

Manipulating sex ratio to increase population growth: the example of the Lesser Kestrel

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Abstract

Small or decreasing populations call for emergency actions like, for example, captive breeding programs. Such programs aim at rapidly increasing population sizes in order to reduce the loss of genetic variability and to avoid possible Allee effects. The Lesser Kestrel *Falco naumanni* is one of the species that is currently supported in several captive breeding programs at various locations. Here, we model the demographic and genetic consequences of potential management strategies that are based on offspring sex ratio manipulation. Increased population growth could be achieved by manipulating female conditions and/or male attractiveness in the captive breeders and consequently shifting the offspring sex ratio towards more female offspring, which are then used for reintroduction. Fragmenting populations into wild-breeding and captive-breeding demes and manipulating population sex ratio both immediately increase the inbreeding coefficient in the next generation (i.e. decrease N_e) but may, in the long term, reduce the loss of genetic variability if population growth is restricted by the number of females. We use the Lesser Kestrel and the wealth of information that is available on this species to predict the long-term consequences of various kinds of sex-ratio manipulation. We find that, in our example and possibly in many other cases, a sex-ratio manipulation that seems realistic could have a beneficial effect on the captive breeding program. However, the possible long-term costs and benefits of such measures need to be carefully optimized.

Introduction

Various kinds of captive-breeding programs are used to possibly prevent threatened populations from becoming extinct (IUCN, 1987). Some of these programs are meant to provide a refuge for 'better times' (Frankham *et al.*, 1986), but most aim at releasing additional individuals into the wild in order to support declining populations and to help prevent further losses of a population's genetic diversity (Lande, 1998; Holsinger, 2000). The strategy has to be well considered, though, because captive-breeding programs could potentially be harmful if the genetic consequences of the various management options are not fully considered (Ryman & Laikre, 1991; Wedekind, 2002b; Woodworth *et al.*, 2002; Linklater, 2003). In the following we assume that the enhanced offspring survival in captivity and the subsequent introduction of individuals into the wild have a positive influence on population size and genetic diversity in the long term.

The rate at which a population loses genetic variability depends on N_e , the genetically effective population size.

With lower N_e , more genetic variability is lost from generation to generation (Frankham, Ballou & Briscoe, 2002). This loss is typically amplified in small populations by various non-genetic factors that, taken together, can cause an Allee effect (Courchamp, Clutton-Brock & Grenfell, 1999; Stephens & Sutherland, 1999). For small populations, it is therefore important to increase population growth rapidly. In some cases, the number of offspring per female is one of the limiting factors with regard to population growth. In such a cases, it may be possible to amplify population growth (and finally achieve an increase of N_e) by manipulating offspring sex ratios and producing a higher ratio of the reproductively limiting sex (Tella, 2001; Clout, Elliott & Robertson, 2002; Wedekind, 2002a). Such manipulation is often possible, either through non-invasive techniques like changing sex-determining ecological or social factors (Kamel & Mrosovsky, 2006; Robertson *et al.*, 2006), or through more invasive techniques such as hormone treatment of embryos or sperm sexing before using assisted reproductive technologies (Wildt & Wemmer, 1999; Pukazhenthi *et al.*, 2006). The aim is to lower the sex ratio,

defined here as the proportion of males, and hence to increase the production of females if they are the limiting factor for population growth.

The Trivers and Willard hypothesis (Trivers & Willard, 1973) could explain some of the ecological or social factors that can influence family sex ratio. The hypothesis assumes that the sex with the higher variance in reproductive success, that is the sex that is likely to experience higher competition during sexual selection, is expected to be preferentially produced by parents who are in good condition. This is assuming that parental condition influences offspring condition, which in turn determines their competitive abilities in later sexual selection. Usually, this means that high-quality males and/or high-quality females tend to produce more sons than daughters (but there are interesting exceptions from this rule; for a review, see Cameron, 2004).

In birds, sexual size dimorphism is widespread, and there is much support for the Trivers and Willard hypothesis in several species (Olsen & Cockburn, 1991; Kilner, 1998; Albrecht & Johnson, 2002; Janota, Soukup & Thompson, 2002; Rathburn & Montgomerie, 2005), especially in most falcons studied so far: the Lesser Kestrel *Falco naumanni* (Tella *et al.*, 1996a; Aparicio & Cordero, 2001), the American Kestrel *Falco sparverius* (Wiebe & Bortolotti, 1992; Smallwood & Smallwood, 1998), the Peregrine Falco *Falco peregrinus* (Olsen & Cockburn, 1991) and the European Kestrel *Falco tinnunculus* (Dijkstra, Daan & Buker, 1990). All these studies found that depending on their condition, females bias the sex ratio of their offspring. Note that such a female-biased sex-ratio is achieved without killing or withholding male progeny, that is without reducing the overall number of offspring. Hence, sex ratio manipulation seems possible in these species and could be used by managers to increase population growth by increasing the frequency of the reproductively more important sex.

Here, we use the Lesser Kestrel as an example for our data-based model because it is a particularly well-studied species. Much is known about its mating behavior and its breeding ecology and physiology. The species shows a strong sexual dichromatism, but only slight differences in size between the sexes (Glutz von Blotzheim, Bauer & Bezzel, 1987). It breeds colonially in a monogamous pair bound, although extra-pair copulation and examples of polygyny have been reported (Negro *et al.*, 1996; Tella *et al.*, 1996b; Alcaide *et al.*, 2005). This small falcon was formerly a widespread species, distributed in most of southern Eurasia, but its western Palearctic population has declined dramatically during the second half of the last century and is now restricted to some countries around the Mediterranean (Cramp & Simmons, 1982; Bustamante, 1997). The Lesser Kestrel is currently listed as a globally threatened species (Tucker & Heath, 1994).

Aparicio & Cordero (2001) showed that skewed offspring sex ratios occur in wild colonies of the Lesser Kestrel and that the skews are dependent on the condition of the parents. If the paternal condition is average, more daughters are born, whereas parents in good or bad conditions produce more sons. It was also observed that males seem to

have a higher variance in reproductive success than females because of occasional polygyny and because of extra-pair mating (Kempenaers *et al.*, 1992). This could explain the condition-dependent sex ratio and is in line with the Trivers and Willard hypothesis. Such a naturally occurring phenomenon could be used to manipulate the sex ratio in captive-breeding programs and therefore to increase the number of females that can be released into the wild. One way to decrease the sex ratio and gain more females could be to lower the conditions of the females from optimal to intermediate, which would not automatically reduce the total number of fledglings (Aparicio & Bonal, 2002) but may have detrimental effects on later offspring productivity (Dijkstra *et al.*, 1990; Tella *et al.*, 1996a; Aparicio & Bonal, 2002; Laaksonen, Lyytinen & Korpimäki, 2004). Hormone treatment is another option, as hormones play a role in sex determination (Pike & Petrie, 2003) and have already been used experimentally to alter offspring sex ratio in different bird species (Correa, Adkins-Regan & Johnson, 2005; Love *et al.*, 2005; Pike & Petrie, 2006). A more indirect and probably less interfering approach is the manipulation of secondary sexual traits of male breeders. The gray wing patch of male Lesser Kestrel for example is associated with all variables related to reproductive performance including the sex ratio of the offspring (Aparicio & Cordero, 2001). These secondary traits could be manipulated to change female perception of male attractiveness. Some studies on birds have already successfully manipulated mate choice and even offspring sex ratio by artificially changing the color and brightness of plumage marks (Hill, 1991; Ballentine & Hill, 2003; Pike & Petrie, 2005). According to Real (1991), the perception of the attractiveness of a mate is most likely not genetically determined but based on available references. Therefore, providing more/less attractive males in an adjacent cage could additionally manipulate female's perception of male attractiveness.

Here, we assume that sex-ratio manipulation is possible, at least within the range of skews observed in the wild. We use previously published data on one well-studied population of Lesser Kestrel to analyze the genetic and demographic effects of sex-ratio manipulation in captive-breeding programs and subsequent release of the offspring into the wild.

The population model

The example: a well-studied population in Spain

Our calculations are based on the data of Hiraldo *et al.* (1996) from a population in Southern Spain. This population has been extensively studied for many years. It consists of c. 1000 breeding pairs divided into 12 colonies. The sex ratio of this population shows no deviation from 0.5 over several years (Negro & Hiraldo, 1992). The main captive breeding program that is currently performed on this population has a capacity of around 18 breeding pairs (M.

Alcaide, pers. comm.). These 18 pairs produce up to 100 fledglings per season, most of which are released into the wild (M. Alcaide, pers. comm.). This reproductive rate corresponds to other Spanish breeding programs for the Lesser Kestrel that produce up to six fledglings per pair (Pomarol *et al.*, 2004).

Hiraldo *et al.* (1996) provide information about the survival rates of adults (S_a) and juveniles (S_j), the probabilities of reproduction for adults (C_a) and yearlings (C_y) and the number of sons (P_m) and daughters (P_f) per reproducing female and per breeding season (Fig. 1). Hiraldo *et al.*'s (1996) work also suggests that, from an ecological point of view, birds of this species can be treated as adults from their second year on and survival rates do not differ between sexes (see also Negro & Hiraldo, 1992).

As outlined above, an offspring sex ratio of 0.3 has been observed in the wild to be linked to male wing patch size. We therefore assume that a sex-ratio manipulation with a shift from 0.5 to 0.3 is possible in captivity, too. In the following, we use this ratio and a conservatively estimated number of 90 fledglings that are raised in captivity and are released into the wild every year. We will also assume that adult survival rates are the same for the wild and the captive populations, although captive individuals are better fed and are therefore expected to be of better condition than in the wild. In our model, the survival also does not change with increasing population size, because the populations are small compared with historical times. In reality, a constant female reproductive rate cannot always be assumed. The average reproductive rate is likely to decrease over time at very small population sizes due to various factors that cause an Allee effect, and it is likely to decrease at very large population sizes because of habitat restrictions. Also, the average reproductive rate is likely to increase over time in small populations that are growing out of the range that is affected by the Allee effect. Nevertheless, our assumption of constant reproductive rates may be fulfilled in intermediate population sizes, and it is conservative in small populations with regard to our main conclusions, regardless of whether these small populations decrease or grow.

Use of the effective population size N_e

Purely demographic models can potentially be misleading with respect to the genetic variability that a population loses over time. We therefore use the effective population size N_e that describes the size of an ideal population that loses genetic variation at the same rate as does the real population and corrects, among other factors, for unequal numbers of males and females in the population (Hartl & Clark, 1997). In order to take the effects of a sex-ratio manipulation into account, we use the correction (Hartl & Clark, 1997)

$$N_e = \frac{4N_m N_f}{N_m + N_f} \quad (1)$$

If the number of eggs and offspring is a limiting factor for population growth, changing the sex ratios towards more females will enhance population growth. This will eventually have a positive effect on N_e , determined by

$$\frac{1}{N_e} = \frac{1}{t} \left(\frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_3} + \dots + \frac{1}{N_t} \right) \quad (2)$$

where t is the number of generations since the start of the manipulation and N_1 is the effective population size at generation 1 (Hartl & Clark, 1997). This equation takes the reduction of genetic variability that occurs in the first generations following the sex ratio manipulation into account.

When we split a population into wild breeders and captive breeders, we increase the variation in reproductive success because the captive breeders will, on average, have a higher reproductive success than the wild breeders. This so-called Ryman–Laikre effect (Ryman & Laikre, 1991) has, for itself, a negative effect on N_e , which is taken into account by

$$\frac{1}{N_e} = \frac{x_{\text{cap}}^2}{N_{\text{ecap}}} + \frac{x_{\text{w}}^2}{N_{\text{ew}}} \quad (3)$$

where x_{cap} and x_{w} are the relative contributions of offspring from the captive and wild population, respectively, N_{ecap} the number of breeders in the captive population and N_{ew} the sex-ratio-adjusted number of wild breeders (Ryman & Laikre, 1991; Utter, 2003). In the following, we assume that

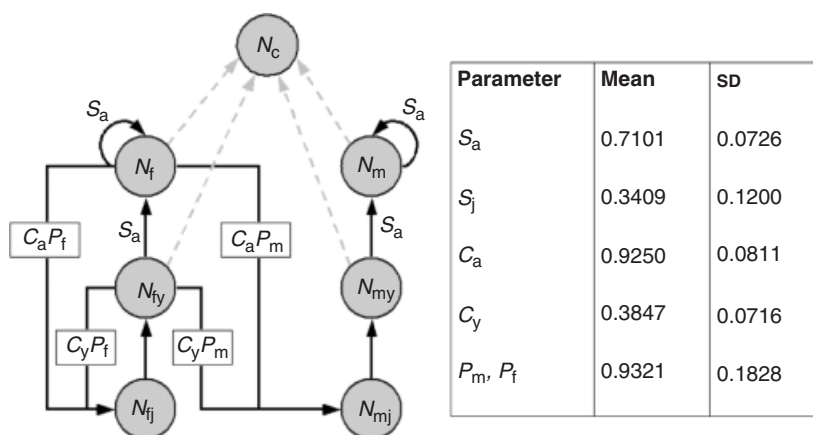


Figure 1 Population model with separation of gender and age classes (juvenile, j; yearling, y and adult, a). The corresponding values (mean and standard deviation) for survival rates (S), proportion of females breeding (C) and male (P_m) and female (P_f) progeny per reproducing female are taken from Hiraldo *et al.* (1996).

the breeding stock in captivity is a subsample of the wild population, as proposed by Miller & Kapuscinski (2003), and that outbreeding depression and adaptation to captivity does not occur or can be neglected.

In order to introduce environmental stochasticity, the following life-history parameters were considered as random variables with a normal distribution (see also the model published by Hiraldo *et al.* (1996): survival rates (S), proportion of females breeding (C) and male (P_m) and female (P_f) progeny per reproductive female. In each simulation, the annual value of the listed parameters is given by the following equation:

$$x(i) = x + (sd) \quad (4)$$

where x is the mean value of any given parameter, s is its standard deviation and d is a random value from a normal distribution with mean 0 and standard deviation 1.

Shifting the sex ratio towards more females could negatively influence the reproductive success of females who have to share a male (e.g. due to a reduction in clutch size, a reduced reproduction probability or reduced offspring survival). We therefore included a parameter κ that can vary from 0 to 1 in the model. Females who share a male have a juvenile survival of κS_j . The number of females with such a

reduced survival is $2(N_f - N_m)$ for sex ratios < 0.5 and 0 for sex ratios ≥ 0.5 .

We start our simulations with a total population of 2000 individuals, 72% of which are adults and 28% yearlings. In each generation, 18 pairs are taken for the captive-breeding program. For our calculations, we assume that birds that are born in captivity are introduced as yearlings into the wild population. As the manipulated sex ratio of these introduced birds shifts the sex ratio of the wild population slightly towards more females, we correct N_e of the wild population for unequal sex ratio [Eq. (1)]. This step is not necessary for the captive population as the sex ratio of these breeders is always 0.5. To take the Ryman–Laikre effect into account, we use [Eq. (3)]. The development of N_e over time is then calculated with [Eq. (2)]. Including all the available life-history parameters (Hiraldo *et al.*, 1996) then enables us to predict the long-term consequences for the population depending on various management strategies.

Results

Starting a captive-breeding program immediately reduces N_e because of the Ryman–Laikre effect [Eq. (3); see the starting points of lines in Fig. 2]. After some generations, however, the supplementation of the wild population by

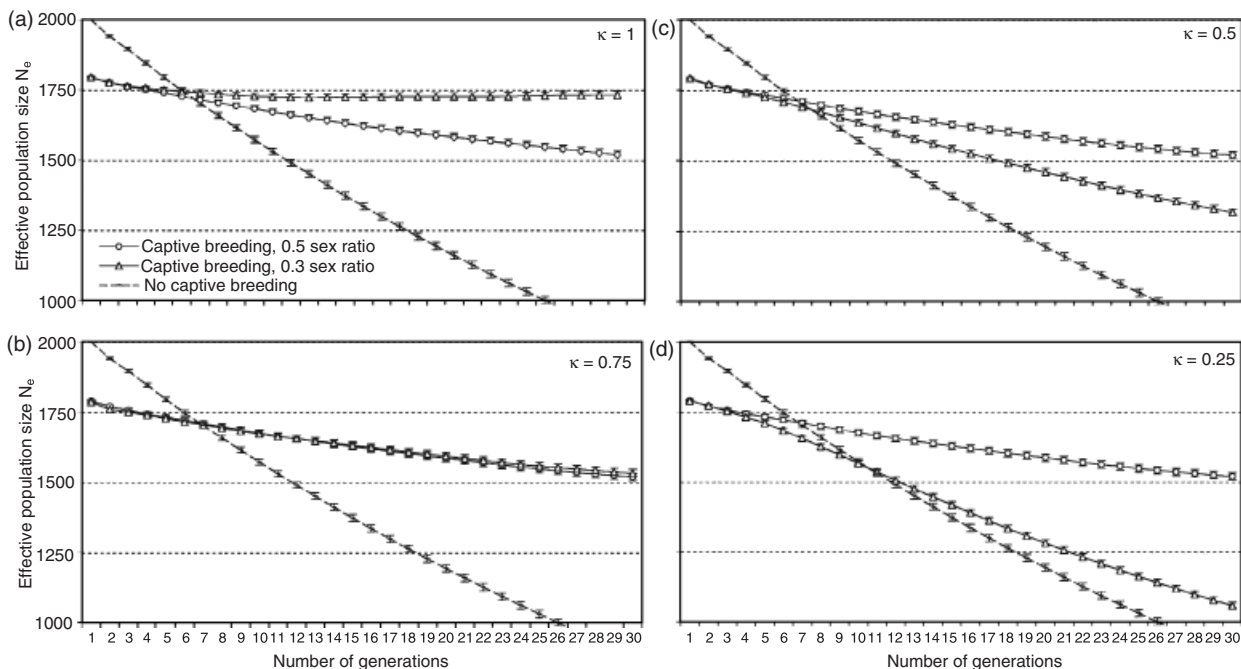


Figure 2 Predicted development of the effective population size (N_e) of the population in Southern Spain that we used as an example. The population starts with a total of 2000 adults, of which 36 are used for a captive-breeding program from which 90 yearlings per generation are released into the wild. The curve with triangles shows the effect of continuous manipulation of the offspring sex ratios in the captive program (sex ratio=0.3), the curve with circles corresponds to sex ratio=0.5 and the remaining curve with no symbols corresponds to a population without supportive breeding. Every point is the mean and standard error of 1000 simulation runs. Panels a–d show the N_e with different levels of κ , which stands for the reduction in reproductive output for females that share males because of a shift in the sex ratio towards more females. The decline of the N_e to 1800 after the first generation of manipulation results from the extraction of 36 individuals for the breeding stock [the Ryman–Laikre effect; see Eq. (3)].

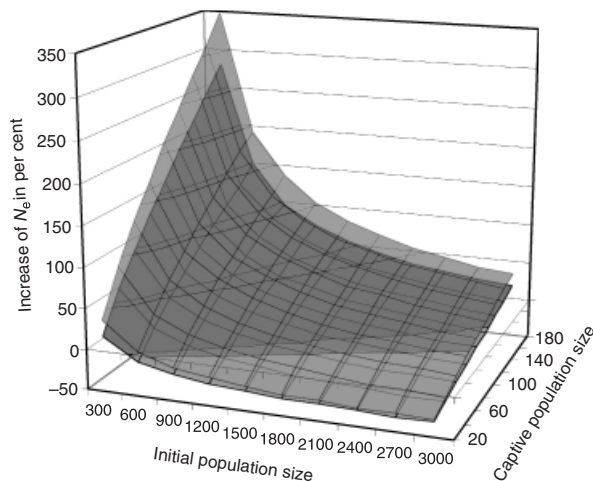


Figure 3 Change of N_e after 20 generations (in per cent, compared with initial N_e , $\kappa=1$). The upper area shows the effect of the manipulated sex ratio; the lower area shows the effect of no sex-ratio manipulation. Areas of increased N_e are shown in dark gray, and those of decreased N_e in light gray. The initial population = initial wild population + captive population. Every intercept point on the areas is the mean of 500 simulation runs.

offspring from the captive population can compensate for this initial loss of genetic variability. In our example, this compensation is reached after six generations of captive breeding and supplementation, assuming an average 0.5 offspring sex ratio in captivity (Fig. 2), but it can take longer if offspring sex ratio is manipulated in captivity (depending on κ ; Fig. 2).

Under the assumptions we made here (Fig. 1) and with an average offspring sex ratio of 0.5 in captivity, introducing 90 fledglings per year from the captive-breeding program into the wild population can only reduce but not stop the decline of the population (Fig. 2). However, manipulating the offspring sex ratio in the captive population towards a relatively higher number of daughters can lead to an increase of N_e over time (Fig. 2a). This compensatory effect is, however, strongly affected by κ , that is by the relative reproductive success of females who share a male: κ close to one leads to beneficial effects of a sex-ratio manipulation (Fig. 2a), while a κ of around 0.75 neutralizes any positive effects of a sex-ratio manipulation (Fig. 2b), and lower κ leads to an increased population decline as a consequence of the sex-ratio manipulation, compared with original sex ratios (Fig. 2c and d).

With any sex-ratio manipulation, we expect an initial decrease of N_e in the manipulated situation because of the negative effects of the deviation from a 0.5 sex ratio [Eq. (1)]. However, this loss turned out to be small and beyond visibility in Fig. 2, because the manipulation in the captive population has only a slight effect on the overall sex ratio in the wild population (in Fig. 2, the total sex ratio in the wild population decreases from 0.5 to about 0.49 after the first generation of sex ratio manipulation and levels off at around 0.47 after several generations). Hence, the popula-

tion growth that is induced by the sex-ratio manipulation turns out to compensate rapidly for the initial slight loss of N_e , at least at high κ (Fig. 2).

Figure 3 shows the relative deviation over 20 generations, that is the increase or decrease of N_e over such a time period, in relation to various initial and captive population sizes for both management scenarios, sex ratio manipulated to 0.3 (upper area) and a sex ratio of 0.5 (lower area). Regardless of whether the net benefit of a captive-breeding program is positive or negative after 20 generations, a sex-ratio manipulation from 0.5 to 0.3 in captive families always results in a higher N_e than no manipulation when κ is close to 1 (Fig. 3). Figure 3 also shows that under our model assumptions (Fig. 1) and $\kappa = 1$, manipulating the sex ratio to 0.3 in the captive population with, for example, 40 breeding pairs would be sufficient to stop the decline of a population that started at a population size of 2700, whereas without sex-ratio manipulation, 50 pairs would be necessary to achieve the same result (Fig. 3).

Discussion

We studied the long-term effects of a management option that has recently been suggested for species where offspring sex ratio is dependent on female condition and/or female's perception of male quality. In such species, manipulation of offspring sex ratios may be possible in captive-breeding populations and may increase the number of females that can be released. This could eventually increase N_e in the wild if female number is a limiting factor for population growth (Tella, 2001; Clout *et al.*, 2002; Wedekind, 2002a). As an example, we used data from an extensively studied population of the Lesser Kestrel to estimate the long-term quantitative effects of sex-ratio manipulation in an existing captive-breeding program. Manipulated sex ratios of 0.3 seem possible in this species (see 'Introduction'). We found that if the reproductive output of females who share a male does not decline below around 25% as compared with females who do not have to share a male, a manipulation that leads to an average offspring sex ratio of 0.3 in the current captive program could not only increase N_e but even stop a predicted further decline of the wild population and lead to some population recovery. Hence, offspring sex-ratio manipulation in captivebreeding programs should be considered as a possibility that may significantly improve the situation of a declining population. We use the Lesser Kestrel as an example; the possible long-term consequences of comparable management options in other small or declining populations could be analyzed analogously.

For our calculations, we assumed an adult sex ratio of 0.5 in the wild population. This is what is usually observed in the Lesser Kestrel (Negro & Hiraldo, 1992; Hiraldo *et al.*, 1996), but adult sex ratios can sometimes be male biased in wild populations of other species (e.g. due to higher female mortality). In these cases, adding females to the population may have a stronger positive effect on population growth than our calculations suggest.

We found that κ , that is the reproductive success of females who have to share a male with other females relative to the reproductive success of females who do not have to share their male, is a crucial factor that may largely decide the success of a sex-ratio manipulation. Although the Lesser Kestrel is usually described as a monogamous species, deviations from perfect monogamy are possible. Polygyny with shared paternal brood care, that is some males providing food to more than one female, and extra-pair copulations (EPC) without shared brood care could be observed in this species (Hiraldo, Negro & Donazar, 1991; Negro *et al.*, 1996; Tella *et al.*, 1996b; Alcaide *et al.*, 2005). There are observations that unpaired females tend to be more prone to extra-pair copulations than paired ones (Negro, Donazar & Hiraldo, 1992; Negro, 1997), that yearlings sometimes help at the nest (Negro, 1997) and that unrelated chicks from neighboring nests are adopted (Tella *et al.*, 1997). It may even be possible that a sex-ratio manipulation leads to an increased proportion of first-year males that breed with the excess of females. Some of this behavioral plasticity may compensate partly for the negative effects that can be caused by a shifted sex ratio. As it is known from other species that EPC and polygyny is related to availability of food resources (Hamerstrom, Hamerstrom & Burke, 1985; Simmons, 1988), (1) κ needs to be determined under conditions that experimentally control for the effects of food resources but allow the birds to show their full behavioral repertoire that may help them to partly compensate for any negative effects, and (2) variation in habitat quality is a key factor that determines the success of the proposed sex-ratio manipulation.

The recent discussion about the management of the Kakapo *Stigops habroptilus* provides another example of how offspring sex-ratio manipulation may help a highly endangered species to recover. The remaining semi-wild population of Kakapo shows a highly skewed sex ratio of two males to one female while population growth largely depends on the number of reproductive females (Trewick, 1997). As in the Lesser Kestrel, the Kakapo has a condition-dependent offspring sex ratio, with females in good condition producing relatively more sons than daughters. Clout *et al.* (2002) and Tella (2001) therefore suggested that the skewed sex ratio could be due to supplementary feeding, although data from sub-fossil remains indicate a similar sex ratio skew in pre-human times (Trewick, 1997). Nevertheless, the most recent study of Robertson *et al.* (2006) provided evidence for the feeding effect and concluded that the supplementary feeding regime needs to be changed in order to increase the relative number of females in future generations.

The Kakapo example suggests that non-invasive methods may be possible and could be used to change sex ratios and increase population growth. By doing so, however, we change the demographic parameters that may have an influence on breeding systems and life-history strategies (Emlen & Oring, 1977). The sex ratio plays an important role in the viability of a population (Jirotkul, 1999; Jiggins, Hurst & Majerus, 2000; Steifetten & Dale, 2006) and under-

standing its consequences is vital for conservation management (Wildt & Wemmer, 1999; Ewen *et al.*, 2001). Also, captive-breeding programs always have to compensate for the immediate negative effects of the Ryman–Laikre effect they cause (Ryman & Laikre, 1991). We found that the Ryman–Laikre effect can be very strong and has to be appropriately combined with other negative consequences of captive breeding (e.g. a κ below 1) in order to fully appreciate the immediate negative consequences of a captive-breeding program. These negative effects need to be compensated by a program-induced population growth and reduced loss of genetic variability to justify the captive breeding. Our calculations outline the parameter space that may lead to such an adequate compensation in terms of demography and genetic variability.

The decline of populations usually has various causes. In the case of the Lesser Kestrel, the main reason for the previous population decline seems to be the degradation of foraging habitats (Donazar, Negro & Hiraldo, 1993; Franco *et al.*, 2004; Ursua, Serrano & Tella, 2005), the spatial relationship between foraging sites and the location of colonies (Garcia *et al.*, 2006; Rodriguez, Johst & Bustamante, 2006), and other factors that may sometimes make the number of nesting cavities restrict population growth (Negro & Hiraldo, 1993; Franco, Marques & Sutherland, 2005, but see Forero *et al.*, 1996). For our present calculations, we assumed that individual survival rates and reproductive success are not, or at least not strongly, reduced with increasing population size, that is that a supplementation from captive-breeding programs has a positive long-term effect on population size (otherwise, there would not be much reason to continue with any supplementation from captive breeding). These assumptions may be justified in a certain range of population sizes. We found that, under these assumptions and at κ close to 1, sex-ratio manipulation in captive-breeding programs can potentially make the difference between a further decline or a recovery of a population.

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