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Polyandrous, sperm-storing females: carriers of male genotypes through episodes of adverse selection

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SUMMARY

In the pseudoscorpion, *Cordylochernes scorpioides*, males experience sexual selection in two disparate and well-defined habitats. Populations inhabit decaying trees for several generations before dispersing under the elytra of the harlequin beetle, *Acrocinus longimanus*. Males compete to monopolize beetle abdomens as strategic sites for inseminating dispersing females. Using single-locus minisatellite DNA profiling to assign paternity for the offspring of dispersing females, we found a strong, positive correlation between male size and reproductive success in the beetle environment. However, this intense selection is undermined by polyandry and the ability of females to store sperm and produce mixed-paternity broods. Although beetle-riding males achieved fertilizations with 70% of the females, paternity could not be assigned for 57% of the offspring. It is likely that many of these offspring were the products of within-tree inseminations since, in a sample of females intercepted in the act of boarding beetles, most (86%) carried sperm from pre-dispersal matings within trees. Polyandry and sperm storage may therefore enable smaller males, unable to monopolize beetle mating territories, to circumvent the bottleneck of dispersal-generated sexual selection and thereby transmit their genes to future tree populations. Sperm stored within females can thus provide the kind of resistant life-history stage shown by recent modelling to be critical for the maintenance of genetic variation by temporally fluctuating selection.

1. INTRODUCTION

Theoretical models of sexual selection generally assume that species occupy homogeneous environments and experience selection through either male competition or mate choice by monogamous females (review in Maynard Smith 1991). Under these conditions, sexual selection often acts as a constant, unidirectional force, driving a population towards a single, optimal male phenotype. Such selection should deplete additive genetic variation (Fisher 1958), yet male sexually selected traits are often precisely those which exhibit the greatest level of variability (Pomiankowski & Møller 1995).

Among mechanisms hypothesized to maintain genetic variation, temporally fluctuating selection, in which the relative fitnesses of different genotypes vary through time, has been repeatedly proposed and rejected as an important process in natural populations (see Ellner & Hairston 1994). Despite a large body of correlative and experimental evidence to the contrary (Nevo 1978; Mackay 1981; Lynch 1987; Hairston & Dillon 1990), it has been argued on theoretical grounds that the conditions required for temporally fluctuating selection to maintain variation (e.g. large oscillations in selection intensity; coarse-grained environments, and lower fitness variance in heterozygotes) are too restrictive to be of general evolutionary significance (Hedrick 1986; Frank & Slatkin 1990).

A recent paper by Ellner & Hairston (1994), in which the effects of temporally varying selection on genetic variation were modelled in populations with overlapping generations, has called into question the generality of previous theoretical conclusions based exclusively on discrete-generation models. These authors concluded that ‘...temporally fluctuating selection can indeed contribute significantly to the maintenance of genetic variation when the effects of overlapping generations and age-specific or stage-specific selection are considered’. The essential result, called the ‘storage effect’, occurs when a genotype persists in some life-history stage that enables it to remain viable for periods long enough to experience the next favourable episode of selection (e.g. long-lived adults in animals, dormant seeds in annual plants, and diapausing eggs). This conclusion was found to apply to haploid, diploid, single-locus or multilocus inheritance.

We propose that sperm storage by polyandrous females, superimposed on male competition in a heterogeneous environment, can provide precisely the kind of storage effect described by Ellner & Hairston (1994), in this case, by ‘smuggling’ male genotypes through episodes of unfavourable selection. In this paper, we report the results of a single-locus DNA profiling study of the harlequin beetle-riding pseudoscorpion, *Cordylochernes scorpioides*, which suggest that intense sexual selection for large male size during

dispersal creates a population bottleneck through which unfavoured male genotypes can pass as a consequence of pre-dispersal mating and sperm storage by polyandrous females.

2. BACKGROUND NATURAL HISTORY

Cordylochernes scorpioides is the most sexually dimorphic member of the subfamily Lamprochernetinae (Beier 1948), with males possessing enlarged pedipalps, the appendages important in mate acquisition and male combat (Weygoldt 1969; Zeh & Zeh 1992). Distributed throughout the rain forests of Central and South America (Beier 1948), *C. scorpioides* inhabits decaying trees in the families Moraceae and Apocynaceae. The pseudoscorpion gains access to these rich but patchily distributed and ephemeral habitats by hitchhiking under the elytra (wing covers) of the 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.* 1992*b*). Populations in dead trees remain marooned for three to five 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 who fight to force off rivals in order to monopolize beetle abdomens as strategic sites for intercepting and inseminating dispersing females (Zeh & Zeh 1992, 1994).

After its 'maiden flight', a beetle typically carries under its elytra a single, large male pseudoscorpion, defending a mating territory on its abdomen. As the harlequin continues its search for oviposition trees and mates, sub-elytral space remains a dynamic site for sexual competition (Zeh & Zeh 1994*b*). Mark-recapture field experiments (Zeh & Zeh 1992) have demonstrated that females or challenging males may transfer from other beetles. The resident male may disembark to reconnoitre other beetles. He may be supplanted by a larger intruder. Tree individuals may board and dispersing individuals may disembark when the harlequin visits standing trees which are mosaics of live and necrotic tissues.

As a consequence of dispersal on harlequin beetles, *C. scorpioides* males experience selection both within trees and on beetle abdomens, two disparate and well-defined habitats which alternate on a regular, cyclical basis. The dispersal phase can thus be viewed as an episode of sexual selection (*sensu* Arnold & Wade 1984) with two multiplicative components to male reproductive success. A male must first succeed in monopolizing a beetle abdomen (W_1). He must then fertilize the eggs of females passing through his mating territory (W_2). Multivariate morphometric comparisons between beetle-riding males and males from pre-dispersal tree populations have documented strong, directional selection for large male size associated with the W_1 component (Zeh & Zeh 1992, 1994).

3. METHODS

(a) Field collection and laboratory rearing

To determine whether the intense, size-based male competition to monopolize mating territories on beetles translates into reproductive success (W_2), we carried out a paternity assignment study of the offspring of females naturally dispersing on harlequin beetles. Females and putative sires were collected at the end of the dispersal phase by capturing beetles ($n = 34$) on three newly fallen host trees (*Parahancornia fasciculata*, Apocynaceae) along the Piste du Kaw, 50 km south-east of Cayenne, French Guiana (Zeh *et al.* 1992*b*; Zeh & Zeh 1994). Any pseudoscorpions present on a beetle's abdomen were removed and photographed for morphometric analyses (for methods, see Zeh & Zeh 1992). Females ($n = 23$) were monitored through nymph hatching, and their offspring reared to adults in the laboratory. Males, females and offspring were frozen at -70 °C, pending DNA profiling.

(b) DNA profiling analysis

For the purpose of paternity assignment, we considered each potential breeding group to consist of a female (or females) and all males collected on the same beetle or present on another beetle captured at the same time on the same tree. An estimate of the reproductive success of 44 putative sires in 15 potential breeding groups was obtained by DNA profiling a sample of five to 12 offspring from each of the 23 females ($n = 168$ offspring in total). DNA extraction protocols, electrophoresis conditions, Southern transfer methods, probe labelling and hybridization procedures are described elsewhere (Zeh *et al.* 1992*a*, 1994). Paternity assessment was carried out by sequential hybridization of *Hae* III- or *Hinf* I-digested genomic blots with two independently segregating, hypervariable single-locus minisatellite probes, *cCscMS13* and *cCscMS23* (Zeh *et al.* 1994). DNA samples from the mother, her offspring and all putative sires were run on the same gel. If a male was a putative sire of the offspring of more than one female, his DNA was aliquoted for running on more than one gel. Heterozygosity (H) and false inclusion probability estimates (P_{FI}) were obtained by calculating mean allele sharing between mothers and/or putative sires in adjacent gel lanes (Wong *et al.* 1987; Zeh *et al.* 1994). Because of the extremely high level of allelic diversity at the two loci, paternity could be assigned by visual comparison, with a male being identified as the father if he possessed the offspring's paternal allele at both loci (see figure 1).

(c) Estimating selection in the harlequin beetle environment

The reproductive success of each male was estimated by calculating the proportion of a female's DNA-profiled offspring sired by that male, multiplying this proportion by the total number of the female's offspring reaching maturity in the laboratory, and summing over females. Directional sexual selection (Lande & Arnold 1983) was estimated by regressing each male's relative reproductive success on a composite size measure of his pedipalps (PC1PALP) and of his cephalothorax (PC1CEPH). These composite size measures were derived from principal component analysis of seven traits of the sexually dimorphic pedipalps (chelal movable finger length; chelal hand length and depth; tibia length and depth, and femur length and depth) and two

traits of the sexually monomorphic cephalothorax (length and posterior width; see Zeh & Zeh 1992, 1994). All nine traits measured are characters fixed in size at the terminal molt to the adult stage (Chamberlin 1931). Selection was also estimated using the non-parametric cubic spline method for Poisson distributions, with confidence intervals being calculated by doubling the standard errors obtained from 100 bootstrap replications (Schluter 1988).

(d) Estimating the proportion of dispersing females storing sperm from within-tree matings

To assess the potential for within-tree, pre-dispersal mating by females to dilute the effect of sexual selection operating in the harlequin beetle environment, we intercepted females ($n = 21$) in the act of boarding newly eclosed harlequin beetles ($n = 2$) on old, dried-out trees ($n = 2$). Mating status of each female, i.e. virgin or mated, was assessed by monitoring her in the laboratory either until she produced a brood or for 2 months following collection. Females not having produced broods by this point were scored as virgins.

4. RESULTS

(a) Paternal false inclusion probabilities

DNA profiling indicated that the potential breeding groups of dispersing pseudoscorpions consisted of unrelated individuals (see figure 1). In fact, allelic diversity within these groups was slightly higher than that previously reported for *C. scorpoides* based on randomly selected individuals (Zeh *et al.* 1994). In 61

adjacent-lane comparisons, we found no cases of identical genotypes and only two instances in which two members of a potential breeding group shared an allele at the *cCscMS13* locus ($P_{FI} = 0.0164$, $H = 0.9918$). Allele sharing was slightly higher for *cCscMS23* ($P_{FI} = 0.0938$, $H = 0.9520$), yielding, for the two probes, a combined probability of falsely assigning paternity to an unrelated male of 0.0015.

(b) Male size and reproductive success

Overall, 18 males (41%) achieved reproductive success and 16 females (70%) produced broods which included offspring fathered by one or more of the putative sires. The remaining 30% of females produced broods in which paternity could not be assigned for any offspring. There was a strong, positive correlation between the reproductive success of beetle-riding males (W_2) and pedipalp size. The selection differential (s_2) was positive and statistically significant for PC1PALP ($s_2 = 0.57$, $p = 0.02$) but was not significant for PC1CEPH ($s_2 = 0.41$, $p = 0.07$). These findings were corroborated by the non-parametric, cubic spline method (graphs not shown). Selection gradients (b) (see Lande & Arnold 1983) suggest that the pedipalp is the direct target of selection (PC1PALP, $b_2 = 0.95$, $p = 0.05$; PC1CEPH, $b_2 = -0.42$, $p = 0.22$), although the statistical power of this result was limited by a high correlation between PC1PALP and PC1CEPH ($r = 0.88$). The effect of the directional selection operating at the W_2 stage is illustrated in figure 2c which plots

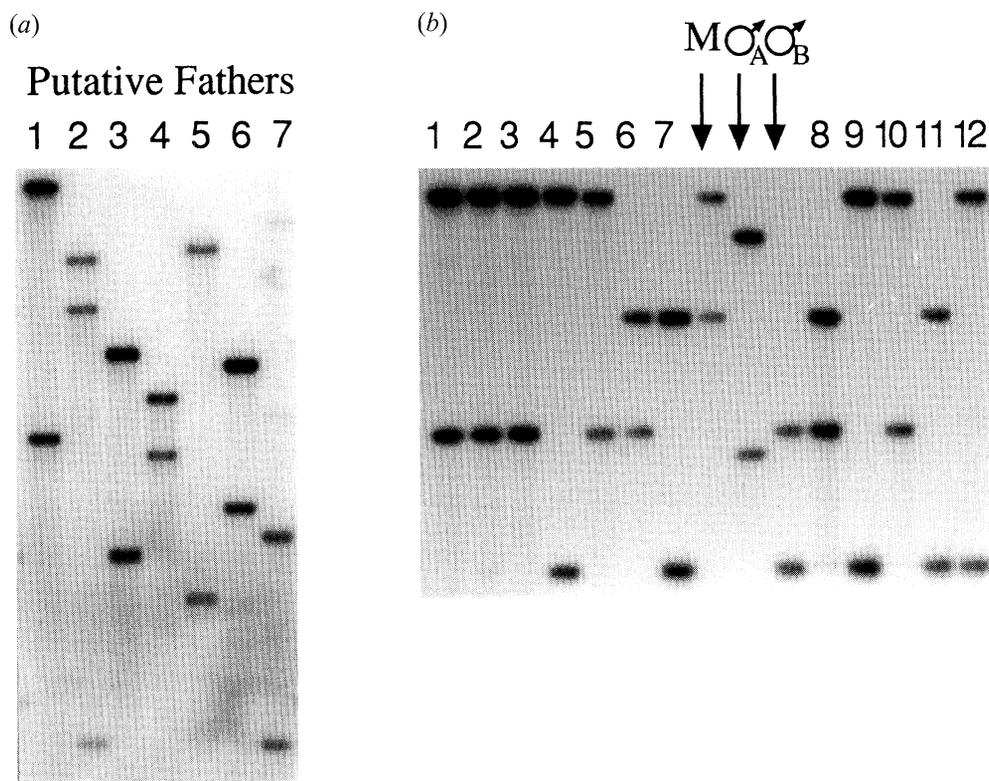


Figure 1. Single-locus minisatellite DNA profiles at the *cCscMS13* locus. (a) DNA from seven putative sires in the largest potential breeding group, illustrating the extreme allelic diversity at this locus. (b) Paternity assignment in a potential breeding group consisting of the female (M) and two putative sires (males A and B). All non-maternal alleles in the 12 offspring can be traced to male B.

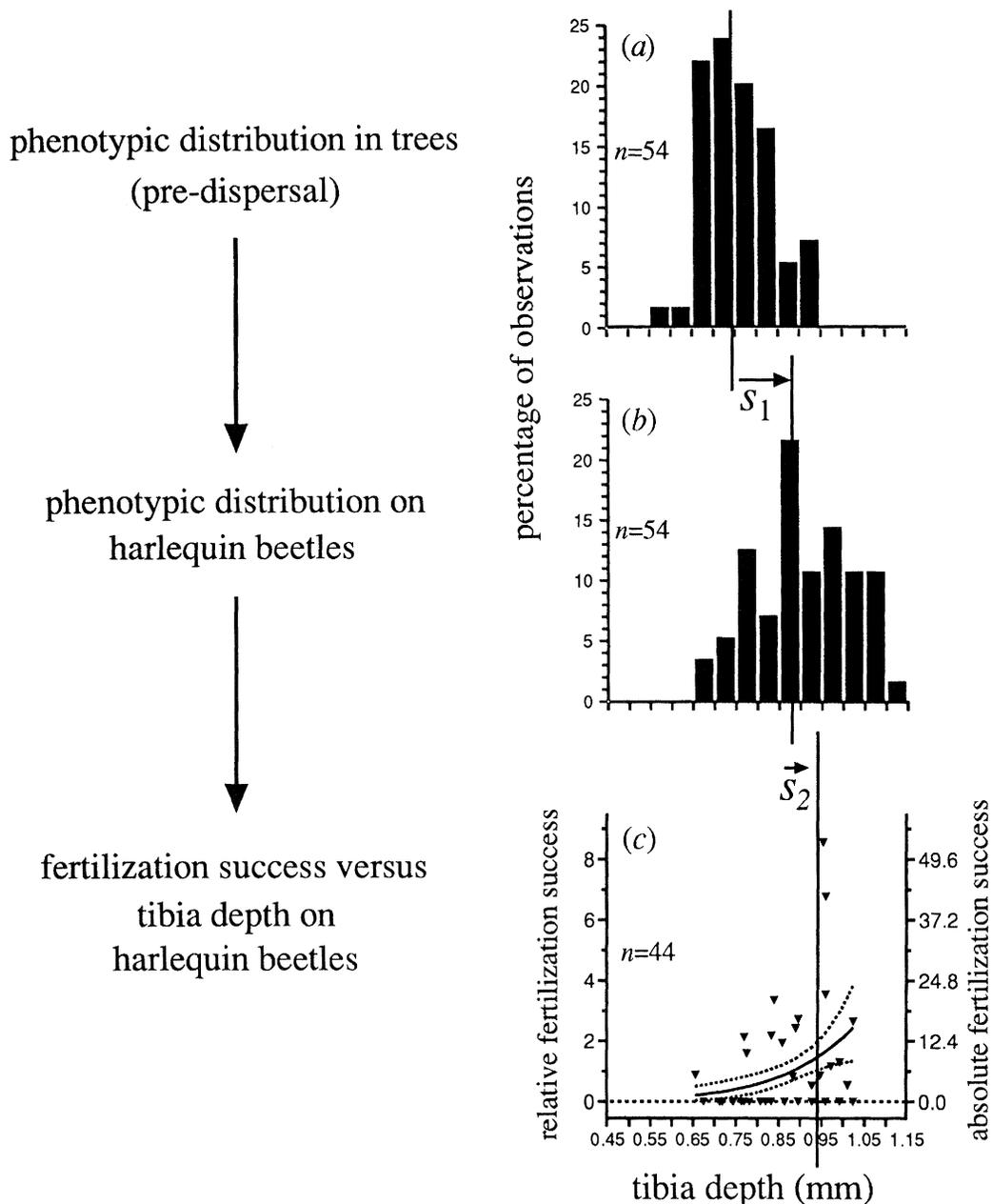


Figure 2. Stages of dispersal-generated sexual selection in *C. scorpioides*. The two histograms illustrate the difference between pedipalp tibia depth distribution of (a) males randomly sampled from pre-dispersal tree populations and (b) that of beetle-riding males. (c) The bivariate plot maps the relative fertilization success of beetle-riding males (as determined by our DNA paternity assignment study) onto tibia depth, and shows the continuation of size-based male competition, at this stage to achieve fertilizations. Non-parametric estimation of the fitness function is represented by a solid line. The dotted lines denote the 95% confidence interval (see text).

relative fertilization success against tibia depth, a highly sexually dimorphic trait of the pedipalp (Zeh & Zeh 1994).

(c) *Multiple paternity*

Due to a high level of mixed paternity, even though 70% of females produced broods which included some offspring of beetle-riding males, fathers could not be identified for 57% of the offspring. A conservative estimate of the number of males involved in siring a female's brood was obtained by counting (and dividing by two) the number of non-maternal alleles present in her sample of offspring. The majority of females (74%)

produced broods sired by two or more males (figure 3). In the most extreme case, paternal alleles present in one set of 10 offspring demonstrated fertilization by at least four males. Our estimates of multiple paternity are unlikely to have been inflated by incidences of mutation. In the 168 offspring profiled in this study, we detected only one maternal allele mutation (see figure 3, offspring number 7), giving an empirically estimated mutation rate of 0.006 at the *cCscMS13* locus.

(d) *Pre-dispersal, within-tree matings by females*

Of the 21 females collected in the act of boarding newly emerged beetles to disperse out of old trees, 18

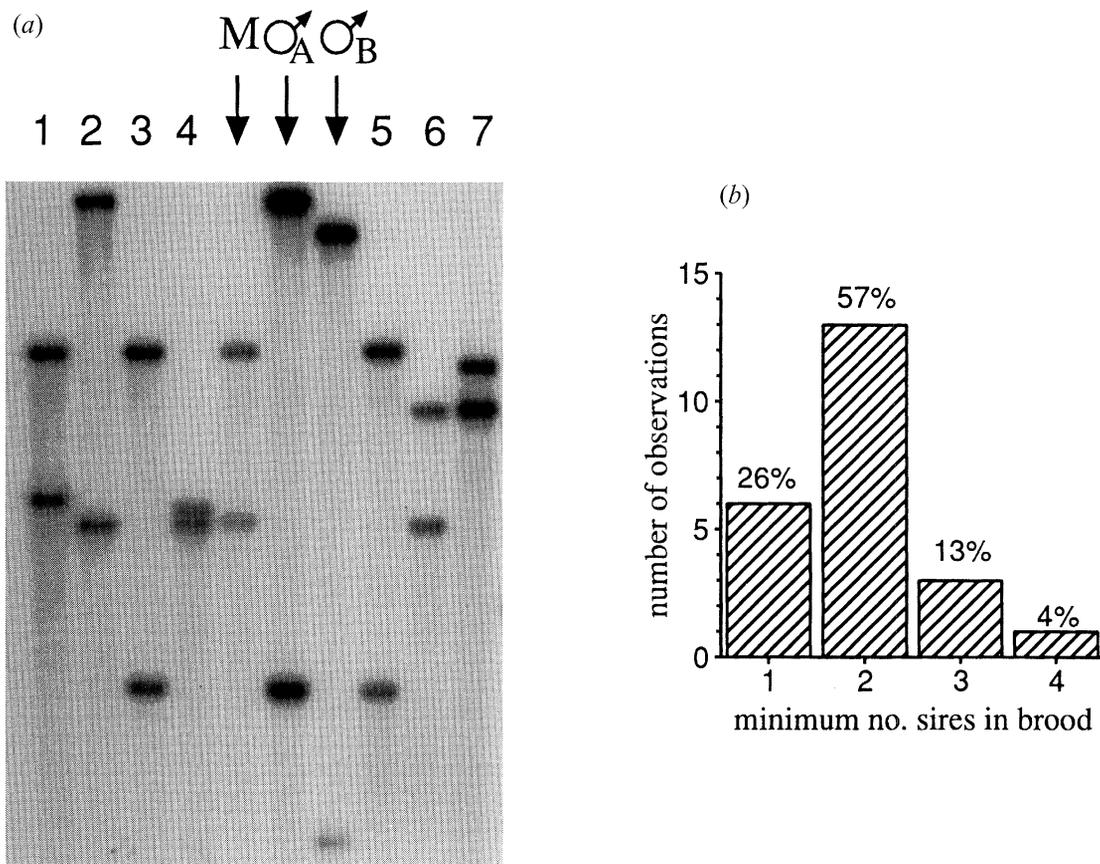


Figure 3. Multiple paternity in the offspring of beetle-riding females. (a) A potential breeding group in which paternity of offspring 2, 3 and 5 can be assigned to putative sire A (*cCscMS13* probe). There are three non-maternal alleles present in the remaining four offspring, indicating that a minimum of two more males were involved in siring this female's brood. Note that offspring 7 carries a mutation of the mother's higher (upper) molecular weight allele. (b) The frequency distribution of broods categorized by the estimated minimum number of fathers (see text).

(86%) subsequently produced broods in the laboratory, demonstrating that, had they not been intercepted, the majority would have entered the dispersal phase carrying viable sperm stored from pre-dispersal matings with males within trees.

5. DISCUSSION

In this pseudoscorpion, dispersal-generated sexual selection disproportionately eliminates smaller males in the first round of competition to monopolize mobile mating territories on beetles, thereby shifting the arena for subsequent competition to the upper end of the source tree population's phenotypic distribution (see figure 2*a, b*). For the highly exaggerated male trait, tibia depth, for example, the mean value for beetle-riding males (0.88 mm) is 1.81 standard deviation units greater than the mean (0.74 mm) for males randomly sampled from pre-dispersal tree populations (Zeh & Zeh 1994). This difference provides an estimate of the first multiplicative component of sexual selection in the beetle environment (s_1).

The results of our DNA profiling analysis reported here indicate that in the second round of competition, this time to achieve fertilizations, it is the largest of these large beetle-riding males that gain the greatest reproductive success. In the case of tibia depth, this

amounts to a further increase in the mean of 0.60 standard deviation units (s_2 ; figure 2*c*). The combined effect of selection in the beetle environment is consequently enormous (more than two standard deviation units). This may well represent the most extreme case of sexual selection for exaggerated male traits so far demonstrated using direct estimates of reproductive success.

Such intense dispersal-generated selection should act to erode variability, yet *C. scorpioides* males have been described as the most morphologically variable pseudoscorpions known (Beier 1948). Male coefficients of variation for sexually dimorphic traits are 15–20%, two to three times higher than those for females (Zeh & Zeh 1992, 1994). Preliminary analysis of a split-brood, paternal half-sib quantitative genetic study of *C. scorpioides*, in which offspring were reared under two environmental conditions, suggests a significant additive genetic component to this variation (Zeh & Zeh unpublished data). We propose that extreme variability in *C. scorpioides* males is maintained because sexual selection is not constant but oscillates through time. The fact that beetle-monopolizing males comprise an élite selected from the upper end of the male phenotypic distribution within trees makes it extremely likely that selection is considerably less intense within trees. Indeed, several lines of indirect evidence suggest that counter-selection for a smaller optimal male

phenotype operates in the tree environment. Laboratory experiments have demonstrated that large size prolongs development in males and delays access to females but confers no mating advantage under the low-density conditions which characterize tree populations (Zeh & Zeh 1992 and unpublished data).

Sexual selection, alternately favouring large male phenotypes on beetles and small male phenotypes within trees, creates the conditions for polyandry and sperm storage by dispersing *C. scorpioides* females to provide the kind of storage effect (Ellner & Hairston 1994) necessary for temporally fluctuating selection to maintain genetic variation. In this study, we found 86% of dispersing females to be storing sperm from pre-dispersal matings within trees. Since last-male sperm precedence and mating order effects are known to break down completely in this pseudoscorpion when females mate with more than two males (Zeh & Zeh 1994), it is highly likely that many of the offspring for whom paternity could not be assigned in this study were the product of pre-dispersal matings within trees. Polyandry and prolonged sperm storage by females may thus enable 'tree males' to circumvent the bottleneck of dispersal-generated sexual selection for large male size and thereby pass on their genes to future tree populations. The strength of the storage effect in this system depends, of course, not only on the nature of selection in the tree environment, which will be the subject of future research, but also on the ratio of pre-dispersal matings to on-beetle matings by dispersing females. This ratio could be assessed by DNA profiling of entire broods of offspring to compare levels of multiple paternity in the broods of females intercepted immediately before and immediately after dispersal.

As molecular evidence increasingly demonstrates that polyandry is a widespread feature of natural populations (Schwartz *et al.* 1989; Amos *et al.* 1993; Birkhead & Møller 1995), it is becoming clear that females can often increase their reproductive success by mating with more than one male (Watson 1991; Madsen *et al.* 1992; Olsson *et al.* 1994; Zeh 1996). Previous studies, particularly those carried out on birds, suggest that polyandry is a force which acts to reinforce the effects of pre-copulatory sexual selection for a single, optimal male phenotype (Kempanaers *et al.* 1992; Hasselquist *et al.* 1996). As such, polyandry would be expected to further erode genetic variability in male sexually selected characters. By contrast, our research on *C. scorpioides* suggests that polyandry can serve as a mechanism which maintains male variability when sexual selection operates in a heterogeneous environment. Although the generality of our findings remains to be assessed by similar studies on other species, many organisms, particularly among the diverse arthropod taxa which exploit ephemeral resources, are subjected to strong, regular fluctuations in environmental conditions (Hamilton 1978; Lynch 1987; Hairston & Dillon 1990). Oscillations in selective pressures (Bryant 1976; Gillespie 1991; Schluter *et al.* 1991), and hence the potential for polyandry to maintain male variability, may thus be considerably more important than is currently appreciated.

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