-first-brood category died and the remaining 13 either produced a second brood sac of embryos, which subsequently aborted ( $N=6$ ), or did not produce another brood sac ( $N=7$ ). To test whether sexually unreceptive first-brood females became receptive with time, the latter females ( $N=7$ ) were given a second opportunity to remate 14 days after aborting their first brood. All seven females were once again found to be sexually unreceptive. Of the seven aborted-first-brood females that had accepted a sperm packet in their second mating, three successfully gave birth to nymphs and four produced a second brood sac that aborted.

The level of sexual receptivity displayed by females whose brood sacs had been experimentally removed did not differ significantly from that of females whose broods had aborted naturally (Fisher's exact test:  $N=43$ ,  $P=1.000$ ), with six of 20 females (30%) accepting a sperm packet (Table 1). Once again, the low rate of successful sperm transfer in these matings could not be attributed to male effects. The mean number of spermatophores deposited by males mated to experimental-removal females ( $1.90 \pm 0.19$ ) did not differ significantly from that deposited by males in the other two categories (Kruskal-Wallis ANOVA:  $H_{61}=0.111$ ,  $P=0.946$ ), and, in each of the 14 replications in which the female was sexually unreceptive, the male deposited at least one spermatophore. Unlike females in the spontaneously aborting category, the majority of females in the experimental-removal group (17 of 20) went on to produce a second brood sac within 14 days of first-brood abortion. It was therefore not possible to give experimental-removal females a second remating opportunity, since gravid females are incapable of accepting sperm and are thus invariably sexually unreceptive.

## DISCUSSION

The results of this study demonstrate that singly mated *C. scorpioides* females that have experienced brood abortion remain sexually unreceptive, in marked contrast

to females that have carried broods to term. Within 24 h of successfully giving birth to nymphs, 87% of females accepted sperm from a new male. This level increased to 95% when three females that had given birth to abnormally small broods (4, 6 and 8 nymphs) were excluded from the analysis. By contrast, the level of sexual receptivity in females whose brood of embryos had spontaneously aborted was significantly lower, with only 33% accepting sperm. Because unreceptive *C. scorpioides* females do not generally reveal their unwillingness to accept sperm until after the male has deposited a spermatophore, it was possible to eliminate differences in male sexual motivation as a possible explanation for differences in rate of sperm transfer to aborting and nonaborting females. Furthermore, randomly selected females whose brood sacs had been experimentally removed were as sexually unreceptive 24 h after brood sac removal as females whose broods had aborted naturally. It thus seems likely that the low level of sexual receptivity displayed by the spontaneously aborting females was the result of embryo abortion per se rather than a consequence of poor female condition. Unfortunately, sexual receptivity of the experimental-removal females could not be tested through time, and it was therefore not possible to completely eliminate the 'poor female quality' hypothesis. However, we have shown elsewhere that, when females are given the opportunity to mate with more than one male prior to first brood production, they suffer a significantly reduced rate of spontaneous abortion compared with females restricted to multiple inseminations by a single male (Newcomer et al. 1999). Poor female quality could therefore provide at best only a partial explanation for the results reported here.

While the precise mechanisms through which abortion depresses sexual receptivity remain to be determined, it seems likely that, in these viviparous females, the endocrine balance required for nourishing broods of developing embryos differs significantly from that of nongestating females. Our results suggest that, when broods are successfully carried to term, birth of the nymphs acts as a switch, triggering a change in maternal hormone production, a return to nongestation concentration levels, and a reinstatement of sexual receptivity. Without such a switch, the hormone balance of aborting females remains set up for nourishing embryos and serves as a block to remating. In mammals, both recurrent spontaneous abortion (Bussen et al. 1999) and low female libido (Petty 1999) are known to be associated with abnormalities in the secretion of the pituitary hormone prolactin. In invertebrates, female sexual receptivity has been linked to levels of both dopamine (Neckameyer 1998) and juvenile hormone (Kerr et al. 1997; Schal et al. 1997) but, to our knowledge, the consequences of spontaneous abortion for hormone balance and female sexual receptivity have not been investigated.

With complete brood failure presumably providing the strongest possible cue to females of a poor-quality first mating partner, the trading-up hypothesis would predict that females in the aborted-first-brood category of this study should have been significantly more receptive to receiving sperm from a different male than females that

had produced a successful first brood. Instead, they were significantly less receptive. Furthermore, by refusing to accept sperm from a different male, these females failed to take advantage of the opportunity to potentially improve their future reproductive success. With none of the sexually unreceptive, aborted-first-brood females bringing a second brood successfully to term, our findings indicate that *C. scorpioides* females that mate with only one male prior to producing their first brood run the risk of becoming locked into a cycle of brood failure followed by sexual unreceptivity.

In this experiment, males were randomly allocated to females as first mates. It might therefore be argued that the results reported here do not provide a legitimate test of the trading-up hypothesis because virgin experimental females were deprived of the opportunity to exercise choice and reject nonpreferred males. The experimental design may thus have exposed females to a risk of spontaneous abortion that is never experienced under natural conditions. Several lines of evidence suggest that this criticism is invalid in the context of the mating behaviour of *C. scorpioides* females. In this pseudoscorpion, as in many other animal species, females encounter potential mates in a sequential fashion and do not have the opportunity to simultaneously evaluate a range of male phenotypes (Zeh et al. 1998). Under such conditions, a female must assess the current male against either an internal standard or her memory of males previously encountered (Gabor & Halliday 1997). Sequential mate choice is thus an iterative decision-making process in which a female must repeatedly choose whether to mate or not to mate. Our previous research has shown that *C. scorpioides* females are almost invariably sexually receptive as virgins but exercise choice at second mating when they discriminate against previous mates and preferentially accept sperm from different males (Zeh et al. 1998). In a study that involved large sample sizes, multivariate morphometric analyses and a measure of male sexual performance, we were unable to detect any evidence of female mate choice based on phenotypic indicators of inherent male genetic quality (Zeh et al. 1998). Furthermore, as described above, *C. scorpioides* females have complete control over sperm transfer and cannot be coerced into accepting sperm packets from males (Zeh et al. 1998). In the study reported here, females were experimentally precluded from engaging in polyandry prior to first brood production. However, as virgin individuals, they were not deprived of their usual opportunity to exercise choice in whether or not to accept sperm. At a more general level, it should also be pointed out that constraints on mate choice provide the very basis for the trading-up hypothesis. Polyandry is hypothesized to result from ecological or social factors that constrain females into accepting less-than-optimal first mates.

The pattern of female sexual receptivity revealed by this study suggests that polyandry in this pseudoscorpion is not a facultative mating strategy in which females use low reproductive success with a first mating partner as a cue for remating with a different male in order to acquire more viable paternal genes for their offspring. Indeed, the negative impact of abortion both on a female's

reproductive success and on her subsequent propensity to remate strongly suggests that *C. scorpioides* females should avoid abortion, rather than using it as a means of optimizing the genetic quality of their offspring. Elsewhere, we have shown that *C. scorpioides* females significantly reduce the rate of total brood abortion by mating with more than one male before fertilizing any eggs (Zeh 1997; Newcomer et al. 1999). In an experiment that controlled for male mating experience and the amount of ejaculate received, females that acquired sperm from two different males prior to producing their first brood reduced their rate of total brood abortion by 33%, thereby increasing their lifetime reproductive success by 32%, compared with females mated twice to a single male (Newcomer et al. 1999). Reduction in spontaneous abortion rate through polyandry could result from reduction in the rate of fertilization of eggs either by genetically incompatible sperm or by sperm carrying intrinsically inferior haploid genomes, incapable of successfully supporting embryonic development. If poor genetic quality of males and/or sperm were the primary cause of embryo failure, the reproductive consequences of mating with a particular male should be consistent across females. However, in a study in which 67 males were each mated to two females, the numbers of nymphs born to each male's two mates were completely uncorrelated (Zeh 1997). Broods of both females failed for only two of the 67 males, whereas, for 25 males, mating resulted in complete brood failure in one female but successful nymph production in the other. Given this absence of consistent effects of male genotype on female reproductive success, the enhanced reproductive success of polyandrous females appears most consistent with the genetic incompatibility avoidance hypothesis.

The generality of the findings reported here is at present unclear, since the impact of spontaneous abortion on female sexual receptivity remains to be investigated in other viviparous species. None the less, our results do suggest that trading-up as a female mating strategy, although supported by studies of several bird species (Petrie & Kempnaers 1998; Jennions & Petrie 2000), may be under greater constraints in viviparous species. Live-bearing females differ from egg-laying females in two important respects. First, viviparity is likely to make females particularly vulnerable to reproductive loss through genetic incompatibility, because the development of the embryo within the mother creates potential for genomic-conflict-based incompatibility that is not present in oviparous species (Zeh & Zeh 1996, 1997, 2000, 2001). With viviparity, conflict can arise not only between male and female mates, but also between mothers and developing embryos and between sibling embryos (see Spencer et al. 1998, 1999). Second, as this study demonstrates, the ability of viviparous females to engage in trading up from an unpropitious first partner may be constrained by detrimental effects of abortion on sexual receptivity that obviously are not experienced by females that lay eggs. For a viviparous female, mating with more than one male before attempting to reproduce would seem to have two advantages over the trading-up strategy. A multimale sperm pool not only minimizes the

risk that all embryos will be aborted but also may result in a mixed-paternity brood, thereby allowing females to shunt maternal resources from any failing, defective embryos to embryos that are developmentally viable. At least in the case of *C. scorpioides*, it seems likely that pre-emptive polyandry rather than facultative polyandry provides these viviparous females with the best defence against the negative impact that complete brood abortion can have on their future reproductive success.

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### References

- Alberman, E. 1988. The epidemiology of repeated abortion. In: *Early Pregnancy Loss: Mechanisms and Treatment* (Ed. by R. W. Beard & F. Sharp), pp. 9–17. New York: Springer-Verlag.
- Beier, M. 1948. Phoresie und Phagophilie bei Pseudoscorpionen. *Österreichische Zoologische Zeitschrift*, **1**, 441–497.
- Birkhead, T. R. & Møller, A. P. 1998. Sperm competition, sexual selection and different routes to fitness. In: *Sperm Competition and Sexual Selection* (Ed. by T. R. Birkhead & A. P. Møller), pp. 757–781. London: Academic Press.
- Bussen, S., Sutterlin, M. & Steck, T. 1999. Endocrine abnormalities during the follicular phase in women with recurrent spontaneous abortion. *Human Reproduction*, **14**, 18–20.
- Gabor, C. R. & Halliday, T. R. 1997. Sequential mate choice by multiply mating smooth newts: females become more choosy. *Behavioral Ecology*, **8**, 162–166.
- Gwynne, D. T. 1984. Courtship feeding increases female reproductive success in bushcrickets. *Nature*, **307**, 361–363.
- Hasselquist, D., Bensch, S. & von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, **381**, 229–232.
- Hertig, A. T. & Rock, J. 1959. A series of potentially abortive ova recovered from fertile women prior to the first missed menstrual period. *American Journal of Obstetrics and Gynecology*, **58**, 968–973.
- Hertig, A. T., Rock, J., Adams, E. C. & Menkin, M. C. 1959. Thirty-four fertilized human ova, good, bad and indifferent, recovered from 210 women of known fertility. *Pediatrics*, **23**, 202–207.
- Hill, J. A. 1995. Immunological factors in recurrent spontaneous abortion. In: *Immunology of Human Reproduction* (Ed. by M. Kurpisz & N. Fernandez), pp. 401–424. Oxford: Bios Scientific.
- Hoogland, J. L. 1998. Why do female Gunnison's prairie dogs copulate with more than one male? *Animal Behaviour*, **55**, 351–359.
- Ivy, T. M., Johnson, J. C. & Sakaluk, S. K. 1999. Hydration benefits to courtship feeding. *Proceedings of the Royal Society of London, Series B*, **266**, 1523–1527.
- Jennions, M. D. & Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews*, **75**, 21–64.
- Kempnaers, B., Verheyen, G. R., van der Broeck, M., Burke, T., van Broeckhoven, C. & Dhondt, A. A. 1992. Extra-pair paternity results from female preference for high quality males in the blue tit. *Nature*, **357**, 494–496.
- Kerr, C., Ringo, J., Dowse, H. & Johnson, E. 1997. Icebox, a recessive X-linked mutation in *Drosophila* causing low sexual receptivity. *Journal of Neurogenetics*, **11**, 213–229.
- Møller, A. P. 1998. Sperm competition and sexual selection. In: *Sperm Competition and Sexual Selection* (Ed. by T. R. Birkhead & A. P. Møller), pp. 55–90. London: Academic Press.
- Neckameyer, W. S. 1998. Dopamine and mushroom bodies in *Drosophila*: experience-dependent and -independent aspects of sexual behavior. *Learning and Memory*, **5**, 157–165.
- Newcomer, S. D., Zeh, J. A. & Zeh, D. W. 1999. Genetic benefits enhance the reproductive success of polyandrous females. *Proceedings of the National Academy of Sciences, U.S.A.*, **96**, 10236–10241.
- Petrie, M. & Kempnaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology and Evolution*, **13**, 52–58.
- Petty, R. G. 1999. Prolactin and antipsychotic medications: mechanisms of action. *Schizophrenia Research*, **35**, S67–S73.
- Schal, C., Holbrook, G. L., Bachmann, J. A. S. & Sevala, V. L. 1997. Reproductive biology of the German cockroach, *Blattella germanica*: juvenile hormone as a pleiotropic master regulator. *Archives of Insect Biochemistry and Physiology*, **35**, 405–426.
- Spencer, H. G., Feldman, M. W. & Clark, A. G. 1998. Genetic conflicts, multiple paternity and the evolution of genomic imprinting. *Genetics*, **148**, 893–904.
- Spencer, H. G., Clark, A. G. & Feldman, M. W. 1999. Genetic conflicts and the evolutionary origin of genomic imprinting. *Trends in Ecology and Evolution*, **14**, 197–201.
- Tregenza, T. & Wedell, N. 1998. Benefits of multiple mates in the cricket *Gryllus bimaculatus*. *Evolution*, **52**, 1726–1730.
- Valhé, B., Dietl, J., Kapp, M., Toth, B. & Arck, P. 1999. Increased blood vessel density in decidua parietalis is associated with spontaneous human first trimester abortion. *Human Reproduction*, **14**, 1628–1634.
- Wetton, J. H. & Parkin, D. T. 1991. An association between fertility and cuckoldry in the house sparrow, *Passer domesticus*. *Proceedings of the Royal Society of London, Series B*, **245**, 227–233.
- Weygoldt, P. 1969. *The Biology of Pseudoscorpions*. Cambridge, Massachusetts: Harvard University Press.
- Zeh, J. A. 1997. Polyandry and enhanced reproductive success in the harlequin-beetle-riding pseudoscorpion. *Behavioral Ecology and Sociobiology*, **40**, 111–118.
- Zeh, D. W. & Zeh, J. A. 1992. Dispersal-generated sexual selection in a beetle-riding pseudoscorpion. *Behavioral Ecology and Sociobiology*, **30**, 135–142.
- Zeh, J. A. & Zeh, D. W. 1994. Last-male sperm precedence breaks down when females mate with three males. *Proceedings of the Royal Society of London, Series B*, **257**, 287–292.
- Zeh, J. A. & Zeh, D. W. 1996. The evolution of polyandry I: Intra-genomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London, Series B*, **263**, 1711–1717.
- Zeh, J. A. & Zeh, D. W. 1997. The evolution of polyandry II: post-copulatory defences against genetic incompatibility. *Proceedings of the Royal Society of London, Series B*, **264**, 69–75.
- Zeh, D. W. & Zeh, J. A. 2000. Reproductive mode and speciation: the viviparity-driven conflict hypothesis. *BioEssays*, **22**, 938–946.
- Zeh, J. A. & Zeh, D. W. 2001. Reproductive mode and the genetic benefits of polyandry. *Animal Behaviour*, **61**, 1051–1063.
- Zeh, D. W., Zeh, J. A., Coffroth, M. A. & Bermingham, E. 1992a. Population-specific DNA-fingerprints in a neotropical pseudoscorpion. *Heredity*, **69**, 201–208.

- Zeh, D. W., Zeh, J. A. & Tavakilian, G. 1992b. Sexual selection and sexual dimorphism in the harlequin beetle *Acrocinus longimanus*. *Biotropica*, **24**, 86–96.
- Zeh, D. W., Zeh, J. A. & May, C. A. 1994. Charomid cloning vectors meet the pedipalpal chelae: single-locus minisatellite DNA probes for paternity assignment in the beetle-riding pseudoscorpion. *Molecular Ecology*, **3**, 517–522.
- Zeh, D. W., Zeh, J. A. & Bermingham, E. 1997. Polyandrous, sperm-storing females: carriers of male genotypes through episodes of adverse selection. *Proceedings of the Royal Society of London, Series B*, **264**, 119–125.
- Zeh, J. A., Newcomer, S. D. & Zeh, D. W. 1998. Polyandrous females discriminate against previous mates. *Proceedings of the National Academy of Sciences, U.S.A.*, **95**, 13732–13736.