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Managing Population Sex Ratios in Conservation Practice: How and Why?

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1. Introduction

Small or declining populations are at increased risk of extinction because of stochasticity and Allee effects (Lande 1998, Courchamp et al. 1999, Stephens and Sutherland 1999, Bourbeau-Lemieux et al. 2011), and several genetic problems that include reduction in genetic variability, an accumulation of deleterious mutations due to random drift, and increased rates of inbreeding depression (Frankham et al. 2002, Hedrick 2005, Allendorf and Luikard 2007). Genetic problems are likely to reduce the average viability of individuals from generation to generation, and they reduce evolutionary potential and therefore the long-term survival expectancies, especially of small populations (Frankham et al. 2002, Hedrick 2005, Allendorf and Luikard 2007). However, genetic problems are only indirectly linked to the census size (N_c). Instead, they are directly dependent on the genetically effective population size (N_e) that is defined as the size of an ideal model population that looses genetic variability at the same rate as the observed population. Usually, N_e is significantly smaller than N_c because of variance in individual reproductive success, deviations from a 1:1 operational sex ratio, and other reasons. Risks of extinction are therefore increased if population sex ratios deviate from 1:1.

We typically expect 1:1 sex ratios in natural populations because of strong frequencydepended selection on the production of sons and daughters (Fisher 1930). However, population sex ratios can be biased by non-random harvest as a consequence of, for example, sex differences in behavior, size, or morphology, or simply as a consequence of hunter preferences (Bunnefeld et al. 2009, Tryjanowski et al. 2009, Marealle et al. 2010). Sex ratios can also be influenced by environmental changes such as, for example, different kinds of chemical pollution or changes in the temperature regime that may cause sex-specific mortality or growth. Environmental changes can even directly influence the production of males and females in species with environmental sex determination (Janzen 1994, Kamel and Mrosovsky 2006), or in species where the genetically determined sex can be reversed during a critical period in life. Such environmental sex reversal has been observed in several fish and amphibians (Wallace et al. 1999, Devlin and Nagahama 2002, Baroiller et al. 2009, Stelkens and Wedekind 2010), may potentially be more likely under many of the rapid environmental changes we are currently observing, but may well have happened frequently even before anthropogenic effects on the environment became ubiquitous (Perrin 2009).

Lastly, parents (especially mothers) of many species are able to manipulate family sex ratio, as will be explained below. There are examples where the combined effects of such parental life-history decisions have lead to distorted population sex ratios (Robertson et al. 2006).

We may be able to manipulate and hence manage population sex ratios to benefit biodiversity if we understand how they are influenced under natural and artificial conditions. We may either aim for maximizing the evolutionary potential and hence the long-term perspectives of a given population, or wish to control the growth of problem populations (e.g. of exotic species). Among the various tools that have been proposed for manipulating sex ratios are the 'sterile male' strategy, the 'Trojan Y chromosome', and recombinant constructs that lead to gender distortion (Gutierrez and Teem 2006, Cotton and Wedekind 2007a, Bax and Thresher 2009). Alternatively, maternal life-history strategies can sometimes be manipulated in order to affect family sex ratios, and some species even allow for sex ratio manipulation by simple manipulations of the micro-ecological conditions during critical stages in ontogeny.

In the following I summarize the current knowledge about how population sex ratios develop, and how they can change due to, for example, changed temperature regimes, different kinds of chemical pollution, or other environmental changes. I will then outline the various tools that could be used to manipulate sex ratios and give some examples from the literature. I will discuss the potential risks and benefits of such manipulations, and I will list a number of key questions that still need to be answered in order to optimize the management of population sex ratios.

2. What affects family sex ratios?

When discussing family sex ratios, it is useful to distinguish between the different possible explanatory levels, especially between proximate and ultimate explanations (Tinbergen 1963). Proximate (mechanistic) explanations of family sex ratio deal with questions about the genetic, physiological, and molecular aspects of, for example, sex determination. Ultimate (evolutionary) explanations concentrate on the adaptive value of a given family sex ratio, especially on the impact of a parent's fitness, without necessarily explaining the proximate aspects. Obviously, proximate arguments often set constraints to what parents may be able to achieve in order to maximize fitness.

If sex determination is purely environmental, as in most reptiles, sex is not determined at conception but later during a specific window of time during embryonic or larval development. The window is often called "the thermosensitive period" because incubation temperature is often the most important sex-determining factor in these species (Valenzuela and Lance 2004). Purely environmental sex determination has been assumed to be quite common also in fish. However, Ospina-Alvarez and Piferrer (2008) argued that among the many species for which sex-determining chromosome have not (yet) been identified, species should only be considered as having a purely environmental sex determination if sex is determined by environmental conditions that can be considered as normal and within the range usually experienced under natural conditions. Applying this condition leaves only few species of four teleost orders with purely environmental sex determination. Among them, three different types of reaction norms dominate: (i) decreased or (ii) increased

frequency of males with increasing temperature, or (iii) high frequency of males at extreme (high or low) temperatures (Devlin and Nagahama 2002, Ospina-Alvarez and Piferrer 2008, Baroiller et al. 2009).

In species with environmental sex determination, the within-population variance in family sex ratio can be very high due to variance in the micro-ecological conditions that affect eggs or larvae. Moreover, regional changes in the environment can easily lead to skewed population sex ratios in some years (Janzen 1994, Kamel and Mrosovsky 2006). Rapid and consistent environmental changes could then have dramatic consequences on population growth especially in small population of limited genetic variability, or in fragmented populations with limited gene flow. However, correlated changes in nesting or spawning time (Janzen et al. 2006, Wedekind and Küng 2010) or other changes in behavior and life history could potentially mitigate some of these negative effects of environmental changes. Moreover, some species seem to have the potential for (rapid) evolution in response to changed environments (Conover and Van Voorhees 1990, Conover et al. 1992, Magerhans et al. 2009).

In many fish and amphibians, sex determination is genetic but reversible by environmental factors during a sensitive period that is typically very early in life. Environmental sex reversal can be induced by various factors, including temperature changes or exposure to hormone active substances (Wallace et al. 1999, Devlin and Nagahama 2002, Baroiller et al. 2009). It is nowadays even used in fish farming to produce more profitable one-sex cultures (Pandian and Sheela 1995, Piferrer 2001, Cnaani and Levavi-Sivan 2009). Distorted sex ratios in the wild could potentially be caused by environmental sex reversal (Olsen et al. 2006, Brykov et al. 2008, Alho et al. 2010). Sex hormones, hormone-active substances, and endocrine disrupting chemicals are frequently released into natural watercourses, for example, in effluents from domestic and industrial sources (Larsson et al. 2000, Parks et al. 2001, Jobling and Tyler 2003). Fish exposed to such chemicals often display reduced reproductive performance (Vos et al. 2000), and exposure to such chemicals could well be responsible for gonadal malformations if, for example, sex reversal was incomplete leading to individuals that display gonadal characteristics of both sexes. A sudden increase in the prevalence of intersex or of other gonadal malformations is indeed frequently observed in natural populations (Harries et al. 1997, Bernet et al. 2004, Penáz et al. 2005, Jobling et al. 2006, Bernet et al. 2008, Bittner et al. 2009). Other possible consequences of exposure to hormones or hormone-active substances may include reductions in gonadal growth, a delayed onset of sexual maturity, inhibition of spermatogenesis, lower egg production, or reduced egg quality (Sumpter and Jobling 1995) (Vos et al. 2000). However, sex ratios in the wild can be skewed for many reasons (Palmer 2000), and environmentally induced sex reversal is often difficult to prove (Nagler et al. 2001, Chowen and Nagler 2004, 2005, Williamson et al. 2008). The prevalence and significance of environmental sex reversal in the wild is therefore still unclear (Wedekind 2010). So far, the consequences of environmentally induced sex reversal have only been analyzed in theoretical studies (Kanaiwa and Harada 2002, Hurley et al. 2004, Cotton and Wedekind 2009). These studies suggest that environmentally induced sex reversal can change population growth and population sex ratios in ways that may sometimes be counter-intuitive. A moderate rate of feminization, i.e. of an environmentally-induced development of the female phenotype despite male sex

chromosomes, could sometimes be beneficial for population growth, especially in the absence of strong viability effects of the sex reversal. However, most possible outcomes of environmental sex reversal are negative with regards to population growth or the persistence of sex chromosomes. For example, strong environmental feminization over several generations leads to high rates of YY individuals and can eventually lead to the extinction of X chromosomes (Cotton and Wedekind 2009). Analogously, continuous environmental masculinization increases the rate of XX individuals and can drive the Y chromosome to extinction (Cotton and Wedekind 2009). If sex chromosomes are lost, i.e. if populations loose their genetic sex determination in response to environmental factors that induce sex reversal, the affected population may quickly go extinct if the environmental forces that cause sex reversal cease.

The frequency-dependent selection on the production of sons and daughters is a consequence of the fact that every sexually produced individual usually has exactly one father and one mother. This explains why 1:1 sex ratios are so common. Such equal sex ratios are easier to achieve if sex determination in purely genetic as compared to if sex determination is environmentally biased. Sex determination is purely genetic in all mammals and birds and in many species of other taxa. However, even in these taxa, equal primary sex ratios are a rule with exceptions, and parents of many species are often able to somehow manipulate family sex ratio. The physiology of such manipulations is often not clear yet, but there are good reasons why skewed family sex ratio may offer fitness benefits. If, for example, one sex is more costly to produce and raise than the other one, parents who are able to weight the relative investment into sons and daughters according to the expected fitness return would achieve higher fitness than parents who would not be able to do so (Charnov 1982).

The relative value of sons and daughters may differ for different parents. This is especially so if the expected fitness return of one type of offspring is more dependent on resources received from the parents than the expected fitness return of the other type of offspring. This is a typical outcome in polygamous species where, for example, few dominant males receive an increased reproductive success at the expense of outcompeted males. In such cases, parents that are in good condition or experience favorable conditions would increase their fitness by producing more offspring of the sex with the greater requirements, while parents in suboptimal condition should rather "play safe" and produce the other sex that promises a lower variance in reproductive success (Trivers and Willard 1973). This hypothesis received much empirical support in a variety of taxa (Gomendio et al. 1990, Cassinello and Gomendio 1996, Bradbury and Blakey 1998).

If family sex ratio can be adjusted in response to parental condition, it seems reasonable to assume that mate attractiveness could influence overall parental investment and maybe even family sex ratio. Indeed, females of various taxa have been observed to produce relatively more sons if mated with an attractive male rather than if mated with an less attractive male (Burley 1982, Ellegren et al. 1996), possibly because sons of attractive males may generally be more likely to achieve high reproductive success than sons of less attractive males. However, the effect could not always be observed (Westerdahl et al. 1997, Saino et al. 1999). Moreover, skewed family sex ratios do not necessarily reflect adaptive parental strategies (Krackow 1995).

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3. Managing population sex ratio

3.1 Why?

There are several good reasons why conservation managers could potentially profit from manipulating population sex ratios (Table 1). First, sex ratios of a small and endangered population are sometimes significantly skewed towards too many females or too many males. Such non-equal sex ratios increase the negative effects of Allee effects and demographic stochasticity, sometimes leading to extinction. For example, the last six individuals of the Dusky Seaside Sparrow (Ammodramus maritimus nigrescens) that remained and were kept in a captive breeding program turned out to be all male. This subspecies is now believed to be extinct (en.wikipedia.org from Feb 6th 2012). Non-equal sex ratios also reduce the genetically effective population size because $N_e = 4N_mN_f/(N_m+N_f)$, with N_m and N_f being the number of mature males and females, respectively (Hartl 1988). In harem-based mating systems, N_e is even better described as $N_e = 4N_mN_f/(2N_m+N_f)$ (Nomura 2002). Therefore, populations with non-equal sex ratios are expected to lose more genetic variability (i.e. evolutionary potential) and suffer more from the negative consequences of inbreeding than populations with equal sex ratios. Moreover, in species where population growth is limited by the availability of oocytes, male-biased sex ratios directly reduce population growth. For example, the remaining population of the critically endangered kakapo (Strigops habroptilus) of New Zealand has been found to be significantly male biased, probably as an undesirable side effect of supplementary feeding (Tella 2001, Clout et al. 2002). Because this parrot is also a species for which population growth is severely limited by egg production, manipulating family sex ratios towards more daughters (by methods that are outlined below) quickly became one of the priorities of the conservation management of this species (Robertson et al. 2006).

Second, if population sex ratios are not significantly skewed, but population size is small and population growth is limited by the availability of oocytes, manipulating sex ratio towards a female bias could sometimes be desirable, especially if very small or rapidly declining populations call for emergency actions. For example, captive breeding programs are typically not only meant as a refuge in response to a temporary ecological crisis, but they often aim at releasing additional individuals into the wild to support small or declining populations and to help preventing further losses of genetic diversity (Young and Clarke 2000). Such captive breeding programs sometimes even include the use of assisted reproductive technologies (Gibbons et al. 1995, Dobson and Lyles 2000, Lanza et al. 2000). There are a number of potential risks that need to be considered in such programs. These risks include, among others, a general increase in the variance in reproductive success and hence a reduction in overall Ne (Ryman and Laikre 1991), potential negative effects of circumventing natural mate preferences (Grahn et al. 1998, Wedekind et al. 2001, Wedekind 2002b, Jacob et al. 2010), and artificial selection favoring certain life-history characteristics (Heath et al. 2003, Wedekind et al. 2007). However, if we can assume that offspring have an enhanced survival in captivity and that the subsequent release of captive bred individuals into the wild has a positive effect of the long-term survival of the population, artificially changing family sex ratios towards a female bias could sometimes even further increase population growth rate. Such manipulations may be feasible within a captive breeding program, for example by manipulating female reproductive strategies, or directly within the

warranted (see text for further explanations and for references). Table 1. Circumstances where different forms of sex ratio manipulation may or may not be

Observation	Aim of intervention	Main reasons for intervention**	Potential intervention technique	Immediate effect of the intervention	Typical taxa for v intervention may promisin
Biased sex ratio in small population, not caused by ESR*	Remove sex ratio bias	1, 2, 3, 4	Manipulate parental strategies	Changes sex ratio of next generation	Polygamous species, o monogamous species rates of extra-pair fert
			Manipulate environment during embryogenesis or early larval stages	Changes sex ratio of next generation	Species with environm determination (e.g. tur crocodiles, some fishe
The growth of a small population is limited by the availability of oocytes	Increase population growth rate	1	Manipulate parental strategies	Changes family sex ratio in order to create a female excess	Polygamous species, o monogamous species rates of extra-pair fert
			Manipulate environment during embryogenesis or early larval stages	Changes sex ratio of next generation to create a female excess	Species with environm determination
			Introduction of Trojan sex chromosome carriers	Daughter-biased family sex ratio in introduced individuals	Fishes and amphibian ZZ/ZW sex determin ESR, and functional V chromosome
Biased sex ratio caused by ESR*	Avoid short-term and long-term consequences of ESR; increase population growth	1, 2, 3, 4, 5	Identify and control driver of ESR	Genotype-phenotype mismatch reduced; strong immediate effects on population size and sex ratio possible (caution : continuous ESR could lead to extinction of one of the sex chromosomes)	Many fishes and amp
Damaging effects of invasive species	Control or reduce population growth rates	6	Introduction of 'Trojan Y chromosomes'	Male-biased family sex ratio in introduced individuals	Many fishes and amp XX/XY sex determinit and functional Y chro
			Introduction of sterile males	Immediate male bias, increased male-male competition, increased number of non-fertilized eggs	Many species
			Introduction of the recombinants "daughterless"	Male-biased family sex ratio in introduced individuals	Some fishes

* Environmentally-induced sex reversal, i.e. mismatch between gender genotype and phenotype ** 1. Typical problems of small populations, i.e. increased risk of extinction because of dem

1. Typical problems of small populations, i.e. increased risk of extinction because of demographic and e effects, or various genetic problems 2. Increased two-sex demographic stochasticity (i.e. increased risk of loosing one sex)

3. Reduced Ne/Nc ratio (i.e. increased genetic drift, reduction of overall heterozygosity, inbreeding depression) 4. Increased risk of losing cultural traits, especially if the sex ratio bias or the low population size is untypical

5. Increased risk of extinction of a sex chromosome

6. Various possible negative effects of an invasion, including a reducing biodiversity, altering ecosystem pr exotics acting as vectors of new diseases, etc.



wild population, for example by releasing individuals that are more likely to produce daughters than sons (Cotton and Wedekind 2007b) (see below). It is important to note that such a sex-ratio manipulation has the immediate effect of reducing the N_e to N_c ratio (because $Ne = 4N_mN_f/(N_m+N_f)$), i.e. it increases the genetic bottleneck that the small population is going through. This increased bottleneck immediately increases demographic stochasticity and leads to a greater loss of genetic variance, higher inbreeding rates, and higher rates of genetic drift and hence of fixation of deleterious mutations. However, if the sex ratio manipulation is carefully applied, these immediate negative effects of the treatment can be outweighed by the increased reproduction rates and the accelerated population growth (Wedekind 2002a, Lenz et al. 2007, Cotton and Wedekind 2009).

Third, invasions by exotic species, for example after a planned or accidental release of a nonnative species, are a major threat to biodiversity in most regions of the world (Myers et al. 2000). Various methods have been proposed to deal with this threat, but some of these methods have frequently created further problems, e.g. the introduction of secondary controlling species (Louda and Stiling 2004). Biasing the sex ratio in such problem populations towards more males could be a largely reversible method that may not only reduce population growth but could even reduce average female fitness. Male harassment of females over mating could by itself accelerate population decline (Rankin and Kokko 2007). At very low population sizes, induced male biases could even enhance Allee effects (Stephens and Sutherland 1999). Sex ratio manipulation may hence be an attractive option in fighting or controlling exotic species.

Family sex ratio manipulation is possible in many taxa. The degree of the invasiveness of the manipulation spans from manipulating environmental conditions during embryo and larval development or manipulating female perception of certain environmental key factors to, for example, sperm sexing prior to assisted reproductive technology in captive breeding programs (Gibbons et al. 1995, Dobson and Lyles 2000, Lanza et al. 2000). With regard to the latter, some methods of micromanipulation and some *in vitro* culture conditions have been discussed as potentially having an effect on embryo sex ratio in mice and cattle (King et al. 1992, Gutierrez et al. 1995). It therefore seems possible that sex ratios could be manipulated if assisted reproductive technology is used to propagate a species. However, in the following discussion of sex ratio manipulation, I will concentrate on methods that are arguably less invasive and comparatively less expensive.

3.2 Manipulating the rearing environment or maternal decisions

Obviously, if sex determination is purely environmental, a simple manipulation of the environment that embryos, larvae, or juveniles experience during the critical window in time in which sex is determined can be sufficient. If this critical time is during egg development, as for example in most if not all turtles, eggs could be collected and incubated at temperatures that result in the desired family sex ratio. Alternatively, the conditions at the egg laying site could be artificially changed (Girondot et al. 1998). Analogous manipulations have been suggested from some amphibians (Solari 1994).

Manipulating family sex ratio is less straightforward in species with genetic sex determination. However, the frequent observation that females are somehow able to manipulate family sex ratio (or the sex of their one offspring) in response to ecological or

social characteristics of the rearing environment may provide a number of options. If, for example, females adjust their family sex ratio in response to a perceived skew in the population sex ratio, skewed sex ratios could potentially be simulated in captive populations, for example by removing and housing members of one sex separately. Alternatively, the sensory stimuli that females use to perceive their social environment could be manipulated, for example by exposing the female to urine of different individuals in order to simulate a skewed population sex ratio (Perret 1996).

The Trivers-Willard hypothesis (Trivers and Willard 1973) predicts that in polygynous species, females in good conditions are more likely to have sons than daughters (see above). Such parental decisions could potentially be manipulated by manipulating the females' condition, for example by a changed feeding regime. The kakapo may be an example here. Supplementary feeding of the few remaining individuals of that species may have led to malebiased sex ratios because females in good conditions turned out to be more likely to have sons than daughters (Tella 2001, Clout et al. 2002). At one point in time, about 70% of all recorded offspring of this species were sons. Robertson et al. (2006) found that the male bias was significantly reduced when female condition was altered. Lenz et al. (2007) used this line of thought to work out the likely genetic and demographic consequences of analogous management actions in an existing captive breeding program for a Spanish population of the lesser kestrel (Falco naumanni), another polygynous bird that shows a correlation between family sex ratio and female condition: more daughters are born by mothers of average conditions, while more son are born by mothers of good condition (Aparicio and Cordero 2001). The authors found that a sex-ratio management within the range that seems possible would significantly increase the efficiency of an existing captive breeding program.

If females adjust their investment into sons and daughters according to male characteristics, it may be possible to exploit the rules that females use to determine the attractiveness of a male relative to all potential mates. Such decision rules are not likely to be entirely genetically fixed but may be rather flexible (Real 1991). Mate choice decisions can be the outcome of simple cost/benefit analyses (Milinski and Bakker 1992), and the perception of the attractiveness of a given male is expected to depend on female experience and hence on a sampling template given by the population. Such a sampling template could be manipulated in order to increase or decrease the perceived attractiveness of a given male. If, for example, the size or the color of a secondary sexual ornament determines sexual attractiveness, exposing the female to several (real or dummy) individuals with very weak sexual ornaments may make a male with medium-sized or medium-colored ornament more attractive. Analogously, exposing the female to several individuals with strong sexual ornaments may make the male with a medium-sized or a medium-colored ornament less attractive. Alternatively, many secondary sexual ornaments could be directly manipulated. Structural ornaments could be artificially elongated, colors could be enhanced painting the ornament, or the male could be presented under light conditions that accentuate the colors in question.

3.3 'Trojan Y chromosomes' and genetic constructs that distort sex ratios

Conservation practice sometimes includes managing potential problem populations (Kolar and Lodge 2002, Hanfling et al. 2011, Poulin et al. 2011). The 'sterile male' strategy is one of the various techniques that has been proposed. The idea is that large numbers of sterile males are produced and released into the wild in order to outcompete wild males for

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mating. So far, the application of this idea has largely concentrated on disease-transmitting insects (Thailayil et al. 2011). However, if females mate with only few males each, and the mating frequency of introduced sterile males is not significantly smaller than the mating frequency of wild males, the 'sterile male' strategy could potentially be applied more widely and also in the context of exotic species that need to be controlled. And even if the idea behind this technique is not primarily based on changing population sex ratio in order to manipulate population growth, it should nevertheless be discussed in the present context. Obviously, releasing large numbers of sterile males leads to a male-biased sex ratio that may, by itself, increase intra-individual competition and lead to a reduction of average female fitness not only because of the increased rate of non-fertilized eggs but also because of the likely negative effects of male-biased sex ratios in some sort of species (Rankin and Kokko 2007). Further recombination methods that have been discussed as possible pest control include sex-specific lethality constructs (Schliekelman and Gould 2000, Schliekelman et al. 2005). The effectiveness of the release of such constructs can be greatly enhanced by complementary management options such as selective harvest of males or females (Bax and Thresher 2009). However, the recombinant approach could lead to undesirable results if, for example, the gene construct jumps to other species (Kapuscinski et al. 2007).

Species with predominantly genetic but environmentally reversible sex determination (i.e. many fish and amphibians) offer another approach, the so-called 'Trojan Y chromosomes' strategy ('Trojan' genetic elements were originally defined as elements that have the potential of driving local populations to extinction (Muir and Howard 2004)). The necessary prerequisites are that (i) the species in question displays male heterogamety (i.e. XX = female and XY = male), and that (ii) the Y-chromosome should not be significantly decayed as it usually is, for example, in most mammals because of the suppressed recombination between the sex chromosomes (Bull 1983, Rice et al. 2008) and the thereby resulting accumulation of deleterious mutations on the Y-chromosome (Muller 1932, Felsenstein 1974). Interestingly, in fish and amphibians with genetic but environmentally reversible sex determination, sex chromosomes are typically not heteromorphic, and the functionality of Y chromosomes seems mostly unrestricted. This for itself leads to a number of interesting evolutionary questions (Perrin 2009), but what is probably most interesting in the present context is the fact that YY individuals are therefore often viable. Such YY individuals can be produced by mating feminized XY individuals with wild-type XY males. YY individuals would normally be males who can only produce XY sons if mated with wild-type XX females. Sex-reversed YY individuals (i.e. females without X chromosomes) would also be expected to have only sons if mated with a wild-type XY male. Moreover, half of these sons would have the YY genotype and could hence only have sons themselves. Gutierrez and Teem (2006) modeled the repeated introduction of YY females as potential tool in conservation management. They found that such introduction of 'Trojan Y chromosomes' can potentially be used to control the growth of problem populations. Critical variables in these scenarios are the relative viability of carriers of these 'Trojan Y chromosomes' and their attractiveness in mate choice, i.e. their mating success relative to the wild-type females and males (Cotton and Wedekind 2009).

Some species that display environmentally reversible sex determination have a sex determination mechanism that is based on female heterogamety (i.e. ZZ = male and ZW = female). Introducing sex-reversed WW individuals would then lead to an increased population growth, especially if the induced sex change had no significant effect on viability

and mating success (Cotton and Wedekind 2007b). Boosting population growth with 'Trojan sex chromosomes' may currently have the highest potential in the conservation of amphibians. Many amphibian display female heterogamety (Hillis and Green 1990), are susceptible to environmental influences during sex determination (Wallace et al. 1999), and WW genotypes may generally be viable and fertile because W chromosomes do typically not seem to be decayed (Perrin 2009).

The potential of 'Trojan sex chromosomes' for boosting or reducing population growth still needs to be experimentally analysed. For now, the concept seems entirely theoretical, i.e. to the best of my knowledge no empirical test of this idea has been published so far. The same seems to be true for a genetic construct that has recently been suggested and modeled by Bax and Thresher (2009) and that would induce a shift in the sex ratio of fish population. The idea here is that if individuals with multiple copies of a genetically engineered aromatase inhibitor gene (D) are introduced into a problem population, all offspring of the D gene carrier that inherit the D gene would phenotypically develop into males regardless of the composition of their sex chromosome. Analogously to Gutierrez and Teem's (2006) original 'Trojan sex chromosomes' idea, the introduction of the D gene into a population could shift the sex ratio in future generations to a male bias that potentially reduces population growth.

4. Conclusions

It may often be possible to manipulate population sex ratios, for example by changing certain ecological or social factors that influence maternal decisions about family sex ratio, or by invasive techniques like, for example, introducing sex-reversed individuals into natural populations to boost or reduce population growth on the long run. If the aim of such manipulations is to support a small and endangered population, it is important to consider the possible dangers of the manipulation. If the sex ratio of a small population is found to be male-biased prior to the intervention, reducing this bias in future generations may generally be beneficial because this would be increasing the N_e to N_c ratio and thereby reducing the negative effects of small population size on population genetics. However, even if we deal with populations in which sex ratio directly determines population growth, any deviation from equal sex ratio towards a female-biased sex ratio reduces the N_e to N_c ratio, i.e. It may create a genetic bottleneck. On the long run, the likely negative effects of such a bottleneck would need to be compensated by the increased population growth that was achieved through the sex ratio manipulation (as, for example, modeled in Lenz et al. (2007)). Furthermore, by changing a population sex ratio we are changing demographic parameters that may significantly influence breeding systems, mate choice, sex-specific use of resources, or other life-history aspects (Emlen and Oring 1977, Andersson 1994). It may even be possible that we thereby risk losing culturally transmitted characteristics that could be linked to, for example, natural breeding systems. The potential costs and benefits of a sex ratio manipulation should therefore carefully optimized for any given situation, i.e. the optimal sex ratio manipulation is likely to differ from case to case.

In the case of small and declining populations, any kind of sex ratio manipulation is likely to fail if the underlying stressors and threats to the population are not appropriately dealt with. Moreover, many of the ideas discussed here are relatively new and lack empirical support. For example, the potential of manipulating female strategies in a given species is often unclear, and we need to learn more about the viability and the fertility of sex-reversed individuals in the wild to better estimate the potential of the 'Trojan Y chromosome'

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strategies to control or boost populations. However, it is clear that population sex ratio can be managed in attempting to reduce genetic bottlenecks and the effects of stochasticity in small or declining populations, and to control the spread of invasive species.

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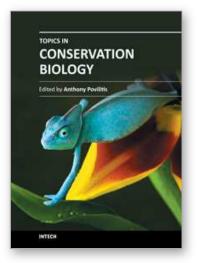
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Conservation biology is called a "crisis discipline." In a world undergoing rapid change, this science informs us about research, technologies, management practices, and policies that can help protect the earth's naturallyoccurring biological diversity. The six chapters of this book provide insightful analysis on managing protected areas (Middle East), conserving biochemical and genetic diversity of carob tree (Tunisia) and wild pear (Japan), determining the health status of Amazon manatee, manipulating sex ratios to benefit wildlife, and narrowing the gap between religion and conservation. The authors approach threats to biological diversity from varied angles, reflecting the interdisciplinary nature of the field. This book offers room for reflection on the definition and utility of the word 'natural' on a planet now overwhelmingly dominated by people.

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