6

Impacts of inbreeding on components of reproductive success

KAREN KOENINGER RYAN, ROBERT C. LACY & SUSAN W. MARGULIS

INTRODUCTION AND OBJECTIVES

Although inbreeding depression may reduce individual fitness at all life-history stages, empirical investigations have been largely limited to studies of juvenile survival in captive mammals. Numerous studies (e.g. Ralls *et al.*, 1979; Ballou & Ralls, 1982; Ralls & Ballou, 1982; Ralls *et al.*, 1988; Lacy *et al.*, 1993, reviewed by Thornhill, 1993) have demonstrated a reduction in the survival of offspring produced by related mates. This narrow focus, however, has led some scientists (e.g. Shields, 1982) to speculate that inbreeding depression is less important than it appears from the size of the effects found. First, if some offspring will usually be lost due to sib–sib competition, losses due to inbreeding depression may not drastically affect the parent's fitness. Second, it is possible (but still largely untested) that inbreeding could result in enhancements to other components of fitness, thereby offsetting reductions in juvenile survival.

It is not clear, however, that inbreeding depression affects mainly juvenile life-history traits (Charlesworth & Charlesworth, 1987). Rather, the effects of inbreeding on early stages of reproduction and other adult life-history traits have been little investigated, especially in non-domesticated animals. Inbred individuals that survive to adulthood may still suffer reduced fitness via reduced adult survival, poor performance in mating competition, reduced fecundity, and less capable parental care. The paucity of data regarding the effect of inbreeding on these adult traits may lead biologists to underestimate the total cost of inbreeding for sexually reproducing species.

The current literature offers little evidence regarding the proximate behavioural and physiological mechanisms underlying inbreeding avoidance and inbreeding depression. However, such data would provide an invaluable resource to biologists who manage small captive and wild populations. In addition to the current practice of using pedigrees to avoid matings between closely related individuals, an understanding of such proximate mechanisms might provide further options for controlling the effects of inbreeding when managers cannot avoid it. Furthermore, mechanisms used by the animals themselves to avoid inbreeding may depress reproduction in small populations consisting largely of related animals, even if no inbreeding occurs. While this would not be inbreeding depression *per se*, it is yet another way in which processes that relate to inbreeding and kinship could have important consequences for managed breeding and conservation programmes.

This chapter has three specific goals. First, we will provide a brief overview of the extensive literature concerning the effects of inbreeding on juvenile life-history traits in non-domesticated vertebrates. Second, we will identify other components of fitness that we consider both important and under-investigated with regard to inbreeding effects. We will provide a more thorough review of the current knowledge in these crucial areas, highlighting our own work concerning inbreeding and fitness in *Peromyscus* mice. Finally, we will suggest priorities for the direction of future research, with the specific aim of providing additional information to conservation biologists who are charged with the task of managing the reproductive effects of inbreeding in small populations of vertebrates.

TERMINOLOGY

We begin with a brief review of the relevant terminology, specifically highlighting the distinction between inbreeding and kinship. The inbreeding coefficient (f) specifies the relatedness of an individual's parents. Inbreeding coefficient describes the proportion of an individual's loci that are homozygous for genes that are identical by descent. The kinship coefficient (k) is a relative property of a pair of individuals. Kinship coefficient describes the probability that a pair of alleles, chosen at random from the same loci in the two individuals, are identical by descent. Kinship, therefore, is a measure of the relatedness between individuals, and is equivalent to the inbreeding coefficient of their potential offspring. A brother and sister, for example, would have a kinship coefficient (k) = 0.25; the inbreeding coefficient of their potential offspring would be $f = 0.25$.

Inbreeding and kinship have often been used interchangeably in the conservation literature, and geneticists sometimes describe populations with high average kinship as being inbred. This confusion of terminology results from the fact that inbreeding and kinship effects are often confounded in small isolated populations. When a population has descended from only a few founders, its constituents would typically have large inbreeding coefficients because their ancestors were related. Furthermore, if the population has remained small and isolated, its constituents would also have high kinship coefficients relative to each other. However, if there is inbreeding avoidance or preferential inbreeding, then the extent of inbreeding in individuals can be decoupled from the average kinship among individuals. The poor reproductive performance commonly observed in small populations may result from inbreeding effects, kinship effects, or both. Identifying the separate effects of inbreeding and kinship, however, may suggest targeted solutions to reproductive problems faced by small vertebrate populations.

COMPONENTS OF FITNESS

Decreased reproductive rates commonly observed in small isolated wild populations have generally been attributed to inbreeding depression. While this is broadly accurate, the various avenues by which kinship and inbreeding may have led to low population growth rates remain largely unexplored. Fitness can be organised into several components (outlined in Figure 6.1): survival to sexual maturity; adult survival; mate acquisition; fecundity; and parental care. We shall organise our discussion, below, according to these several components.

INBREEDING DEPRESSION OF JUVENILE SURVIVAL

The negative impact of inbreeding on juvenile survival is well documented. In their seminal studies, Ralls and Ballou reported increased juvenile mortality due to inbreeding for many captive mammal populations using data from zoological records (Ralls *et al.*, 1979, 1988; Ballou & Ralls, 1982; Ralls & Ballou, 1982). Individuals were scored as either surviving or not surviving half the estimated time to sexual maturity. Inbred offspring suffered increased mortality during this period. Similar trends have been reported in channel catfish, common iguana, great tits, oldfield mice, and many other vertebrates (reviewed by Thornhill, 1993).

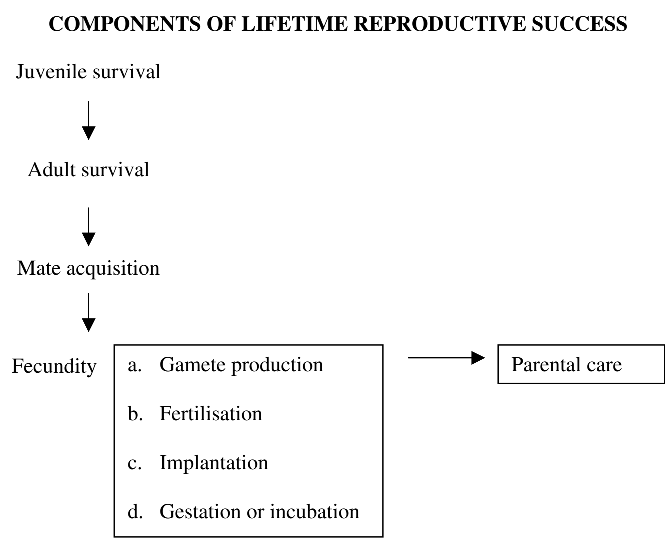

Figure 6.1 In this chapter we review the literature regarding the effects of inbreeding and kinship at each of these components of fitness, drawing attention to those components of lifetime reproductive success that are particularly under-studied.

The sheer volume of evidence that inbreeding can negatively impact juvenile survival has led many scientists to assume prematurely that this is its primary effect. In other words, inbred individuals that survive to adulthood are typically assumed not to suffer from inbreeding depression (Margulis, 1998a). On the contrary, there is still much to learn regarding the importance of inbreeding and kinship for the early stages of reproduction and other adult life-history traits.

INBREEDING DEPRESSION OF ADULT SURVIVAL

Those inbred individuals that survive to adulthood may still suffer inbreeding depression via reduced adult survival. Although the consequences of inbreeding for the survival of inbred adults have received relatively little attention, evidence is building (Pusey & Wolff, 1996). Chen (1993), for example, released inbred and outbred adult land snails into the field. Inbred snails were less likely to be recaptured than their outbred counterparts. Similarly, Keller *et al.* (1994) found that inbred song sparrows were less likely to survive a natural population crash resulting from severe winter weather.

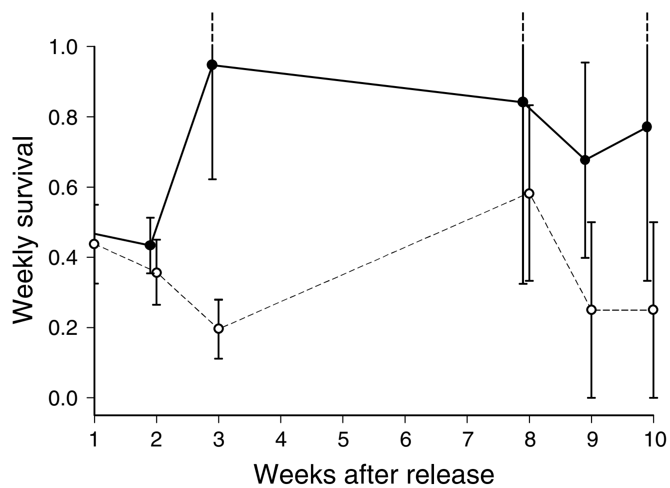

Figure 6.2 Survival of inbred and non-inbred mice (*Peromyscus leucopus*) over 10 weeks. Solid circles represent the mean survivorship values for non-inbred mice and open circles represent values for inbred mice. Bars represent standard errors of the estimates. Symbols and error bars are slightly offset to show the area of overlap. Non-inbred animals had higher survival than inbred animals during all six time intervals. The ratio of inbred survival to non-inbred survival is 0.558 ± 0.121, averaged over the six estimates shown. None of the survival estimates from single time periods differs significantly between inbred and non-inbred individuals. When the estimates are used as repeated measures of survival for groups of inbred and non-inbred individuals, the overall difference is statistically significant. (From Jiménez *et al.*, 1994.)

Inbred white-footed mice (*Peromyscus leucopus*) also suffered inbreeding depression via reduced adult survival. Jiménez *et al.* (1994) released marked inbred and non-inbred adult white-footed mice into a forested area following several generations of captive breeding. Traps were set on 27 occasions during the 10 weeks following their release. All recaptured mice were identified, weighed, and re-released. Inbred males lost body mass throughout the experiment, while non-inbred males regained body mass lost during the first few days following their release. Furthermore, the weekly survival of inbred mice (both male and female) was only 56% of the survival of non-inbred mice (Figure 6.2).

MATE ACQUISITION

Both inbreeding and kinship can affect mate acquisition in small vertebrate populations. Inbred adults may be at a disadvantage in direct intrasexual competition over mates if they are less vigorous than their outbred

P1: FDJ/IKJ P2: FDJ/IKJ QC: FDJ
CU568-Holt 0521812151 June 19, 2002 3:29 Char Count= 0

counterparts. Additionally, 'choosy' members of the opposite sex may prefer outbred mates. Under these competitive circumstances, inbreeding depression might be much more severe than otherwise expected. Kinship between potential mates would affect mate acquisition in systems where individuals actively avoid inbreeding. Specifically, individuals would be expected to choose the least-related mate available. In severe cases, where all available mates are close relatives, animals may delay mating or refuse to mate entirely. Such behaviours could have severe consequences for the growth of small populations.

Effect of inbreeding on mate acquisition

Those inbred individuals that survive to adulthood and remain alive long enough to reproduce may still suffer inbreeding depression if they are less able to acquire a mate. Maynard-Smith (1956) and Sharp (1984) suggested that mate choice and intrasexual competition may favour outbred individuals in many species. If this is indeed a common phenomenon, it represents an additional cost of inbreeding to the reproductive success of inbred adults. Inbreeding reduces competitive male mating ability in *Drosophila melanogaster* (Simmons & Crow, 1977; Miller *et al*., 1993) and decreases male display rates in guppies (*Poecilia reticulata*) (Farr, 1983). Yet the effect of inbreeding of adults on mate choice and intrasexual competition has received little attention elsewhere, with at least one exception which we describe below.

In a recent study of house mice (*Mus domesticus*), Meagher *et al*. (2000) demonstrated an 81% reduction in male reproductive success due to inbreeding. Inbred ($f = 0.25$) and outbred ($f = 0$) adult mice were released into semi-natural enclosures, and their behaviour and offspring production were monitored. Inbred males had only 19% as many pups that survived to weaning compared with outbred males. The reduced reproductive success of inbred males was attributed to their inability to obtain breeding territories. Fewer inbred males became territorial compared with outbred males. Furthermore, those few inbred males that did acquire territories acquired suboptimal territories containing fewer female residents and, later, producing fewer pups. This inbreeding depression would not have been detected if investigators had focused only on survival of inbred juveniles.

Effect of kinship on mate acquisition

Many animals are known to bias social behaviour according to differences in their kinship to conspecifics (reviewed by Fletcher & Michener, 1987, and Hepper, 1991). Numerous species avoid mating with their first order (parents, full sibs) or second order (half-sibs, aunts/uncles) relatives (e.g. McGuire & Getz, 1981; Dewsbury, 1982; Barnard & Fitzsimons, 1988). Such incest avoidance can sometimes be useful to population managers, if it allows sexually mature opposite-sex relatives to be housed together with little risk of unwanted births.

Although the abilities of animals to detect smaller differences in their kinship to potential mates have been largely untested (but see Slater & Clements, 1981; Bateson, 1982; Barnard & Fitzsimons, 1988; Keane, 1990), they could have important implications for managed breeding. If animals delay or withhold sexual responsiveness toward even distantly related conspecifics, this inbreeding avoidance mechanism could slow the growth of small, isolated populations (Lacy, 2000). We illustrate this possibility with an example from our own experimental studies of inbreeding, kinship and reproduction in a captive population of the monogamous oldfield mouse (*Peromyscus polionotus*) (Ryan, 2000; K. Ryan & R. Lacy, unpublished data). In this population, males chose between distantly related unfamiliar females according to very small differences in their kinship to these potential mates. Moreover, these mate preferences had consequences for their subsequent reproductive success.

Male oldfield mice were allowed to express a social preference between two distantly related, unfamiliar potential mates. The mean kinship coefficient of the choosing male to either of the females was less than the kinship of first cousins. The two females also differed only slightly in their kinship to the choosing male. The mean difference between the two females in their kinship to the choosing male was less than the difference between first cousins and first-cousins-once-removed. Despite these small kinship differences, males consistently favoured the less related of the two females.

These male social preferences between potential mates had further consequences for their subsequent reproductive success (Ryan & Altmann, 2001). Immediately following the social preference tests (above), choosing males were paired either with the female they had preferred or with the female they had rejected. Males that had been paired with their preferred female sired more offspring compared with males that had been paired with their rejected female. Moreover, several of the pairs containing rejected females never produced any offspring, and two of these involved serious fights resulting in the death of one of the mice.

These results suggest an important role for both kinship and mate choice in the design of captive breeding programmes and in the conservation of small natural populations. Not only did oldfield mouse males discriminate based on remarkably small kinship differences, but they apparently used this information to choose the more suitable mate. These unexpected results call for similar investigations in other species (see McLain, 1998; Drickamer *et al.*, 2000). Moreover, they serve as preliminary evidence of the potential benefits of including opportunities for mate choice in managed breeding programmes.

FECUNDITY

Both inbreeding and kinship between mates could affect fecundity in sexually reproducing species. Fecundity is defined here as the number of offspring produced per unit time. Inbred adults may suffer reduced fecundity if they have inferior gamete production, if they are physiologically less capable of fertilisation or implantation, or if they exhibit inadequate gestation (mammals) or incubation (many other vertebrates). Similarly, kinship between mates could affect fecundity if related mates exhibit inferior fertilisation, implantation, gestation or incubation.

Effect of inbreeding on fecundity

Those inbred adults that remain alive long enough to reproduce, and that acquire a mate, might still suffer inbreeding depression via reduced fecundity. Small isolated populations of lion (Wildt *et al.*, 1987), for example, exhibited both reduced genetic variation and higher incidences of sperm abnormalities when compared with a larger continuous population. This possible inbreeding depression was attributed to lower testosterone concentrations. Male Florida panther were more likely to be unilaterally or bilaterally cryptorchid (having one or both testicles not descended), had lowered testicular and semen volumes, poorer sperm motility, and more morphologically abnormal sperm compared with larger, continuously distributed puma populations (Barone *et al.*, 1994). If these physiological abnormalities of inbred adult males reduce their fecundity (as expected), they represent inbreeding depression. Additionally, captive inbred gazelles exhibited decreases in semen volume, sperm motility and morphology both within and across species (Roldan *et al.*, 1998; Gomendio *et al.*, 2000). Sperm quality was correlated with fluctuating asymmetry, suggesting that a phenotypic trait could be used by females as an indicator of sperm quality and therefore level of inbreeding during mate choice.

Both female and male *Peromyscus polionotus* adults in our lab suffered inbreeding depression via reduced fecundity. S. Margulis & A. Walsh

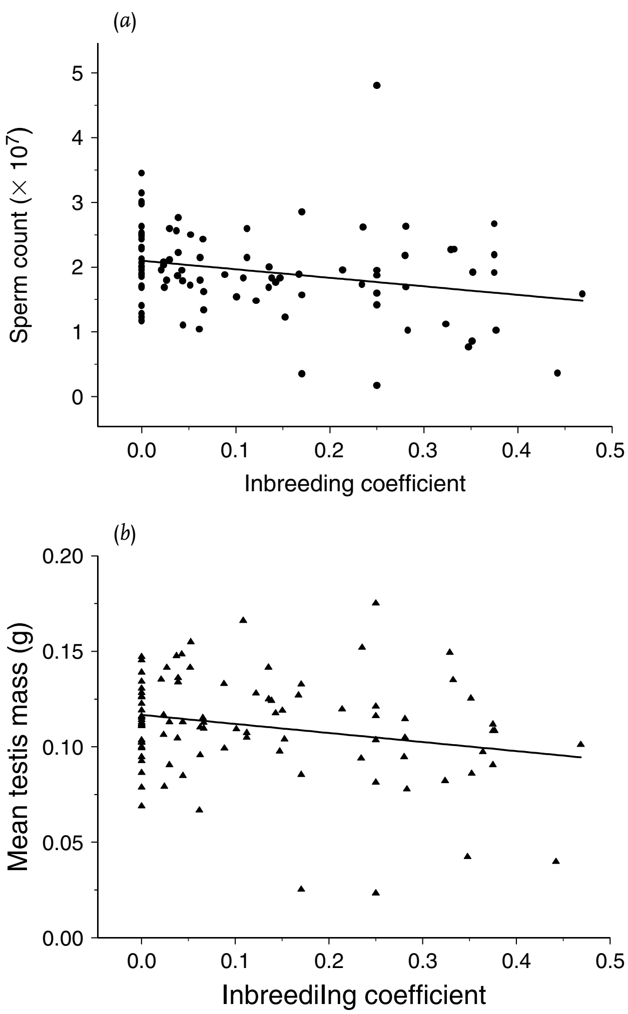

Figure 6.3 Inbreeding depression of male gamete production in oldfield mice (*Peromyscus polionotus*). (a) Sperm count ($F_{1,88} = 6.24,\ P < 0.01$) and (b) testis mass ($F_{1,91} = 5.18,\ P < 0.025$) declined with increasing inbreeding coefficient (f) of adult male oldfield mice. (From S. Margulis & A. Walsh, unpublished data).

(unpublished data) compared the sperm counts and testis size of 93 males. Both testis mass and sperm count per gram testis were negatively correlated with increasing inbreeding coefficient of the male (Figure 6.3). Likewise, inbred female oldfield mice that survived to adulthood also suffered inbreeding depression via reduced fecundity. Inbred dams are less likely to produce litters; when they do reproduce, they are less likely to re-breed to produce a second litter; and the average number of pups born per litter is

P1: FDJ/IKJ P2: FDJ/IKJ QC: FDJ
CU568-Holt 0521812151 June 19, 2002 3:29 Char Count= 0

reduced (Lacy *et al.*, 1996). In addition, inbred females ($f > 0.10$) displayed a greater latency to the birth of their first litter compared with their outbred ($f < 0.10$) conspecifics, regardless of their kinship to the sire (Margulis & Altmann, 1997; Margulis, 1998a). The specific behavioural or physiological mechanisms responsible for this inbreeding depression in female reproduction have not yet been elucidated. They might include abnormal ovulation, fertilisation, implantation, or gestation by inbred females.

Effect of kinship on fecundity

When mates are related (i.e. when their potential offspring are inbred), they often exhibit reduced fecundity. Decreased offspring production by related mates has been demonstrated for several vertebrate species, including geese (Rave *et al.*, 1999), house mice (Krackow & Matuschak, 1991) and oldfield mice (Lacy *et al.*, 1996).

Possible behavioural mechanisms for the reduced fecundity of related mates include latency or refusal to engage in adequate mating behaviour. Those oldfield mice males, for example, that were paired with the (typically less-related) female that they had previously preferred in a social preference test received a greater proportion of receptive lordosis behaviours from their mates (Ryan, 2000).

Possible physiological mechanisms for the reduced fertility of related mates include impaired fertilisation and inferior gestation or incubation. In a small isolated human population, for example, couples sharing alleles at the major histocompatibility complex (MHC) exhibited an increased incidence of recurrent spontaneous abortion (Ober *et al.*, 1992; see Hedrick, Chapter 7, for a discussion of the MHC in relation to breeding). It has been suggested that successful implantation of mammalian embryos requires that the maternal immune system recognise the foetus by its different MHC gene products. Mates that share many MHC alleles by common descent, therefore, would be histoincompatible and more prone to recurrent spontaneous abortion. This maternal–foetal histoincompatibility might provide a mechanism for the reduced fecundity of related mates (reviewed by Jordan & Bruford, 1998).

INBREEDING DEPRESSION OF PARENTAL CARE

Those inbred adults that remain alive long enough to reproduce, that acquire a mate, and that produce offspring, might still suffer inbreeding depression if they exhibit inadequate parental care. Margulis (1998b) observed the parental behaviour of inbred and outbred oldfield mice at regular

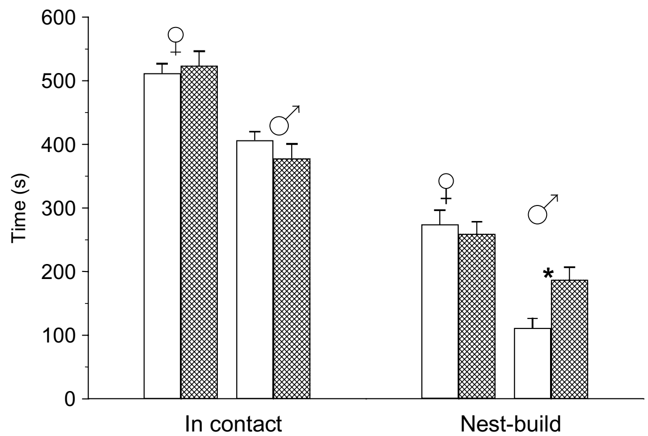

Figure 6.4 The effect of parental inbreeding on parental behavior during the postpartum period. Seconds (of 600) spent in contact with pups (left) and nest-building (right) for inbred (white) and outbred (hatched) males and females. *$P < 0.05$. (From Margulis, 1998b.)

intervals following the birth of their litters. Inbred males were less capable fathers compared with their outbred counterparts. Inbred fathers spent less time nest-building and less time in contact with their pups compared with outbred fathers; both behaviours serve an important thermoregulatory function in this monogamous species (Figure 6.4). In contrast, inbred adult females were better mothers than their outbred counterparts; they had shorter latencies to begin nest-building and nuzzled their pups more frequently. However, superior maternal skills only slightly offset the reduced fecundity of inbred females. Inbred females still weaned fewer offspring compared with outbred females.

SUMMARY AND PRIORITIES FOR FUTURE RESEARCH

The deleterious effects of inbreeding for juvenile survival have been known for more than a century (Darwin, 1859). Moreover, the importance of inbreeding depression for the management and conservation of small vertebrate populations has been discussed for more than two decades (e.g. Frankel & Soulé, 1981; Soulé, 1987; Lacy, 1993; Frankham, 1995). Although the primary threats to many species are anthropogenic (e.g. habitat destruction and over-harvesting), inbreeding within the resulting small and isolated populations may increase their susceptibility to these threats and to other stochastic events (Lacy, 1997; Taylor, Chapter 5).

Despite this rather long history, we know surprisingly little regarding the effects of inbreeding on components of fitness other than juvenile survival. Inbred individuals that survive to adulthood might still suffer inbreeding depression via reduced adult survival, inability to obtain mates, reduced fecundity, and/or insufficient parental care. The effects of inbreeding on these adult life-history traits have rarely been reported. If inbreeding depression is indeed detrimental to early stages of reproduction and other adult life-history traits, then we have greatly underestimated its impact. In this chapter we have reviewed the limited literature concerning inbreeding depression of these various components of fitness, and we emphasise the need for additional studies of this nature.

Likewise, we still know too little regarding the physiological and behavioural mechanisms that mediate inbreeding avoidance and inbreeding depression. An understanding of such proximate mechanisms might suggest means by which managers can mitigate the deleterious effects of inbreeding, when inbreeding cannot be avoided. In this chapter we have reviewed the limited literature regarding the proximate physiological and behavioural mechanisms that mediate inbreeding depression, and again we emphasise the need for additional studies of this nature.

The well-documented reduction in juvenile survival with increased inbreeding may represent only a fraction of the risk associated with inbreeding depression. Inbred adults may also suffer reduced survival and reproductive success. There is a need for additional investigations regarding the impact of inbreeding and kinship on adult life-history traits and the mechanisms of these effects. Such studies would provide invaluable information to conservation biologists charged with managing captive and wild populations of threatened species.

ACKNOWLEDGEMENTS

Our studies of kinship and inbreeding in *Peromyscus* have been funded by the Animal Behavior Society, the Chicago Zoological Society, the US National Science Foundation, Sigma Xi, and the University of Chicago. We thank Glen Alaks and Allison Walsh for years of animal care and assistance with data collection. We thank the symposium organisers and participants for helpful comments and discussion.

REFERENCES

Ballou, J. & Ralls, K. (1982). Inbreeding and juvenile mortality in small populations of ungulates: a detailed analysis. *Biological Conservation* **24**, 239–272.

Barnard, C. J. & Fitzsimmons, J. (1989). Kin recognition and mate choice in mice: fitness consequences of mating with kin. *Animal Behaviour* **38**, 35–40.

Barone, M. A., Roelke, M. E., Howard, J., Brown, J. L., Anderson, A. E. & Wildt, D. E. (1994). Reproductive fitness of the male Florida panther: comparative studies of *Felis concolor* from Florida, Texas, Colorado, Chile, and North American Zoos. *Journal of Mammalogy* **75**, 150–162.

Bateson, P. (1983). Optimal outbreeding. In *Mate Choice* (Ed. P. Bateson), pp. 257–277. Cambridge University Press, Cambridge.

Charlesworth, D. & Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences . *Annual Review of Ecology and Systematics* **18**, 237–268.

Chen, X. (1993). Comparison of inbreeding and outbreeding in hermaphoditic *Areanta arbustorum* (land snail). *Heredity* **71**, 456–461.

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection*. Murray, London.

Dewsbury, D. (1982). Avoidance of incestuous breeding between siblings in two species of *Peromyscus* mice. *Biology of Behavior* **7**, 157–169.

Drickamer, L. C., Gowaty, P. A. & Holmes, C. M. (2000). Free female mate choice in house mice affects reproductive success and offspring viability and performance *Animal Behaviour* **59**, 371–378.

Farr, J. A. (1983). The inheritance of qualitative fitness traits in guppies, *Poecilia reticulata*. *Evolution* **37**, 1193–1209.

Fletcher, D. J. C. & Michener, C. D. (Eds.) (1987). *Kin Recognition in Animals*. Wiley, New York.

Frankel, O. H. & Soulé, M. E. (1981). *Conservation and Evolution*. Cambridge University Press, Cambridge.

Frankham, R. (1995). Inbreeding and extinction: a threshold effect. *Conservation Biology* **9**, 792–799.

Gomendio, M., Cassinello, J. & Roldan, E. R. S. (2000). A comparative study of ejaculate traits in three endangered ungulates with different levels of inbreeding: fluctuating asymmetry as an indicator of reproductive and genetic stress. *Proceedings of the Royal Society of London B* **267**, 875–882.

Hepper, P. (Ed) (1991).*Kin Recognition*. Cambridge University Press, Cambridge.

Jiménez, J. A., Hughes, K. A., Alaks, G., Graham, L. & Lacy, R. C. (1994). An experimental study of inbreeding depression in a natural habitat. *Science* **266**, 271–273.

Jordan, W. C. & Bruford, M. W. (1998). New perspectives on mate choice and the MHC. *Heredity* **80**, 239–245.

Keane, B. (1990). The effect of relatedness on reproductive success and mate choice in the white-footed mouse, *Peromyscus leucopus*. *Animal Behaviour* **39**, 264–273.

Keller, L. F., Arcese, P., Smith, J. N. M., Hochachka, W. M. & Stearns, S. C. (1994). Selection against inbred song sparrows during a natural population bottleneck. *Nature* **372**, 356–357.

Krackow, S. & Matuschak, B. (1991). Mate choice for non-siblings in wild house mice: evidence from a choice test and a reproductive test. *Ethology* **88**, 99–108.

Lacy, R. C. (1993). Impacts of inbreeding in natural and captive populations of vertebrates: implications for conservation. *Perspectives in Biology & Medicine* **36**, 480–496.

Lacy, R. C. (1997). Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* **78**, 320–335.
Lacy, R. C. (2000). Considering threats to the viability of small populations using individual based models. *Ecological Bulletin* **48**, 39–51.
Lacy, R. C., Alaks, G. & Walsh, A. (1996). Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. *Evolution* **50**, 2187–2200.
Lacy, R. C., Petric, A. M. & Warneke, M. (1993). Inbreeding and outbreeding depression in captive populations of wild species. In *The Natural History of Inbreeding and Outbreeding* (Ed. N. W. Thornhill), pp. 352–374. University of Chicago Press, Chicago.
Margulis, S. W. (1998a). Differential effects of inbreeding at juvenile and adult life history stages in *Peromyscus polionotus*. *Journal of Mammalogy* **79**, 326–336.
Margulis, S. W. (1998b). Relationships among parental inbreeding, parental behaviour and offspring viability in oldfield mice. *Animal Behaviour* **55**, 427–438.
Margulis, S. W. & Altmann, J. (1997). Behavioural risk factors in the reproduction of inbred and outbred oldfield mice. *Animal Behaviour* **54**, 397–408.
Maynard-Smith, J. (1956). Fertility, mating behavior, and sexual selection in *Drosophila subobscura*. *Journal of Genetics* **54**, 261–279.
McGuire, M. R. & Getz, L. L. (1981). Incest taboo between sibling *Microtus ochrogaster*. *Journal of Mammalogy* **62**, 213–215.
McLain, D. K. (1998). Non-genetic benefits of mate choice: fecundity enhancement and sexy sons. *Animal Behaviour* **55**, 1191–1201.
Meagher, S., Penn, D. J. & Potts, W. (2000). Male–male competition magnifies inbreeding depression in wild house mice. *Proceedings of the National Academy of Sciences USA* **97**, 3324–3329.
Miller, P. S., Glasner, J. & Hedrick, P. W. (1993). Inbreeding depression and male-mating behavior in *Drosophila melanogaster*. *Genetica* **88**, 29–36.
Ober, C., Elias, S., Kostyu, D. D. & Hauck W. W. (1992). Decreased fecundability in Hutterite couples sharing HLA-DR. *American Journal of Human Genetics* **50**, 6–14.
Pusey, A. & Wolff, M. (1996). Inbreeding avoidance in animals. *Trends in Ecology and Evolution* **11**, 201–206.
Ralls, K. & Ballou, J. (1982). Effects of inbreeding on infant mortality in captive primates. *International Journal of Primatology* **3**, 491–505.
Ralls, K., Ballou, J. D. & Templeton, A. (1988). Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* **2**, 185–193.
Ralls, K., Brugger, K. & Ballou, J. (1979). Inbreeding and juvenile mortality in small populations of ungulates. *Science* **206**, 1101–1103.
Rave, E. H., Fleischer, R. C., Duvall, F. & Black, J. M. (1999). Factors influencing reproductive success in captive populations of Hawaiian Geese, *Branta sandviencensis*. *Wildfowl* **49**, 36–44.
Roldan, E. R. S., Cassinello, J., Abaigar, T. & Gomendio, M. (1998). Inbreeding, fluctuating asymmetry and ejaculate quality in an endangered ungulate. *Proceedings of the Royal Society of London B* **265**, 243–248.
Ryan, K. K. (2000). Consequences and causes of mate choice by monogamous male oldfield mice, *Peromyscus polionotus*. Ph.D. dissertation, University of Chicago.
Ryan, K. K. & Altmann, J. (2001). Selection for male choice based primarily on mate compatibility in the oldfield mouse, *Peromyscus polionotus*. *Behavioral Ecology and Sociobiology* **50**, 436–440.

Sharp, P. L. (1984). The effect of inbreeding on competitive male mating ability in *Drosophila melanogaster*. *Genetics* **106**, 601–612.
Shields, W. (1982). *Philopatry, Inbreeding, and the Evolution of Sex*. SUNY Albany Press, Albany, NY.
Simmons, M. J. & Crow, J. F. (1977). Mutations affecting fitness in *Drosophila* populations. *Annual Review of Genetics* **11**, 49–78.
Slater, P. J. B. & Clements, F. A. (1981). Incestuous mating in zebra finches. *Zeitschrift fur Tierpsychologie* **57**, 201–208.
Soulé, M. E. (1987). *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
Thornhill, N. W. (Ed) (1993). *The Natural History of Inbreeding and Outbreeding*. University of Chicago Press, Chicago.
Wildt, D. E., Bush, M., Goodrowe, K. L., Packer, C., Pusey, A. E., Brown, J. L., Joslin, P. & O'Brien, S. J. (1987) Reproductive and genetic consequences of founding isolated lion populations. *Nature* **329**, 328–331.