Promiscuity in Sand Lizards (*Lacerta agilis*) and Adder Snakes (*Vipera berus*): Causes and Consequences

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We review postcopulatory phenomena in the Swedish sand lizard (*Lacerta agilis*) and adder (*Vipera berus*), and in particular, links between female promiscuity, determinants of paternity, and offspring viability. In both species, females mate multiply and exhibit a positive relationship between the number of partners and offspring viability. We conclude that this relationship is most likely the result of variable genetic compatibility between mates arising from postcopulatory phenomena, predominantly assortative fertilization with respect to parental genotypes. However, males who were more successful at mate acquisition were also more successful in situations of sperm competition, suggesting a possible link between male (diploid and haploid) genetic quality per se and probability of fertilization. Neither the number of partners nor the number of matings influenced the risk of infertility in sand lizards, suggesting that selection for reduced risk of infertility is not a sufficient explanation for maintaining female promiscuity in this population. Finally, we conclude that the relatively low genetic variability exhibited by our study populations may have facilitated detection of genetic benefits compared to more outbred ones. However, recent work derived from outbred populations in other taxa suggest a greater generality of the principles we discuss than previously may have been appreciated.

Promiscuity, or the tendency to mate with multiple partners without a prolonged pair bond, has in the last decade become appreciated as one of the most significant of reproductive behaviors and a prerequisite for all selection processes relating to sperm competition and cryptic female choice (Birkhead and Møller 1992, 1998; Smith 1984). Several selection scenarios may explain its evolution. In taxa such as insects, where a male's nuptial gift to the female, the spermatophylax, may constitute some 30% of his body mass, females are selected to increase their access to these resources by repeat matings (Simmons and Siva-Jothy 1998). In species where there is no direct gain to the female from mating multiply with different partners, evolution of female promiscuity is, however, more difficult to explain. Under the assumption that mating per se carries some cost (e.g., risk of pathogen transfer, increased predation, etc.; Magnhagen 1991), any Darwinian explanation requires a net benefit to the female for the persistence of this behavior.

In addition to the direct resources that females may obtain from mating with many males ("nuptial gifts," access to re-sources defended by the male, increased paternal care, etc.; Birkhead and Møller 1998), females may also gain genetic benefits from mating multiply (Birkhead and Parker 1997). Traditional model species in studies of polyandry (insects and birds; Birkhead and Parker 1997) lend themselves poorly to evaluation of genetic effects. In insects, offspring cannot be genetically screened at hatching/parturition and then be monitored through life in natural populations. Thus the concepts and relative importance of "good" genes or "complementary" genes are unlikely to be tested in natural populations in this taxon. Similarly, in species where postparturient parental effects strongly influence offspring fitness, such as via feeding of nestlings in birds and weaning in mammals, genetic components of fitness may be overlooked as contributors to an individual's lifetime reproductive success. Furthermore, recent work has demonstrated that females can differentiate between half-sibs depending on the quality of their respective fathers, and accordingly allocate resources differently between them (Cunningham and Russell 2000; Gil et al. 1999). Thus studies of the evolution of fe-

male promiscuity would strongly benefit from model systems in which males transfer no resources except genes to the female, where nourishment of follicles and ovulation is synchronous for the entire clutch, and where there is no parental care. This is the case for the majority of squamate reptile species (i.e., lizards and snakes; Olsson and Madsen 1998).

Two alternative views of genetic effects have come to dominate the sexual selection literature in recent years: "good genes" (Møller and Alatalo 1999; von Schantz et al. 1999; Williams 1966:184) and "compatible genes" (sensu Zeh and Zeh 1996, 1997). The good genes hypothesis has the implicit assumption that some genes (or alleles) are superior to others and hence all females in the population should prefer to mate with males carrying them. "Genetic compatibility," however, considers the genetic architecture of both the male and the female. By incorporating interindividual differences in genotype, a given male may be a good partner for one female but not for another. For example, a female heterozygous for a lethal recessive allele should preferably mate with a male who is homozygous dominant at this locus, since a mating with a heterozygous male would on average kill 25% of her offspring. In theory, a male who is completely void of deleterious recessives would be equally complementary to all females. In this review, "genetic benefits" from female promiscuity can accrue under either the good genes or compatible genes models.

In a recent review we demonstrated that females in more than 80% of reptiles (33 of 41 species) mate with multiple partners (Olsson and Madsen 1998). We make no attempt at analyzing these data in accordance with the comparative method protocol, but merely conclude that multiple mating in reptiles seems to be phylogenetically widespread. It occurs in most snakes, territorial and nonterritorial lizards, and all species of turtles for which there is published information (Olsson and Madsen 1998). For the two species that we have worked on in more detail, the Swedish sand lizard (*Lacerta agilis*) and the adder (*Vipera berus*), information is available on the genetic variability and spatial structure of genotypes within populations, demography, viability of young in relation to degree of maternal promiscuity, and genotypic effects on offspring viability and male probability of paternity. We review this information from a perspective of evolution of female promiscuity and dis-cuss the possible applicability of our findings to other taxa.

Materials and Methods

Study Species

Sand lizards are small, ground-dwelling lizards (females to 20 g, males to 15 g) distributed throughout most of Europe and western Asia (Bischoff 1984). The mating period and subsequent oviposition take place in May–June. Females normally progress through one ovarian cycle per annum in Sweden (Olsson and Shine 1997b,c), and can readily be monitored (e.g., with respect to visiting partners) because of the prolonged male mate guarding.

Most work on reproductive behavior referred to in this review took place in a natural population at Asketunnan (50 km south of Gothenburg on the Swedish west coast). Individually marked lizards were monitored throughout the mating season and when females approached oviposition they were brought to laboratory facilities at the University of Gothenburg. Once the eggs were laid, the females were released at the study site and the eggs incubated at 25°C, which is the optimal incubation temperature for this species (Zakharov 1989). We also estimated the genetic variation of this population using microsatellites, minisatellites, and major histocompatibility complex (MHC) class I probes (developed by Håkan Wittzell, University of Lund). Results were compared with corresponding estimates of genetic variation in relatively smaller relic populations, and in two larger more outbred populations in southern Sweden and in Hungary (Gullberg et al. 1998a,b; Madsen et al. 2000).

In the laboratory we staged matings between individual lizards to test predictions from theories of sperm competition and cryptic female choice. Initially we exploited a Mendelian inherited dorsal stripe for assigning paternity (Olsson et al. 1994a), but DNA fingerprinting (DFP) and species-specific microsatellite probes (Gullberg et al. 1998c) were later developed for this purpose to avoid genetic constraints on the choice of males in mating trials (Gullberg et al. 1997, 1998c; Olsson et al. 1994a). See Olsson 1994a for a more detailed description of methods.

The adder is one of the most geographically widespread of all reptile species, occurring throughout Europe and western Asia (Steward 1971). Similar to sand lizards, its distribution in Sweden is insular with local populations varying in size from less than 50 to more than 250 snakes (Madsen et al. 1996 and references therein). Most of the work referred to in the present review took place in the Smygehuk population on the south coast of Sweden (Madsen et al. 1992). We also staged matings in a laboratory population to look for indications of sperm competition (Stille et al. 1986, 1987). Largely the field and laboratory techniques agreed with those described for sand lizards above, differing only in that adder females were monitored using telemetry (Madsen and Shine 1992a,b). Genetic variability was scored using DFP, a species-specific MHC locus I probe (developed by H. Wittzell) and allozymes (Madsen et al. 1996). For a more detailed description of methods, see Madsen and Shine (1992a,b, 1994).

Results

Spatial Distribution, Mating System, and Male Reproductive Behavior

During the mating season, female sand lizards utilize a home range averaging 15% the size of the male range, 160 m² versus 1100 m², respectively, within which they are visited by courting males (Olsson 1988, 1994a). Females are sexually receptive for approximately 10 days and during this period they do not express mate choice but mate with all males capable of courting (Olsson 1992, 1993a, 1994a; Olsson et al. 1996c). In staged mating experiments, mated males that are guarding a female win contests significantly more often than unmated males (Olsson 1994a). Thus prior mating motivates a male to invest relatively more into costly contests than just potential mate acquisition. Males, however, do interrupt mate guardings prior to ovulation, that is, while the female is still receptive (Olsson et al. 1996c).

In sand lizards, clutch size is strongly positively correlated with female size (Olsson 1993b). Because males prefer to mate with larger females (Olsson 1993b), we also expected males to invest relatively longer time into guarding larger females. Guarding duration, however, was not related to female body size, clutch size, or time to ovulation (Olsson et al. 1996c). Furthermore, there was no relationship between guarding duration and the operational sex ratio. Thus males appear not to adjust guarding duration in relation to availability of females or to the degree of competition for them. Recently, however, we found that the size of a male's lateral green area (his "badge"), an important component in male status signaling (Ols-

son 1994a–c), was strongly negatively correlated with male mate guarding duration (Olsson et al. 2000). Thus males who are more successful in both mate guarding and mate acquisition tend to invest relatively more time in acquiring additional partners rather than into a prolonged guarding of an already mated female (Olsson et al. 2000).

The mating system and spacing pattern of adders largely agree with those of sand lizards. Prior to parturition, female adders are immobile (Madsen and Shine 1992a) and are visited by males with which they mate in sequence, independent of their size (Madsen et al. 1992). However, larger males are superior to smaller males in acquiring mates, and males moving greater distances during the mating season exhibit a higher mating success than those moving shorter distances (Madsen et al. 1993).

Male Reproductive Success Under Sperm Competition

In sand lizards, the average mate guarding period in the natural population is 1.4 days (Olsson et al. 1996c). Thus if males have been selected to allocate an optimal time to mate guarding versus mate acquisition (sensu Parker 1978a,b), we would expect males that guard a female for ≥ 1 day to sire more offspring in sperm competition with other males. To test this assumption, a female was mated twice in succession with an interval of 1 h and 24 h, respectively. The second male mating within 1 h of the first male was thus predicted to sire relatively more offspring than one allowed to mate 24 h subsequent to the first male. In neither group (1 h or 24 h), however, was there a difference in the first or second males' probability of siring offspring, nor did first or second males differ in reproductive success compared across the two copulation intervals (Olsson et al. 1994a). The most apparent result was the wide variation in first and second males' reproductive success (from 0 to 100% in both groups). Reproductive success was not only unrelated to mating order, but also to male body size, interval between copulations, and number of prior male copulations. The only trait that could be linked to male reproductive success was the time since his previous copulation, suggesting that replenishment of spermatozoa influenced male fitness. In this analysis, however, relatedness of partners was not considered, and the large variance in male mating success suggested that some factor(s) other than number of spermatozoa in the ejaculate influenced a male's reproductive success.

In staged sperm competition experiments in adders, we demonstrated that females mated to several males showed within-clutch multiple paternity (Stille et al. 1986, 1987). Our sample size was at the time inadequate ($N = 5$) for a more extensive analysis of determinants of paternity, but there was a nonsignificant trend for a first male advantage, which was confirmed in a subsequent study (Höggren and Tegelström 1995).

Female Promiscuity and Paternal Genetic Effects

A pragmatic explanation for multiple matings in females would be that single-mating females suffer from reduced fertility due to insufficient number of transferred spermatozoa, or to a risk of mating with an infertile male. Furthermore, on average, males emerge 17 days earlier than females from hibernation (Olsson 1988), but when females were experimentally forced to emerge on the same day as males they suffered a 30% reduction in fertility (Olsson and Madsen 1996). Thus female sand lizards may initially have been under selection to mate repeatedly in order to reduce the risk of infertility. Infertile eggs are characteristically flaccid in this species, a trait which can be used to discriminate them from fertile unhatched eggs (the latter being zygotes that died in the early stages of development). Neither the number of partners nor the number of matings could, however, be linked to risk of infertility (Olsson and Shine 1997a).

Genetic benefits stand out as a strong candidate for explaining the evolution of female promiscuity in a species where females gain no additional resources or fertility benefits from mating with more than one male. A basic assumption of a genetic benefit model of sexual selection is that males show enough additive genetic variation to admit selection for pre- or postcopulatory female choice. To test for variation in male genetic "quality," we looked for a relationship between male longevity and hatching success of their corresponding clutches, sired with females mating with only one partner. Hatching success did not change through a male's life, but males that lived longer sired clutches with higher hatching success (Olsson and Madsen 1995). Although there was a similar trend in females, the relationship between female longevity and hatching success was not statistically significant (Olsson and Madsen 1995). Furthermore, the male effect was still significant when the effect of female longevity was controlled for in a partial correlation analysis (Olsson and Madsen 1995). Thus, in spite of a relatively low level of genetic variation in this population (Olsson et al. 1994b,c, and below), males varied in some genetic component that influenced the success of embryonic development (Olsson and Madsen 1995).

We also partitioned the different paternal effects of males competing in staged sperm competition trials (i.e., by comparing differences in half-sib phenotypes; Olsson et al. 1996a). Some males consistently produced the largest young from a given egg volume. These eggs incubated for relatively longer and the neonates had a relatively higher growth rate, resulting in a larger body size and a higher probability of survival (Olsson et al. 1996a).

Genetic Benefits of Promiscuity

Females with more partners produced clutches with higher hatching success, lower incidence of malformations, and better offspring survival during their first year of life (i.e., when offspring mortality is highest in the wild; Olsson et al. 1994b,c). Thus there appeared to be indirect genetic benefits of having more than one sexual partner.

Conventional sperm competition theory makes no predictions with respect to offspring viability. Thus under this hypothesis, genes carried in the head of the haploid spermatozoa are considered silent with respect to sperm performance (Parker 1992). In our first contribution on this topic (Madsen et al. 1992), we suggested that female adders perhaps set the stage for arena trials between males of different genetic quality. Thus males with a poor diploid genotype (homozygous for relatively more deleterious recessives) would be more likely to have spermatozoa that not only carried relatively more deleterious recessives but also were poorer in other crucial aspects (e.g., swimming ability, acrosome function, etc.). We have failed so far to test this hypothesis explicitly, but there is some circumstantial evidence in its support, as follows.

In sand lizards, males that were relatively more successful at acquiring partners were also more successful at siring offspring in sperm competition (Olsson et al. 1996c). Thus suites of genetically determined male fitness components could be positively interrelated. Madsen et al.'s (1992) extension of the sperm competition hypothesis, linking sperm performance to male genotypic quality, does not predict a

positive relationship between genetic relatedness of partners and the probability of paternity of competing males. Such a relationship was, however, evident in a detailed analysis of our sand lizard data (Olsson et al. 1996d, 1997b). In the natural population, and in staged mating experiments in the laboratory, males less related to the female sired more offspring within clutches than did competing males related more closely to the female (Olsson et al. 1996d). All experiments examining postcopulatory phenomena, however, run the risk of misidentifying proportional paternity if some eggs succumb before the assignment of paternity can take place, and our study was no exception in this respect. Sand lizard females ovulate their eggs approximately 6 days prior to oviposition, suggesting that an embryo dying in the first stages of development spends a week decomposing, which makes tissue sampling for molecular screening of paternity impossible (Olsson et al. 1999). We controlled for this in the most conservative way possible (Olsson et al. 1997b) by assigning eggs that failed to hatch to the males most closely related to the female, under the assumption that these embryos died due to inbreeding depression. We then reanalyzed the data, which confirmed the robustness of our first conclusion, that is, the more related a male was with a female, the smaller proportion of the clutch he sired (Olsson et al. 1997b).

Our interpretation of the adder data agree with those of the sand lizard. Multiple mating by a female results in fitness benefits stemming from phenotypically superior young. Of interest, in adders both the number of partners and the number of matings correlate positively with offspring viability (Madsen et al. 1992), whereas in sand lizards only the correlation with the number of partners was statistically significant (Olsson et al. 1994b). However, this discrepancy follows from the fact that female adders avoid remating the same partner (Madsen et al. 1992), whereas in sand lizards females may mate repeatedly with the same male (Olsson et al. 1994b). Thus mechanistically there seems to be no difference between these two systems; the fitness benefits appear to result from having spermatozoa from more males in the oviduct.

Genetic Variation in Sand Lizards and Adders

To our knowledge, only one study has examined the relationship between allelic polymorphism and degree of promiscuity:

Petrie et al. (1998) found that bird species with relatively more genetic variability tend to have more extrapair paternity. In most cases, however, the two variables were measured in different populations. Our study populations have also been genetically screened at the population level, and we therefore review these results.

Our sand lizard population (Asketunnan) shows lower genetic diversity than did larger populations in the southern part of the distributional range, but more genetic variation than in most small relic populations (Gullberg et al. 1998a,b). This result is particularly clear when genetic variability was estimated using the MHC class I probe rather than probes for the selectively neutral mini- and microsatellites (Madsen et al. 2000). In a Hungarian population, the average number of DFP alleles was 9.8, whereas in the Swedish populations the average number was only 2.7, with corresponding band-sharing values of 0.19 and 0.61, respectively (Gullberg et al. 1998b). For microsatellites, the average numbers of alleles per locus were 8.0 and 3.3 in the Hungarian and Swedish populations, with expected heterozygosities of 0.89 and 0.45, respectively (Gullberg et al. 1998a).

Until recently the Smygehuk adder population was severely inbred, exhibiting a mean band sharing of DNA fragments of approximately 80% (Madsen et al. 1999) and a lower level of heterozygosity due to fixation or near-fixation of alleles than other populations to which it was compared (Madsen et al. 1996). Smygehuk adder females showed signs of inbreeding depression, such as a smaller relative litter size than outbred females, a higher proportion of malformed young, and a higher incidence of stillborn offspring (Madsen et al. 1996). It is highly unlikely that these effects were due to exogenous toxins such as pesticides (Madsen et al. 1996), and the final evidence that a genetic erosion led to the continuous decline in population size and recruitment came from an experimental introduction of new genes into the population (Madsen et al. 1999). Males from populations more than 250 km away were released into the population and allowed to reproduce with the remaining females before being removed. After this infusion of new genes, the population showed a remarkable recovery, leading to a larger population size than ever recorded previously (Madsen et al. 1999).

Consanguineous Copulations and Risk of Inbreeding Depression

In sand lizards we recorded malformations in about 10% of the hatchlings from

clutches of wild-caught females (Olsson and Madsen 1995; Olsson et al. 1994b,c). We therefore staged a laboratory experiment to (1) investigate whether matings between close kin still resulted in malformations (or, alternatively, if detrimental recessives had been purged) (Hedrick 1994; Kirkpatrick and Jarne 2000); (2) describe the prevalence and characteristics of any malformations that might arise; and (3) compare the laboratory data with those from free-ranging females.

Sand lizard females kept under ad libitum food conditions lay multiple clutches and this can be exploited for mating a female in sequence with partners of differing relatedness. Females mated to brothers had a malformation frequency of 18%, but those same females when mated to unrelated males produced no malformed offspring (Olsson et al. 1996b). Thus deleterious recessives had not been eliminated from the population to the extent that consanguineous matings were harmless in terms of offspring viability (Olsson et al. 1996b). Furthermore, the morphological characteristics of the malformations resulting from sib matings (e.g., cranial deformations, limb asymmetries) agreed in detail with those malformations observed in clutches from the natural population (Olsson et al. 1996b). Not surprisingly, offspring from clutches with no malformed young survived significantly better than offspring from clutches in which young were malformed. Of greater interest, however, normal-looking young with malformed siblings (or half siblings) showed significantly lower survival than offspring from clutches in which no malformations were recorded (Olsson et al. 1996b). Furthermore, offspring from parents that on average were more heterozygous at DFP loci had a higher probability of survival, supporting the proposition that the level of heterozygosity at the genome-wide level influenced offspring survival (Olsson et al. 1997a).

In response to costs and benefits resulting from kin matings, theory predicts that inbreeding avoidance mechanisms should evolve (e.g., Waser et al. 1986 and references therein). This may be the genetic underpinning to sex-biased natal dispersal in sand lizards, with sons exhibiting more pronounced dispersal than daughters (on average 57 m versus 25 m per annum, respectively; Olsson et al. 1996b). In spite of this, inbreeding avoidance is apparently imperfect. More detailed support for this notion comes from our work on degree of relatedness between females and their

consorting males. Females and males with an age difference large enough for a mother and son had significantly higher band sharing than those consorting pairs where the males and females could have been siblings, or father and daughter (Olsson et al. 1997a). Although we did not have the data to demonstrate the exact pedigree relationships between the lizards in this study, the molecular data indicated that matings between mothers and sons were the most likely consanguineous copulations in this population (males mature a year before females, on average, so this scenario is consistent with predictions from demography).

Genetic Restoration of an Adder Population: A Link to Sperm Choice?

Because females will mate with closely related males, we expect malformed young to be produced in relation to the frequency of matings between relatively closely related partners (i.e., at a frequency larger than zero). Following the introduction of new males into the population, however, no malformed young have been recorded (Madsen T, unpublished data). Thus this seems to suggest that spermatozoa from males more distantly related to a female are utilized for fertilization more often than determined by chance.

Discussion

Our studies show that female sand lizards and adder snakes mate promiscuously. Here we describe these results in relation to offspring viability, determinants of paternity, and a potential link between the two.

Female Promiscuity, Determinants of Paternity, and a Link to Offspring Viability

Multiple matings could result in increased offspring viability for several reasons, such as material benefits in the ejaculate (Keller 1994; review in Simmons and Siva-Jothy 1998). However, unlike the relatively large nuptial gifts in insects that are consumed by the female, an ejaculate in sand lizards makes up less than 0.1% of the male's body mass (Olsson M, unpublished data). Furthermore, the female would need to absorb the nutrients from the reproductive tract. To our knowledge, intrauterine resorption has never been described in reptiles, but if it exists, resources acquired this way would be negligible in a female's total energy budget. This argument is further supported by the absence of correlations between the number of matings and clutch size, offspring mass, hatching success, and incidence of malformations (Olsson et al. 1994b). Thus the hypothesis of direct benefits from promiscuity can safely be rejected.

It seems indisputable that promiscuity in adders and sand lizards results in increased offspring viability for genetic reasons. To what degree is this due to the fact that our study populations show less genetic variation than outbred counterparts? We suggest that the more limited genetic variation in our study populations is likely to increase our ability to detect genetic benefits because of an amplification of parental incompatibility by inbreeding depression. However, we also stress that similar phenomena may commonly occur in natural populations but are overlooked simply because accumulated information is not fine enough to admit analysis of genetic interactions of parents and their effects on offspring viability. In support of this notion, two bird studies have accumulated unusually detailed information on parental relatedness and hatching success in outbred populations, and both demonstrate pedigree-unrelated genetic incompatibility resulting in reduced hatching success (Bensch et al. 1994; Kempenaers et al. 1996). Similar results have been demonstrated in a very large population of pythons in tropical Australia. The recapture rate of young was best explained by the identity of the female, also after nongenetic maternal effects were statistically removed (Madsen and Shine 1998). Furthermore, in *Chordylochernes scorpioides* pseudoscorpions, in which females avoid remating the same male, promiscuity increases lifetime reproductive success through a reduction in the number of spontaneous abortions (Newcomer et al. 1999; Zeh et al. 1998). In field crickets, an increased number of partners resulted in increased hatching success (Treganza and Wedell 1998). Thus in a wide range of taxa, including insects, arachnids, reptiles, and birds, promiscuity seems to result in increased offspring viability even when inbreeding can be ruled out.

Are positive genetic effects on offspring viability necessarily linked to determinants of paternity? The following two kinds of answers may apply. Perhaps the answer is "no," such that the probability of paternity is unrelated to the genetic content of the spermatozoa. Under this hypothesis, the risk of having malformed young would be related to the numerical relationship between spermatozoa from a genetically "poor" male versus the summed number of spermatozoa from all "good" males. The risk of having malformed offspring would then be a "fair raffle" (sensu Parker 1990). Alternatively, if the answer is "yes," the haplotype of the spermatozoa does influence the probability of having malformed offspring. This might occur either via sperm competition (i.e., assuming that the fertilization performance of a spermatozoa depends critically on its diploid or haploid genotype), or because assortative fertilization by the female (or egg membrane) places constraints on some males' probability of fertilization.

What is the evidence for these respective scenarios? The first scenario, with dilution of "poor" by "good" spermatozoa as the mechanism, not only predicts that having more spermatozoa from "good males" should reduce the risk of getting poor young, it also predicts that a male's chances of siring offspring per se is linearly related to the number of transferred spermatozoa. In sand lizards, this is contradicted by the fact that time since previous mating and male body size (and hence testis size) were unrelated to male reproductive success when male relatedness to the female was taken into account (Olsson et al. 1996d).

The second scenario is depicted in Madsen et al.'s (1992) hypothesis, suggesting that a male with a relatively superior genotype (e.g., with few homozygous deleterious recessives) shows positive correlations between components of fitness. This hypothesis gains some support from the fact that sand lizard males that are good at mate acquisition also seem to be competitive in situations of sperm competition. The hypothesis does not, however, predict a relationship between partner relatedness and a male's probability of paternity. Only one hypothesis makes this specific prediction: cryptic female (or egg) choice. The two hypotheses are, however, not mutually exclusive and both processes may operate simultaneously.

Assortative Fertilization

The complex cell-cell interactions between gametes at fertilization have been studied in much greater detail in taxa other than reptiles (e.g., Vacquier 1998). Perhaps the best studies of sperm-egg interactions come from work on sea urchins (reviewed in Foltz 1994; Foltz and Lennarz 1994; Hofman and Gabe 1994; Minor et al. 1989; Vaquier et al. 1995). In short, the ma-

jor constituent of the sea urchin sperm acrosome is the protein bindin, which after exocytosis coats the surface of the acrosomal process and is responsible for the adhesion of the sperm to the egg (e.g., Minor et al. 1989). Most studies on the evolutionary biology of bindin have addressed across-species fertilization, that is, aiming to explain barriers to hybridization, and speciation phenomena (Biermann 1998; Metz et al. 1998; Metz and Palumbi 1996; Palumbi 1992, 1998). Recently Palumbi and colleagues suggested, however, that polymorphism in gamete recognition alleles also begs the question: What is its functional significance within species? In an elegant experiment, Palumbi (1999) demonstrated that eggs are not neutral in their sperm choice but show preference for their own genotype. Palumbi's experiment demonstrates strong effects on fertilization by alleles at a single locus and a polymorphism maintained by epistatic interactions between males and females. At least three evolutionarily important generalizations seem to be emerging from their work: (1) There is no universal system by which gametes recognize each other, with the proteins involved in gamete recognition not being homologous in different phyla. (2) Gamete recognition proteins evolve quickly between closely related species. (3) Genes for gamete recognition can be highly polymorphic also within species (Palumbi 1998).

Gamete recognition has been studied in even greater detail in plants (e.g., Delph and Havens 1998; Howard 1999; Wilson and Burley 1983), where relatively more of the genome's alleles are transcribed prior to fertilization. For example, in *Tradescantia paludosa,* more than 20,000 genes are expressed in the pollen, compared to 30,000 in the diploid "adult" (Willing and Mascarenhas 1984). Furthermore, pollen are less frequently rejected when being of a relatively rare self-incompatibility genotype (at the *S* locus), leading to diversifying selection and some of the highest levels of allelic polymorphism recorded (Clark and Kao 1991; Richman and Kohn 1996). Furthermore, traits expressed pre- and postfertilization often show positive correlations within individual plants so that, for example, pollen tube growth is positively correlated with plant growth (Delph and Havens 1998).

It is, however, becoming widely appreciated that genes in the haploid genome are also frequently expressed in animals (e.g., Braun et al. 1988; Nayernia et al. 1996, 1999; Willison and Ashworth 1987).

Erickson (1990) concluded in a review a decade ago that "a plethora of such [postmeiotic] gene transcription has now been found in mammals—so much that one wonders why it should be so common." Of importance, these postmeiotically expressed traits include, for example, tail morphology of the spermatozoa, which has been argued to be of prime importance in sperm competition (Roldan and Gomendio 1999). Furthermore, in humans, genes for similar traits are situated on the Y chromosome (Roldan and Gomendio 1999), which lacks a homologue and hence has portions that are not recombined. Thus heritability for the traits encoded by these genes should be high and evolutionary response to selection rapid. Like humans, sand lizard males have heterogametic sex chromosomes. In adders, genetic sex determination has not been examined in detail, but only female heterogamety is known in snakes (Gorman 1973).

The complexity of intrauterine phenomena and the potential for females or eggs to skew the probability of fertilization between spermatozoa of different genetic origin is further illustrated by studies of flower beetles, *Tribolium* sp. (Wade et al. 1994). When a female is inseminated with spermatozoa from an allospecific male, his spermatozoa successfully fertilize the eggs. However, when the female is inseminated with spermatozoa from both allo- and conspecific males, the conspecific spermatozoa sire virtually all offspring (Wade et al. 1994). Similar phenomena have been demonstrated in grasshoppers (Bella et al. 1992; Hewitt et al. 1989) and crickets (Gregory and Howard 1997). In *Drosophila,* conspecific sperm precedence is clearly not a simple effect of sperm storage, but rather is due to a chemical compound in the seminal fluid of the conspecific male (Price 1997; review of assortative fertilization in Markov 1997; see also Jennions and Petrie 2000). Recent work has also demonstrated male × female interactions as determinants of fertilization in crickets and fruit flies (Clark et al. 1999; Stockley 1999), suggesting that genetic gamete discrimination operates not only between but also within species of *Drosophila*.

Evidence thus seems to be emerging that females and/or eggs can influence a male's probability of fertilization, not only by mechanically "shuffling" spermatozoa from storage sites to fertilization sites in the female reproductive tract in insects (e.g., Eberhard 1996), but also via physiological mechanisms. In mammals it has

long been known that fertilization is an immunological process (Bedford 1965; Cohen and McNaughton 1974) and that immunological incompatibility results in infertility (Dondero et al. 1978). This is further supported by an elegant study by Rulicke et al. (1998) in which it was demonstrated that in vitro fertilized mice have a much stronger tendency to bias the probability of fertilization toward MHC-compatible spermatozoa when infected with a hepatitis virus then when not. Further support for the fertilization process as a barrier to production of inviable offspring comes from experiments on monkeys. Intracytoplasmic sperm injection (ICSI) results in an increased level of embryonic malformations (Hewitson et al. 1999), which supports concerns about the widespread ICSI practice in humans (Edwards 1999; Flaherty et al. 1995). It is important to realize, however, that DNA-damaged spermatozoa can successfully penetrate the egg membrane in many taxa (e.g., Ahmadi and Ng 1999), suggesting that postpenetration processes may also be critical links between sperm haplotype and offspring viability.

Analysis of postcopulatory phenomena is thus made complex by interactions between genetic and nongenetic factors in the female reproductive tract, and the difficulty in separating male and female effects (Olsson et al. 1999). For example, fast-swimming turkey spermatozoa are more likely to fertilize eggs than slow-swimming ones, which could be "the first illustration of a measurable sperm trait predictive of paternity success" (Donaghue et al. 1999). However, sperm motility is likely to be a trait related to male genetic quality (Wildt et al. 1987; cf. pollen and adult characteristics in plants). Thus an alternative explanation to such a result is "egg choice" of a "good" male genotype.

Conclusions

In summary, postcopulatory phenomena are processes amenable to genetic analysis. Numerical sperm competition and sperm performance undoubtedly are important factors in determining male reproductive success. This is evidenced, for example, by a broad taxonomic covariation between relative testis size and variation in mating systems (e.g., Birkhead and Møller 1998; Short 1979). However, it has also long been known that the first spermatozoa to reach fertilization sites do not always fertilize the eggs (Piko 1969), and one reason for this could be gametic in-

compatibility. In most studies of sperm competition, consanguinity of mates and rivals has not been analyzed, even when molecular data are available for the assignment of paternity. Yet such information may shed light on the female benefits of polyandry, its possible relation to gamete recognition, probability of paternity, and breeding success. When this was done in sand lizards and adders, we found evidence primarily for genetic compatibility of partners, but also some indirect evidence for male "good genes." In a recent review, Birkhead (1998) highlighted the complexity of postcopulatory processes and urged researchers to exercise caution and stringency in the interpretation of cryptic female choice. We do the same, while extending this plea to studies of numerical sperm competition, in particular those studies where molecular data make analysis of partner consanguinity possible. Studies of postcopulatory phenomena undoubtedly require multifaceted approaches, including modern molecular genetic techniques as well as the quantification of ejaculate characteristics.

References

Ahmadi A and Ng S-C, 1999. Fertilizing ability of DNA-damaged spermatozoa. J Exp Zool 284:696–704.

Bedford JM, 1965. Effect of environment on phagocytosis of rabbit spermatozoa. J Reprod Fertil 9:249–265.

Bella JL, Butlin RK, Ferris C, and Hewitt GM, 1992. Asymmetrical homogamy and unequal sex ratio from reciprocal mating-order crosses between *Chorthippus paracellus* subspecies. Heredity 68:345–352.

Bensch S, Hasselqvist D, and von Schantz T, 1994. Genetic similarity between parents predicts hatching failure: noninsestuous inbreeding in the great reed warbler. Evolution 48:317–326.

Biermann C, 1998. The molecular evolution of sperm bindin in six species of sea urchins (Echinoida: Strongylocentrotidae). Mol Biol Evol 15:1761–1771.

Birkhead TR, 1998. Cryptic female choice: criteria for establishing female sperm choice. Evolution 52:1212–1218.

Birkhead TR and Møller AP, 1992. Sperm competition in birds: evolutionary causes and consequences. London: Academic Press.

Birkhead TR and Møller AP, 1998. Sperm competition and sexual selection. San Diego: Academic Press.

Birkhead TR and Parker GA, 1997. Sperm competition and mating systems. In: Behavioural ecology—an evolutionary approach (Krebs JR and Davies NB, eds). Oxford: Blackwell Science.

Bischoff W, 1984. *Lacerta agilis* (Linneaus 1758). Zauneidechse. In: Handbuch der Reptilien und Amphibien Europas 2/I (Böhme W, ed). Wiesbaden: AULA-Verlag; 23–68.

Braun RR, Behringer RR, Peschon JJ, Brinster RL, and Palmiter RD, 1988. Genetically haploid spermatids are phenotypically diploid. Nature 337:373–376.

Clark AG, Begun DJ, and Prout T, 1999. Female × male interactions in *Drosophila* sperm competition. Science 283:217–220.

Clark AG and Kao T-H, 1991. Excess nonsynonymous substitution at shared polymorphic sites among self-incompatibility alleles of *Solonaceae.* Proc Natl Acad Sci USA 88:9823–9827.

Cohen J and McNaughton DC, 1974. Spermatozoa: the probable selection of a small population by the genital tract of the female rabbit. J Reprod Fertil 39:297–310.

Cunningham EJA and Russell AF, 2000. Egg investment is influenced by male attractiveness in the mallard. Nature 404:74–77.

Delph LF and Havens K, 1998. Pollen competition in flowering plants. In: Sperm competition and sexual selection (Birkhead TR and Møller AP, eds). San Diego: Academic Press; 149–173.

Dondero F, Cerasaro M, Nigotra M, and Coghi IM, 1978. Sperm-antibody testing in infertility. Lancet 5:313.

Donoghue AM, Sonstegard TS, King LM, Smith EJ, and Burt DW, 1999. Turkey sperm mobility influences paternity in the context of competitive fertilization. Biol Reprod 61:422–427.

Eberhard WG, 1996. Female control: sexual selection by cryptic female choice. Princeton, NJ: Princeton University Press.

Edwards RG, 1999. Widening perspectives of intracytoplasmic sperm injection. Nature Med 5:377–378.

Erickson RE, 1990. Post-meiotic gene expression. Trends Genet 6:264–269.

Flaherty S, Payne D, Swann N, and Matthews C. 1995. Assessment of fertilization failure and abnormal fertilization after intracytoplasmic sperm injection. Reprod Fertil Dev 7:197–210.

Foltz KR, 1994. The sea urchin egg receptor for sperm. Semin Dev Biol 5:243–253.

Foltz KR and Lennarz WJ, 1994. The molecular basis of sea urchin gamete interactions at the egg plasma membrane. Dev Biol 158:46–61.

Gil D, Graves J, Hazon N, and Wells A, 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. Science 286:126–128.

Gorman GC, 1973. The chromosomes of the reptilia, a cytotaxonomic interpretation. In: Cytotaxonomy and vertebrate evolution (Chiarelli AB and Capanna E, eds). New York: Academic Press; 349–424.

Gregory PG and Howard DJ, 1997. A postinsemination barrier to fertilisation isolates two closely related ground crickets. Evolution 48:705–710.

Gullberg A, Olsson M, and Tegelström H, 1997. Male mating success, reproductive success and multiple paternity in a natural population of sand lizards: behavioural and molecular genetics data. Mol Ecol 6:105–112.

Gullberg A, Olsson M, and Tegelström H, 1998a. Colonization, genetic diversity, and evolution in the Swedish sand lizard (*Lacerta agilis*). Biol J Linn Soc 65:257–277.

Gullberg A, Olsson M, and Tegelström H, 1998b. Evolution in populations of Swedish sand lizards: genetic differentiation and loss of variability revealed by multilocus DNA fingerprintng. J Evol Biol 12:17–26.

Gullberg A, Tegelström H, and Olsson M, 1998c. Microsatellites in the sand lizard (*Lacerta agilis*): description, variation, inheritance, and applicability. Biochem Genet 35:281–295.

Hedrick PW, 1994. Purging inbreeding depression and the probability of extinction: full-sib mating. Heredity 73:363–372.

Hewitson L, et al. 1999. Births of ICSI monkeys: unique checkpoints during the first cycle at fertilization. Nat Med 5:431–433.

Hewitt GM, Mason P, and Nichols RA, 1989. Sperm precedence and homogamy across a hybrid zone in the alpine grasshopper *Podisma pedestris*. Heredity 62:343–353.

Hofman A and Gabe CG, 1994. Bindin, a multifunctional sperm ligand and the evolution of new species. Semin Dev Biol 5:233–242.

Höggren M and Tegelström H, 1995. DNA fingerprinting shows within-season multiple paternity in the adder (*Vipera berus*). Copeia 1995:271–277.

Howard, DJ, 1999. Conspecific sperm and pollen precedence and speciation. Annu Rev Ecol Syst 30:109–132.

Jennions MD and Petrie M, 2000. Why do females mate multiply? A review of the genetic benefits. Biol Rev 75:21–64.

Keller L, 1994. Rewards of promiscuity. Nature 230:229–230.

Kempenaers B, Adriensen F, van Noordwijk AJ, and Dhondt AA, 1996. Genetic similarity, inbreeding and hatching failure in blue tits: Are unhatched eggs infertile? Proc R Soc Lond B 263:179–185.

Kirkpatrick M and Jarne P, 2000. The effects of a bottleneck on inbreeding depression and the genetic load. Am Nat 155:154–167.

Madsen T, Olsson M, Gullberg A, Wittzell H, and Tegelström H. 2000. Population size and genetic diversity in sand lizards (*Lacerta agilis*) and adders (*Vipera berus*). Biol Conserv 94:257–262.

Madsen T and Shine R, 1992a. Determinants of reproductive success in female adders, *Vipera berus*. Oecologia 92:40–47.

Madsen T and Shine R, 1992b. Temporal variability in sexual selection acting on reproductive tactics and body size in male snakes. Am Nat 141:167–171.

Madsen T and Shine R, 1994. Lifetime reproductive success in adders. J Anim Ecol 63:561–568.

Madsen T and Shine R, 1998. Quantity or quality: determinants of maternal reproductive success in tropical pythons (*Liasis fuscus*). Proc R Soc Lond B 265:1521–1525.

Madsen T, Shine R, Loman J, and Håkansson T, 1992. Why do female adders copulate so frequently? Nature 355:440–441.

Madsen T, Shine R, Loman J, and Håkansson T, 1993. Determinants of mating success in male adders, *Vipera berus*. Anim Behav 45:491–499.

Madsen, T, Shine R, Olsson M, and Wittzell H, 1999. Restoration of an inbred adder population. Nature 402:34–35.

Madsen T, Stille B, and Shine R, 1996. Inbreeding depression in an isolated population of adders, *Vipera berus*. Biol Conserv 75:113–118.

Magnhagen C, 1991. Predation risk as a cost of reproduction. Trends Ecol Evol 6:183–186.

Markov TA, 1997. Assortative fertilization in *Drosophila*. Proc Natl Acad Sci USA 94:7756–7760.

Metz EC, Gomez-Gutierrez G, and Vacquier VD, 1998. Mitochondrial DNA and bindin gene sequence evolution among allopatric species of the seas urchin genus *Arbacia*. Mol Biol Evol 15:185–195.

Metz EC and Palumbi SR, 1996. Positive selection and sequence rearrangements generate extensive polymorphism in the gamete recognition protein bindin. Mol Biol Evol 13:397–406.

Minor JE, Ga B, and Davidson H, 1989. The molecular biology of bindin. In: The molecular biology of fertilization (Schatten H and Schatten G, eds). New York: Academic Press; 73–88.

Møller AP and Alatalo R, 1999. Good-genes effects in sexual selection. Proc R Soc Lond B 266:85–91.

Nayernia K, Adham I, Kremling H, Reim K, Schlicker M, Schlüter G, and Engel W, 1996. Stage and developmental specific gene expression during mammalian spermatogenesis. Int J Dev Biol 40:379–383.

Nayernia K, von Mering MHP, Kraszucka K, Burfeind P, Wehrend A, Köhler M, Schmid M, and Engel W, 1999. A novel testicular haploid expressed gene (THEG) involved in mouse spermatid-sertoli cell interaction. Biol Reprod 60:1488–1495.

Newcomer SD, Zeh JA, and Zeh DW, 1999. Genetic ben-

efits enhance the reproductive success of polyandrous females. Proc Natl Acad Sci USA 96:10236–10241.

Olsson M, 1988. Ecology of a Swedish population of the sand lizard, *Lacerta agilis*—a preliminary report. Mertensiella 1:86–91.

Olsson M, 1992. Contest success in relation to size and residency in male sand lizards (*Lacerta agilis*). Anim Behav 44:86–388.

Olsson M, 1993a. Contest success and mate guarding in male sand lizards (*Lacerta agilis*). Anim Behav 46: 408–409.

Olsson M, 1993b. Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). Behav Ecol Sociobiol 32:337–341.

Olsson M, 1994a. Nuptial coloration in the sand lizard (*Lacerta agilis*): an intrasexually selected cue to fighting ability. Anim Behav 48:607–613.

Olsson M, 1994b. Rival recognition affects male contest behavior in sand lizards (*Lacerta agilis*). Behav Ecol Sociobiol 35:249–252.

Olsson M, 1994c. Why are sand lizard (*Lacerta agilis*) males not equally green? Behav Ecol Sociobiol l35:169–173.

Olsson M, Gullberg A, Shine R, Madsen T, and Tegelström H, 1996a. Paternal genotype influences incubation period, offspring size, and offspring shape in an oviparous reptile. Evolution 50:1328–1333.

Olsson M, Gullberg A, and Tegelström H, 1994a. Sperm competition in the sand lizard, *Lacerta agilis.* Anim Behav 48:193–200.

Olsson M, Gullberg A, and Tegelström H, 1996b. Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*). J Evol Biol 9:229–242.

Olsson M, Gullberg A, and Tegelström H, 1997a. Determinants of breeding dispersal in the sand lizard (*Lacerta agilis*). Biol J Linn Soc 60:243–256.

Olsson M, Gullberg A, and Tegelström H, 1996c. Mate guarding in male sand lizards (*Lacerta agilis*). Behaviour 133:367–386.

Olsson M, Gullberg A, Tegelström H, Madsen T, and Shine R, 1994b. Rewards of 'promiscuity.' Nature 37: 230.

Olsson M and Madsen T, 1995. Female choice on male quantitative traits—why is it so rare? Behav Ecol Sociobiol 36:179–184.

Olsson M and Madsen T, 1996. Costs of mating with infertile males selects for late emergence in female *Lacerta agilis.* Copeia 1996:462–464.

Olsson M and Madsen T, 1998. Sexual selection and sperm competition in reptiles. In: Sperm competition and sexual selection (Birkhead T and Møller A, eds). San Diego: Academic Press; 503–564.

Olsson M, Norberg A, Tegelström H, Madsen T, and Shine R, 1994c. Can female adders multiply?: promiscuous lizard females have more viable young. Nature 369:528.

Olsson M, Pagel M, Shine R, Madsen T, Doums C, Gullberg A, and Tegelström H, 1999. Sperm choice and sperm competition: suggestions for field and laboratory studies. Oikos 84:172–175.

Olsson M and Shine R, 1997a. Advantages of multiple matings to females: a test of the infertility hypothesis using lizards. Evolution 5:1684–1688.

Olsson M and Shine R, 1997b. The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). Am Nat 149:179–188.

Olsson M and Shine R, 1997c. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. J Evol Biol 10:369–381.

Olsson M, Shine R, Madsen T, Gullberg A, and Tegelström H, 1997b. Sperm choice by females. Trends Ecol Evol 12:445–446.

Olsson M, Shine R, Madsen T, Gullberg A, and Tegelström H, 1996d. Sperm selection by females. Nature 383:585.

Olsson M, Wapstra E, Madsen T, and Silverin B, 2000. Testosterone, ticks and travels: a test of the immuno-competence-handicap hypothesis in free-ranging sand lizards. Proc R Soc Lond B 267:

Palumbi SR, 1992. Marine speciation on a small planet. Trends Ecol Evol 7:114–118.

Palumbi SR, 1998. Species formation and the evolution of gamete recognition loci. In: Endless forms: species and speciation (Howard D and Berlocher S, eds). Oxford: Oxford University Press; 271–278.

Palumbi SA, 1999. All males are not created equal: fertility differences depend on gamete recognition polymorphisms in sea urchins. Proc Natl Acad Sci USA 96: 12632–12637.

Parker GA, 1978a. Evolution of competitive mate searching. Annu Rev Entomol 23:173–196.

Parker GA, 1978b. Searching for mates. In: Behavioural ecology—an evolutionary approach (Krebs JR and Davies NB, eds). Oxford: Blackwell Scientific; 214–244.

Parker GA, 1990. Sperm competition games: raffles and roles. Proc R Soc Lond B 242:120–126.

Parker GA, 1992. Snakes and female sexuality. Nature 355:395–396.

Petrie M, Doums C, and Møller AP, 1998. The degree of extra-pair paternity increases with genetic variability. Proc Natl Acad Sci USA 95:9390–9395.

Piko L, 1969. Gamete structure and sperm entry in mammals. In: Fertilization: comparative morphology, biochemistry and immunology (Metz CB and Monroy A, eds). New York: Academic Press; 325–403.

Price CSC, 1997. Conspecific sperm precedence in *Drosophila.* Nature 388:663–666.

Richman AD and Kohn JR, 1996. Learning from rejection: the evolutionary biology of single-locus incompatibility. Trends Ecol Evol 11:497–502.

Roldan ERS and Gomendio M, 1999. The Y chromosome as a battle ground for sexual selection. Trends Ecol Evol 14:58–62.

Rulicke T, Chapuisat M, Homberger FR, Macas R, and Wedekind C, 1998. MHC-genotype of progeny influenced by parental infection. Proc R Soc Lond B 265: 711–716.

Short RV, 1979. Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the great apes. Adv Study Behav 9:131–158.

Simmons LW and Siva-Jothy MT, 1998. Sperm competition in insects: mechanisms and the potential for selection. In: Sexual selection and sperm competition (Birkhead T and Møller A, eds). San Diego: Academic Press; 503–564.

Smith RL, 1984. Sperm competition and the evolution of animal mating systems. Orlando, FL: Academic Press.

Steward JW, 1971. The snakes of Europe. Newton Abbot, UK: David and Charles.

Stille B, Madsen T, and Niklasson M, 1986. Multiple paternity in the adder, *Vipera berus.* Oikos 47:173–175.

Stille B, Niklasson M, and Madsen T, 1987. Within season multiple paternity in the adder, *Vipera berus.* Oikos 49:232–233.

Stockley P, 1999. Sperm selection and genetic incompatibility: Does relatedness of mates affect male success in sperm competition? Proc R Soc Lond B 266: 1663–1669.

Treganza T and Wedell N, 1998. Benefits of multiple mates in the cricket *Gryllus bimaculatus.* Evolution 52: 1726–1730.

Vacquier VD, 1998. Evolution of gamete recognition proteins. Science 281:1995–1998.

Vaquier VD, Swanson WJ, and Hellberg ME, 1995. What have we learned about sea urchin sperm bindin? Dev Growth Differ 37:1–10.

von Schantz T, Bensch S, Grahn M, Hasselqvist D, and Wittzell H, 1999. Good genes, oxidative stress and condition-dependent sexual signals. Proc R Soc Lond B 266:1–12.

Wade MJ, Patterson H, Chang NW, Johnson NA, 1994. Postcopulatory, prezygotic isolation in flour beetles. Heredity 72:163–167.

Waser PMS, Austad N, and Keane B. 1986. When should animals tolerate inbreeding? Am Nat 128:529–537.

Wildt DE, Bush M, Goodrowe KL, Packer C, Pusey AE, Brown JL, Joslin P, and O'Brien SJ, 1987. Reproductive and genetic consequences of founding isolated lion populations. Nature 329:328–331.

Williams GC, 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton, NJ: Princeton University Press.

Willing RP and Mascarenhas JP, 1984. Analysis of the complexity and diversity of mRNAs from pollen and shoots of *Zea mays.* Plant Physiol 75:865–868.

Willison K and Ashworth A, 1987. Mammalian spermatogenic gene expression. Trends Genet 3:351–355.

Wilson MF and Burley N, 1983. Mate choice in plants: tactics, mechanisms, and consequences. Princeton, NJ: Princeton University Press.

Zakharov VM, 1989. Future prospects for population phenogenetics. Sov Sci Rev F Physiol Gen Biol 4:1–79.

Zeh JA, Newcomer SD, and Zeh DW, 1998. Polyandrous females discriminate against previous mates. Proc Natl Acad Sci USA 95:13732–13736.

Zeh JA and Zeh D, 1996. The evolution of polyandry I: intragenomic conflict and genetic compatibility. Proc R Soc Lond B 263:1711–1717.

Zeh JA and Zeh D, 1997. The evolution of polyandry II: post-copulatory defences against genetic incompatibility. Proc R Soc Lond B 264:69–75.

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