
Sexual Selection and Life-History Decisions: Implications for Supportive Breeding and the Management of Captive Populations

CLAUS WEDEKIND

Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, Scotland, United Kingdom, email c.wedekind@ed.ac.uk

Abstract: *Natural breeding systems and various kinds of mate-choice or sperm-choice rules (e.g., as proposed in the “good genes” models of sexual selection) are expected to have important implications for the genetics of the next generation. Moreover, mate-choice decisions may be connected to life-history decisions about current and future parental effort. Considering these genetic and conditional aspects of free mating could improve the long-term success of breeding programs in conservation. In some cases, free mate choice might be more genetically advantageous than random mating because it may promote offspring health and enable host populations to react to coevolving pathogens. However, breeding systems are not evolved to avoid extinction. In small and endangered populations, some forms of natural breeding systems and mate preferences need to be carefully manipulated to avoid an extensive reduction of the effective population size (N_e). In general, supportive breeding should minimize the variance in reproductive success that is not linked to viability traits. However, minimizing reproductive skew might not be the best conservation strategy if potential mates differ in their heritable viability. If a reproductive skew can be positively linked to heritable viability or increased parental effort, there might be a way to optimize this skew with respect to the survival prospects of a population.*

Selección Sexual y Decisiones de Historia de Vida: Implicaciones sobre la Reproducción de Apoyo y el Manejo de Poblaciones Cautivas

Resumen: *Se especula que los sistemas de reproducción natural y varios tipos de reglas que se refieren a la selección de pareja o a la selección de esperma (propuestos en los modelos de “buenos genes” de selección sexual) tengan implicaciones importantes para la genética de la siguiente generación. Además, las decisiones de selección de pareja pueden estar conectadas con las decisiones de historia de vida en cuanto a los esfuerzos actuales y futuros de los padres. La consideración de estos aspectos genéticos y condicionales de apareamiento libre puede mejorar el éxito de largo plazo de los programas de reproducción para la conservación. En algunos casos, la selección del apareamiento libre puede ser genéticamente ventajoso si se compara con el apareamiento aleatorio debido a que podría promover la salud de la descendencia y facilitar que las poblaciones hospederas reaccionen a patógenos que coevolucionan. Sin embargo, los sistemas reproductivos no han evolucionado para evitar la extinción. En poblaciones pequeñas y amenazadas, algunas formas de sistemas de reproducción natural y preferencias de pareja necesitan ser cuidadosamente manipuladas para evitar una reducción extensiva del tamaño poblacional efectivo (N_e). En general, la reproducción de apoyo debería minimizar la variación en el éxito reproductivo que no está vinculada con las características de viabilidad. Sin embargo, la minimización del sesgo reproductivo podría no ser la mejor estrategia de conser-*

Paper submitted May 8, 2001; revised manuscript accepted October 31, 2001.

vación si las parejas potenciales difieren en su viabilidad heredable. Si un sesgo reproductivo puede ser vinculado positivamente con la viabilidad heredable o a un incremento del esfuerzo parental, podría haber una forma de optimizar este sesgo con respecto a la esperanza de supervivencia de una población.

Supportive Breeding, Genetic Variance, and Sexual Selection

Supportive breeding, the practice of supporting weak wild populations by releasing individuals that were bred in captivity, is an important method for the conservation of vertebrates. Its first aim is to maintain or increase population size, but such intervention programs could have harmful long-term effects, especially if the potential impact of such programs on the genetics of a population is not given enough consideration (Hedrick & Miller 1994; Lande 1998).

As a first rule, maladaptive hybridization and outbreeding depression should be avoided (Hindar & Balstad 1994), although breeding individuals from different populations may in exceptional cases be advantageous, especially if a given population suffers from inbreeding depression (Madsen et al. 1999). A second important genetic risk is the fact that dividing a population into wild-breeding and captive-breeding components can have a negative impact on the effective population size (N_e , the size of an ideal population that loses genetic variance at the same rate as the real population) because it increases the variance in reproductive success and thereby increases inbreeding in the total population (Ryman & Laikre 1991; Ryman et al. 1995, 1999; Nomura 1999; Wang & Caballero 1999). Recent empirical studies provide support for this "Ryman-Laikre effect" (Tessier et al. 1997), and an increase in the inbreeding coefficient can eventually lead to the extinction of a population (Saccheri et al. 1998).

A third potential problem is the fact that supportive breeding normally circumvents potential mate-choice decisions, whereas in nature individuals normally compete for access to mating partners and they choose their mates (Andersson 1994). It is not surprising that mating in nature is usually not random with respect to genetics if one considers the two main genetic advantages of sex: (1) recombination followed by selection results in the efficient removal of damaged genes (Kondrashov 1993), and (2) recombination creates genetic diversity, which is important in coevolutionary arms races, especially in host-parasite coevolution (Jaenike 1978). Circumventing sexual selection could relax the selection on sexual antagonism and consequently have a positive effect on female fecundity after some generations (Holland & Rice 1999). Apart from this, however, circumventing mate choice is likely to

have negative consequences for the genetics of a population, especially in cases where N_e has not yet become very small, because sexual selection can select against deleterious mutations and can enhance mean resistance to pathogens in a population.

The Significance of Sexual Selection for "Good Genes"

Free mate choice usually takes into account at least the degree of kinship between two individuals (Pusey & Wolf 1996). Apart from this, most researchers categorize the possible criteria used in mate choice among unrelated individuals into three groups (Andersson 1994): (1) criteria that offer direct benefits, such as good parental care and nuptial gifts; (2) "Fisher-traits," criteria that are attractive just to members of the other sex and that do not have any further information content; and (3) criteria that reveal "good genes." This last group of criteria is of special interest here because these "good genes" are expected to increase the survival prospects of the common offspring. "Good genes" in the context of sexual selection are mainly alleles on loci that are important in the coevolution of pathogens and their hosts (Hamilton & Zuk 1982). Mate choice for good genes could result in subsequent generations of hosts that are better adapted to the local pathogens and therefore less susceptible (reviewed by Grahn et al. 1998; Westneat & Birkhead 1998; Møller et al. 1999; Jennions & Petrie 2000). Such mate preferences may therefore influence the evolution of parasite virulence in natural host-parasite systems (Wedekind 2002a).

Mate choice is only one form of sexual selection. Others are selection on sperm by the female reproductive tract, selective fertilization, or selective support of the embryo or the offspring (Birkhead & Møller 1993; Wedekind 1994a; Eberhard 1996; Birkhead 2000). This "cryptic female choice" could potentially be connected to host-parasite coevolution (Wedekind et al. 1996; Rüllicke et al. 1998) or at least help prevent inbreeding (e.g., Olsson et al. 1996).

How important is viability-based sexual selection? In a review and meta-analysis, Møller and Alatalo (1999) indicate that viability-based sexual selection is widespread across taxa, but its effect on offspring survival varies. Male secondary sexual characters revealed, on average, 1.5% of the variance in variability

of the offspring, but Møller and Alatalo (1999) stress that the studies they summarize may only partly estimate the full fitness consequences of mate choice in terms of offspring survival. Indeed, a recent experimental study (Wedekind et al. 2001) demonstrates that the good-genes effect of mate choice can be strong: optimal mate choice reduces pathogen-correlated egg mortality in a whitefish (*Coregonus* sp.) by 67% compared with random mating (i.e., total egg survival until hatching increases by 12%). Male breeding ornamentation accounted for 32% of this variance in offspring mortality.

Uniform or Variable Preferences for Mates or Sperm

Some kinds of mate preferences are uniform and some are variable, in that all members of one sex have the same or different mate preferences. This is important for the conservation of small populations because it influences the variance in reproductive success among individuals. This variance influences N_e and with it important aspects of the genetic long-term viability of small and endangered populations.

A preference for individuals in good health and vigor (Hamilton & Zuk 1982) is an example of a uniform preference. The mechanisms suggested by Hamilton and Zuk (1982) and later von Schantz et al. (1999) lead to populations in which all individuals of one sex have the same mate preference. The members of the opposite sex can then be ranked in a universally valid order of attractiveness, and less attractive individuals would be taken as mates only if the more attractive ones are not available. This is expected to increase variance in reproductive success and therefore decrease N_e . The effect often exists even in species believed to be monogamous, because females sometimes actively solicit extra-pair copulations with more attractive or more viable males than the ones they are paired with socially (Hasselquist et al. 1996; Petrie et al. 1998).

Another example of a uniform preference was suggested by Brown (1997): instead of revealing "good" alleles on loci that are important in host-parasite coevolution, sexual ornaments may reflect the degree of individual heterozygosity at key loci or at many loci. The respective mate preferences may then lead to some higher degree of genetic diversity in the offspring than would random mating, but there would be a corresponding variance in reproductive success that covaries with individual heterozygosity. This would also lead to somewhat decreased N_e .

Inbreeding avoidance is a simple expression of variable preferences, because with inbreeding avoidance members of the opposite sex cannot be ranked in a universally valid order of attractiveness. Consequently, in

populations where only inbreeding avoidance matters, the variance in reproductive success is expected to be low compared with the above mating systems, and the difference between N_e and the actual population size (N_a) is low.

A frequent byproduct of inbreeding avoidance mechanisms is offspring with increased degrees of heterozygosity on certain loci. This is especially so for the major histocompatibility complex (MHC) because these loci are often involved in kin recognition processes (Brown & Eklund 1994; Penn & Potts 1999). It is also possible in some systems, however, that mate preferences specifically aim at reaching heterozygosity on such important loci as those in the MHC (discussed by Brown 1997; Wedekind & Fürti 1997); recent examples of fitness advantages for MHC heterozygotes are described by Thursz et al. (1997) and Carrington et al. (1999). Although there is a conceptual difference between such a mating system and inbreeding avoidance, it may sometimes be difficult to discriminate between these two types of mating preferences. The mechanisms that lead to heterozygosity on specific loci could originally have evolved as a means to avoid inbreeding. Its effect on N_e may be about the same as the effect of inbreeding avoidance: the deviation from N_a would be small.

There are good-genes models that predict variable mate preferences and that therefore differ from the original idea of Hamilton and Zuk (1982). At loci important for the host-parasite interaction (e.g., immunogenes), certain combinations of alleles may be more beneficial than others. If individuals choose their mates to produce such beneficial allele combinations, their preferences have to depend on their own genotypes and their partners'. Consequently, individuals with different resistance genes show different preferences, and there is no universal order of sexual attractiveness with respect to signals that reveal heritable disease resistance or immunogenes (Wedekind 1994a, 1994b). Wedekind and Fürti (1997) specifically searched for evidence of such preferences but did not find any. However, Tregenza and Wedell (2000) list cases of mate preferences that result in beneficial allele combinations. Rüllicke et al. (1998), for example, showed that gamete fusion depends on the MHC and on the presence or absence of an epidemic of mouse hepatitis virus.

Fisherian models, in which preferences exist for criteria that are sexually attractive but do not reveal anything apart from that, typically assume that the females of a population have similar preferences for ornamental traits (Andersson 1994). This would again lead to an increased variance in individual reproductive success and thereby decrease N_e .

Many of the above kinds of sexual selection (summarized in Table 1) predict uniform mate preferences. However, a number of empirical studies provide evidence for genetic variation in female mate preference (Bakker & Pomiankowski 1995; Jennions & Petrie 1997). In real sys-

Table 1. Different kinds of mate preferences and the influence they are expected to have on variance in reproductive success, on effective population number (N_e) compared with the absolute population number (N_a), and on the virulence of coevolving pathogen populations.

Type of mate preference	Variance in reproductive success	N_e compared with N_a	Future virulence of coevolving pathogens ^a
Inbreeding/selfing	low	low ^b	very high
Random mating	low	medium-high	high
Inbreeding avoidance Preference	low	high	medium
for heterozygous offspring	low	high	low
for heterozygous mates	medium	medium	low
for health and vigor	high	low	low
for complementary disease resistances	low	high	low
for beauty traits (Fisherian traits)	high	low	low ^c
for direct benefits (e.g., paternal care)	low	high	low ^c

^aRough estimates according to host genetic variance and how much any reproductive skew is linked to viability traits.

^bFrom Caballero and Hill (1992).

^cLow if ornamental traits or the amount of direct benefits correlate with general viability.

tems, it is possible that different forms of sexual selection act at the same time and interfere with one another. Moreover, intersexual selection, the competition of members of the same sex for access to mating partners, often interferes strongly with free mate choice. The combination of both inter- and intrasexual selection determines the breeding system of an animal and is expected to have a strong effect on the life-history decisions of parents.

Captive Populations and Breeding Systems

In captive populations, natural breeding systems and mate-choice decisions often may not be circumvented. However, breeding systems are not evolved to be optimal with respect to the long-term survival of small populations. Indeed, some breeding systems may be damaging to the genetics of a population over the long term (Blumstein 1998). A recent study of the N_e of captive-bred Lake Victoria cichlids is an alarming example (Fiumera et al. 2000). It may therefore be of interest to intervene in the animals' mate choice and breeding behavior and to create a controlled situation that prevents the captive population from generating high inbreeding coefficients.

Different breeding systems have different effects on N_e and N_a (Table 2). They are also likely to vary in their influence on the future virulence of coevolving pathogens because they create different degrees of genetic variance in the next generation. For reviews on breeding systems in different taxa, see, for example, Davies (1991) and Taborsky (1994).

Life-History Decisions






Evolutionary theory predicts that parents should weigh their investment in each individual offspring according to the potential fitness return of the offspring (Fisher

1930). If the relative reproductive value of sons and daughters differs for different females or different males, sex-allocation theory predicts that the females should adjust the sex ratio of their offspring according to their own condition or according to their mate's attractiveness (Trivers & Willard 1973). This may have important consequences for conservation (Wedekind 2002b).

Life-history theory also predicts that females should alter their investment in particular breeding attempts according to the likelihood of its success and to male attractiveness (Williams 1966). Accordingly, some female birds lay more eggs (Petrie & Williams 1993) or larger eggs (Cunningham & Russell 2000) after copulating with preferred males. In the latter case the females produce offspring of better body condition when paired with preferred males. Gil et al. (1999) found that females deposit higher amounts of testosterone and 5 alpha-dihydrotestosterone in their eggs when mated to more attractive males. In American Kestrels (*Falco sparverius*), hormones provided by the females influence the survival of the offspring (Sockman & Schwabl 1999), and in canaries (*Serinus canaria*) the social rank of juveniles is positively correlated with the concentration of yolk testosterone in the eggs from which they hatched, suggesting that the development of aggressive behavior in offspring might be subject to modification by maternal testosterone (Schwabl et al. 1997).

There is evidence that such conditional maternal effects also exist in taxa other than birds. The tapeworm *Schistocephalus solidus*, for example, produces large eggs if given the opportunity to outbreed, but relatively small ones if forced to reproduce by selfing (Wedekind et al. 1998). There is also evidence that a comparable effect exists in our own species. In some human populations, the degree of MHC similarity influences mate preferences (Ober et al. 1997; Wedekind & Furi 1997); in one study, the birth weight of the baby and the weight of the placenta were negatively correlated to the degree

Table 2. Different kinds of breeding systems and the influence they are expected to have on population growth in terms of absolute numbers (N_a) and effective numbers (N_e), and on the virulence of coevolving pathogen populations.

Breeding system	Population growth		Future virulence of coevolving pathogens*
	N_a	N_e	
	low	low	high
	low	low-medium	medium
	high	medium	medium
	high	high	low
	high	high	low

*According to host genetic variance and how much any reproductive skew is linked to viability traits.

of similarity of MHC alleles between the parents (Reznikoff Etievant et al. 1991).

Such a change in life history is expected to have evolved under natural selection. Accordingly, Saino et al. (1999) found that an increased parental effort is traded against "own survival" and future reproductive potential. This kind of trade-off calculation may not work for captive-bred populations in a protected environment, so some supportive- and captive-breeding programs may profit from taking into account the animals' life-history decisions regarding mating and mate choice. Such decisions could potentially be manipulated to optimize parental effort with respect to population growth.

Current Breeding Programs: Minimizing Inbreeding and Reproductive Skew

Traditional methods of supportive breeding normally avoid direct inbreeding when possible (Montgomery et al. 1997; but see Templeton & Read 1984). Apart from this, details about the methods used in supportive breeding can be crucial with respect to N_e . Imagine, for example, a situation where only sperm of a few males is available to fertilize the eggs of many females in a fish hatchery. Such a skewed effective sex ratio would correspond to the third situation in Table 2 and would produce a negative effect on N_e . The negative effect would be enhanced if the reproductive variance among the males were carelessly increased (e.g., by using different amounts of sperm from the few males available, by using their milt sequentially, or by striping the males' milt directly one after another into the container that already holds all the egg and thereby giving the first males a reproductive advantage).

If we assume that all males are equal in genetic quality to all females (an assumption that often may not hold) and that the only aspect that matters is the genetic varia-

tion in the freshly fertilized eggs, the following methods probably would be best for increasing the long-term survival of a population via supportive breeding (my example is a fish hatchery, but analogous methods could be used in other breeding programs). (1) Try to catch a number of adults that result in an N_e of at least 50 (a rule of thumb suggested by Ryman et al. 1999). (2) Try to catch an equal number of males and females to avoid disturbance of sex ratio in the wild, or at least avoid using far fewer males than females, because $N_e = 4N_mN_f/(N_m + N_f)$ (e.g., using only six males to fertilize the eggs of 20 females results in an effective population number of <20), and the high relatedness among the offspring would further enhance the Ryman-Laikre effect. If, however, more males than females have already been brought to the hatchery, they should all be used, regardless of the skewed sex ratio, because N_e in the captive population increases with every male used. (3) Pool and carefully mix equal amounts of sperm from all the males (with appropriate methods, sperm can normally be stored for some hours). Use this mix to fertilize the eggs, either at once after they have been pooled in a container (Billard 1985) or in each female's batch in separate containers. When each batch is fertilized separately, the potential negative effects of swollen or broken eggs on the fertilization of healthy eggs is avoided. Mixing the sperm corresponds to the fifth situation in Table 2, with all the potential genetic benefits of multiple mating. However, by minimizing the potential negative effects of sperm interaction and restricting the transmission of pathogens, combining the gametes of one male and one female each could be a beneficial method (Crim & Glebe 1990). This method would correspond to the fourth situation in Table 2.

Incorporating Mate Preference into Breeding Programs

Different methods used in supportive breeding appear to be analogous to different forms of natural breeding systems, with their various consequences for N_e and N_a . There is an important difference, however, between the natural and the artificial situation: in the natural situation, male and female viability, health and vigor, or immunocompetence, are expected to correlate positively with reproductive skews. In supportive breeding, chance events may often decide reproductive skews, and the correlation between viability traits and reproductive success may be broken.

Supportive breeding should minimize variance in reproductive success that is not linked to viability traits. If individuals differ in their heritable viability, however, minimizing reproductive skew and thereby maximizing N_e might not be the best conservation strategy. If a re-

productive skew can be linked to viability traits, there might be a way to optimize this skew with respect to the survival prospects of a population.

For example, some whitefish (*Coregonus* sp.) populations in Switzerland are mainly if not exclusively maintained by supportive breeding in hatcheries because of recent eutrophication of the lakes and consequent oxygen problems for naturally spawned eggs (Ventling-Schwank & Müller 1991). Wedekind et al. (2001) found in one of these populations that parents differ in their heritable viability: the resistance of the eggs to a virulent egg parasite is strongly influenced by maternal and paternal effects. Moreover, the males' breeding ornamentation correlates positively with the offspring's resistance.

To maximize the long-term viability of these whitefish populations, hatcheries could use one of the following two procedures. Mating regime A would minimize reproductive skew, which would lead to higher levels of genetic variation in the freshly fertilized eggs (i.e., a good $N_e:N_a$ ratio). However, this initial genetic variation and the absolute egg number are likely to be reduced later by directed selection from egg pathogens. Mating regime B would give the well-ornamented males higher reproductive success than the weakly ornamented males. This would lead to a somewhat lower genetic variation in the freshly fertilized eggs, but would reduce the effects of selection by pathogens (i.e., it would lead to an increased mean survival of the offspring). The egg population would start with a relatively low $N_e:N_a$ ratio, but at hatching N_a would still be high compared to the N_a that results from mating regime A. Consequently, the N_e resulting from mating regime B could sometimes be higher than the N_e that results from mating regime A. Moreover, regime A may even support present pathogen populations because it produces more-susceptible offspring. This could increase the pathogen pressure on other eggs and, because pathogen resistance is not an all-or-none trait, this would further reduce population size. Of course, it is not a trivial problem to find the supportive-breeding regime that optimally includes variation in heritable fitness and any potential beneficial effects of natural mate choice.

Captive Populations and Mate Choice

In captive populations there are several ways of accounting for the fact that males often are not equal with respect to genetic quality and that female mate choice may be taking this into account. First, allow for free mate choice in (nearly) monogamous populations. This may be beneficial because of the good-gene effects of sexual selection and the increased parental investment of females (or males) who had attractive mates.

Second, allow for some degree of mate choice in non-monogamous populations but intervene if necessary in order to keep N_e as close as possible to N_a (i.e., high re-

productive variance is avoided among the males and females of a population). Females may be presented to different males so that some degree of free mate choice can occur, but the manager would intervene appropriately if a few individuals become too successful at the cost of the reproduction of others (e.g., by removing them for some time). In cases where presenting different males is not possible, mate-preference tests of the type that have been used in behavioral research (Anderson 1994; Penn & Potts 1999) may be considered. If, for examples, odors are important in sexual communication, it may be possible to provide odor samples of different males and to interpret the females' reaction to them before bringing males and females together. Such behavioral tests also could be performed in advance of artificial insemination and other methods of assisted reproductive technology that are often used in captive breeding (Gibbons et al. 1995; Dobson & Lyles 2000). These preference tests may even support the immediate success of the assisted reproductive technology because they may reduce the risk of miscarriage (Wedekind 1994a).

Third, allow for free mate choice in a population that is not monogamous, disregarding the possibility that this may lead to high reproductive variance and a reduction in N_e . The negative effect of the likely increased inbreeding coefficients over time would then need to be compensated for by the good-genes effects of sexual selection and by parental life-history decisions. Again, comparing the good-genes effects in sexual selection with the effects of increased inbreeding coefficients is a challenging task that requires good data and realistic models for each particular type of population. It may therefore be too early to suggest a rule of thumb for conservation managers. At the least, the larger the population, the more likely it probably is that good-genes effects may outweigh the increased inbreeding coefficients that come with increased variance in reproductive success. For small populations with a polygamous breeding system, allowing for free mate choice is a risky strategy (Fiumera et al. 2000).

Acknowledgments

I thank T. Little, M. Mackinnon, E. Main, G. K. Meffe, A. F. Read, A. Rivero, and the reviewers for discussion or comments on the manuscript. I am supported by the Swiss National Science Foundation.

Literature Cited

- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey.
- Bakker, T. C. M., and A. Pomiankowski. 1995. The genetic-basis of female mate preferences. *Journal of Evolutionary Biology* 8:129-171.

- Billard, R. 1985. Artificial insemination of salmonids. Pages 116–128 in R. N. Iwamoto and S. Sower, editors. *Salmonid reproduction: an international symposium*. Washington Sea Grant Program, Seattle.
- Birkhead, T. 2000. Promiscuity. Faber and Faber, London.
- Birkhead, T., and A. P. Møller. 1993. Female control of paternity. *Trends in Ecology & Evolution* **8**:100–104.
- Blumstein, D. T. 1998. Female preferences and effective population size. *Animal Conservation* **1**:173–177.
- Brown, J. L. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology* **8**:60–65.
- Brown, J. L., and A. Eklund. 1994. Kin recognition and the major histocompatibility complex: an integrative review. *The American Naturalist* **143**:435–461.
- Caballero, A., and W. G. Hill. 1992. Effective size of nonrandom mating populations. *Genetics* **130**:909–916.
- Carrington, M., G. W. Nelson, M. P. Martin, T. Kissner, D. Vlahov, J. J. Goedert, R. Kaslow, S. Buchbinder, K. Hoots, and S. J. O'Brien. 1999. HLA and HIV-1: heterozygote advantage and B*35-Cw*04 disadvantage. *Science* **283**:1748–1752.
- Crim, L. W., and B. D. Glebe. 1990. Reproduction. Pages 529–553 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland.
- Cunningham, E. J. A., and A. F. Russell. 2000. Egg investment is influenced by male attractiveness in the mallard. *Nature* **404**:74–77.
- Davies, N. B. 1991. Mating systems. Pages 263–294 in J. R. Krebs, and N. B. Davies, editors. *Behavioural ecology*. Blackwell Scientific, Oxford, United Kingdom.
- Dobson, A. P., and A. M. Lyles. 2000. Black-footed ferret recovery. *Science* **288**:985–988.
- Eberhard, W. G. 1996. *Female control: sexual selection by cryptic female choice*. Princeton University Press, Princeton, New Jersey.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, United Kingdom.
- Fiumera, A. C., P. G. Parker, and P. A. Fuerst. 2000. Effective population size and maintenance of genetic diversity in captive-bred populations of a Lake Victoria cichlid. *Conservation Biology* **14**:886–892.
- Gibbons, E. F., B. S. Durrant, and J. Demarest, editors. 1995. *Conservation of endangered species in captivity*. State University of New York Press, Albany.
- Gil, D., J. Graves, N. Hazon, and A. Wells. 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. *Science* **286**:126–128.
- Grahn, M., A. Langesfors, and T. von Schantz. 1998. The importance of mate choice in improving viability in captive populations. Pages 341–363 in T. M. Caro, editor. *Behavioral ecology and conservation biology*. Oxford University Press, Oxford, United Kingdom.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites. *Science* **218**:384–387.
- Hasselquist, D., S. Bensch, and T. von Schantz. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the Great Reed Warbler. *Nature* **381**:229–232.
- Hedrick, P. W., and P. S. Miller. 1994. Rare alleles, MHC and captive breeding. Pages 187–204 in V. Loeschke, J. Tomiuk, and S. K. Jain, editors. *Conservation genetics*. Birkhauser, Basel, Switzerland.
- Hindar, K., and T. Balstad. 1994. Salmonid culture and interspecific hybridisation. *Conservation Biology* **8**:881–882.
- Holland, B., and W. R. Rice. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proceedings of the National Academy of Sciences USA* **96**:5038–5088.
- Jaenike, J. 1978. An hypothesis to account for the maintenance of sex within populations. *Evolutionary Theory* **3**:191–194.
- Jennions, M. D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society* **72**:283–327.
- Jennions, M. D., and M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society* **75**:21–64.
- Kondrashov, A. S. 1993. Classification of hypotheses on the advantage of amphimixis. *Journal of Heredity* **84**:372–387.
- Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction. Pages 29–51 in G. M. Mace, A. Balmford, and J. R. Ginsberg, editors. *Conservation in a changing world*. Cambridge University Press, Cambridge, United Kingdom.
- Madsen, T., R. Shine, M. Olsson, and H. Wittzell. 1999. Conservation biology: restoration of an inbred adder population. *Nature* **402**:34–35.
- Møller, A. P., and R. V. Alatalo. 1999. Good-genes effects in sexual selection. *Proceedings of the Royal Society of London, Series B* **266**:85–91.
- Møller, A. P., P. Christie, and E. Lux. 1999. Parasitism, host immune function, and sexual selection. *Quarterly Review of Biology* **74**:3–20.
- Montgomery, M. E., J. D. Ballou, R. K. Nurthen, P. R. England, D. A. Briscoe, and R. Frankham. 1997. Minimizing kinship in captive breeding programs. *Zoo Biology* **16**:377–389.
- Nomura, T. 1999. Effective population size in supportive breeding. *Conservation Biology* **13**:670–672.
- Ober, C., L. R. Weitkamp, N. Cox, H. Dytch, D. Kostyu, and S. Elias. 1997. HLA and mate choice in humans. *American Journal of Human Genetics* **61**:497–504.
- Olsson, M., R. Shine, T. Madsen, A. Gullberg, and H. Tegelstrom. 1996. Sperm selection by females. *Nature* **383**:585.
- Penn, D. J., and W. K. Potts. 1999. The evolution of mating preferences and major histocompatibility complex genes. *The American Naturalist* **153**:145–164.
- Petrie, M., C. Doums, and A. P. Møller. 1998. The degree of extra-pair paternity increases with genetic variability. *Proceedings of the National Academy of Sciences of the United States of America* **95**:9390–9395.
- Petrie, M., and A. Williams. 1993. Peahens lay more eggs for peacocks with larger trains. *Proceedings of the Royal Society of London, Series B* **251**:127–131.
- Pusey, A., and M. Wolf. 1996. Inbreeding avoidance in animals. *Trends in Ecology & Evolution* **11**:201–206.
- Reznikoff Etievant, M. F., J. C. Bonneau, D. Alcalay, B. Cavellier, C. Toure, R. Lobet, and A. Netter. 1991. HLA antigen-sharing in couples with repeated spontaneous abortions and the birthweight of babies in successful pregnancies. *American Journal of Reproduction and Immunology* **25**:25–27.
- Rülicke, T., M. Chapuisat, F. R. Homberger, E. Macas, and C. Wedekind. 1998. MHC-genotype of progeny influenced by parental infection. *Proceedings of the Royal Society of London, Series B* **265**:711–716.
- Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population-size. *Conservation Biology* **5**:325–329.
- Ryman, N., P. E. Jorde, and L. Laikre. 1995. Supportive breeding and variance effective population size. *Conservation Biology* **9**:1619–1628.
- Ryman, N., P. E. Jorde, and L. Laikre. 1999. Supportive breeding and inbreeding effective number: reply to Nomura. *Conservation Biology* **13**:673–676.
- Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**:491–494.
- Saino, N., S. Calza, P. Ninni, and A. P. Møller. 1999. Barn swallows trade survival against offspring condition and immunocompetence. *Journal of Animal Ecology* **68**:999–1009.
- Schwabl, H., D. W. Mock, and J. A. Gieg. 1997. A hormonal mechanism for parental favouritism. *Nature* **386**:231.
- Sockman, K. W., and H. Schwabl. 1999. Female kestrels hormonally regulate the survival of their offspring. *American Zoologist* **39**:369.
- Taborsky, M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior* **23**:1–100.

- Templeton, A. R., and B. Read. 1984. Factors eliminating inbreeding depression in a captive herd of Speke's gazelle (*Gazella spekei*). *Zoo Biology* **3**:177-199.
- Tessier, N., L. Bernatchez, and J. M. Wright. 1997. Population structure and impact of supportive breeding inferred from mitochondrial and microsatellite DNA analyses in land-locked Atlantic salmon *Salmo salar* L. *Molecular Ecology* **6**:735-750.
- Thursz, M. R., H. C. Thomas, B. M. Greenwood, and A. V. S. Hill. 1997. Heterozygote advantage for HLA class-II type in hepatitis B virus infection. *Nature Genetics* **17**:11-12.
- Tregenza, T., and N. Wedell. 2000. Genetic compatibility, mate choice and patterns of parentage. *Molecular Ecology* **9**:1013-1027.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**:90-91.
- Ventling-Schwank, A. R., and R. Müller. 1991. Survival of coregonids (*Coregonus* sp.) eggs in Lake Sempach, Switzerland. *Verhandlungen der Internationalen Vereinigung für Limnologie* **24**:2451-2554.
- von Schantz, T., S. Bensch, M. Grahn, D. Hasselquist, and H. Wittzell. 1999. Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society of London, Series B* **266**:1-12.
- Wang, J. L., and A. Caballero. 1999. Developments in predicting the effective size of subdivided populations. *Heredity* **82**:212-226.
- Wedekind, C. 1994a. Mate choice and maternal selection for specific parasite resistances before, during and after fertilization. *Philosophical Transactions of the Royal Society of London, Series B* **346**:303-311.
- Wedekind, C. 1994b. Handicaps not obligatory in sexual selection for resistance genes. *Journal of Theoretical Biology* **170**:57-62.
- Wedekind, C. 2002a. Implications of sexual selection for virulence management. Pages 248-261 in U. Dieckmann, J. A. J. Metz, M. W. Sabelis, and K. Sigmund, editors. *Adaptive dynamics of pathogen host interaction*. Cambridge University Press, Cambridge, United Kingdom.
- Wedekind, C. 2002b. Manipulating sex ratios for conservation: short-term risks and long-term benefits. *Animal Conservation*: **5**:13-20.
- Wedekind, C., and S. Fürti. 1997. Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London, Series B* **264**:1471-1479.
- Wedekind, C., M. Chapuisat, E. Macas, and T. Rüllicke. 1996. Non-random fertilization in mice correlates with the MHC and something else. *Heredity* **77**:400-409.
- Wedekind, C., D. Strahm, and L. Schärer. 1998. Evidence for strategic egg production in a hermaphroditic cestode. *Parasitology* **117**:373-382.
- Wedekind, C., R. Müller, and H. Spicher. 2001. Potential genetic benefits of mate selection in whitefish. *Journal of Evolutionary Biology* **14**:980-986.
- Westneat, D. F., and T. R. Birkhead. 1998. Alternative hypotheses linking the immune system and mate choice for good genes. *Proceedings of the Royal Society of London, Series B* **265**:1065-1073.
- Williams, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *The American Naturalist* **100**:687-690.

