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Review

Minimizing genetic adaptation in captive breeding programs: A review

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ABSTRACT

Captive breeding for species of conservation concern is the act of bringing rare or endangered animals into captivity with the hope of rearing sustained captive populations for eventual reintroduction into the wild. Within captivity, genetic changes can occur that may reduce a species' ability to persist once a population is reintroduced back into its natural habitat. We sought to determine the efficacy of recommendations made to minimize genetic adaptation to captivity by addressing the following questions: (i) Are these recommendations already being carried out in captive programs? (ii) How practical is each recommendation? and (iii) Which recommendations call for future investigation? We performed an extensive search of the published literature for studies of non-domestic, non-model, captive animals in which the investigators used and reported a strategy that can minimize genetic adaptation to the captive environment. We found different forms of each recommendation already being executed in captive programs to varying degrees. In all, we reviewed 90 articles covering four broad categories of strategies. We conclude that the best approach to minimize genetic adaptation is to reduce the number of generations that a species spends in captivity. If this is not possible, then we suggest attempting to minimize generations first by delaying reproduction and then by cryopreservation of germplasm. Other strategies are effective to varying degrees depending on the species' natural history. A large gap in the current literature is the interactive effects of multiple strategies being implemented simultaneously, future research should focus on this issue.

Contents

1. Introduction

Captive breeding for species of conservation concern is the act of bringing rare or endangered animals into captivity with the hope of rearing sustained captive populations for eventual reintroduction into the wild. Captive breeding and reintroduction was considered a successful conservation solution for a few threatened species such as the Guam rail (*Gallirallus owstoni*) and black-footed ferret (*Mustela nigripes*; Derrickson and Snyder, 1992; Miller et al., 1996). The apparent success of these high profile cases led to an increase in the popularity of captive breeding as a practical answer to population decline (Ebenhard, 1995; Seddon et al., 2007). By 2003, 489 animal species were the focus of reintroduction programs (Seddon et al., 2005).

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However, it has been well documented that the act of bringing a species from the wild into a captive breeding program has a negative effect if the species is reintroduced back into the wild. In a review by Fischer and Lindenmayer (2000), 13% of reintroduction programs of captive-born populations were considered successful versus 31% of wild-born translocations (with success judged as a self-sustaining and viable population). In an earlier review by Beck et al. (1994), only 11% of reintroduction programs of captive-born populations were considered successful. Other reviews have shown that captive individuals had a lower success rate than translocations of wild-caught individuals that were never in captivity (38% versus 75%, Griffith et al., 1989; 50% versus 71%, Wolf et al., 1996).

Within captivity, genetic changes can occur that may reduce a species' ability to persist once a population is reintroduced back into its natural habitat (Swinnerton et al., 2004; Araki et al., 2007b; Hedrick and Fredrickson, 2008). As species in captive breeding programs are frequently endangered they are often maintained in small numbers. Inherent to all small populations, both natural and captive, the most well-known sources of genetic change include loss of genetic diversity, inbreeding depression, and accumulation of new deleterious mutations (Bryant and Reed, 1999; Charpentier et al., 2005; Xu et al., 2007).

Within captive breeding programs an additional source of genetic change is genetic adaptation to captivity. Genetic adaptation to captivity is caused by both natural and artificial selection on the organism in the captive environment (Frankham and Loebel, 1992; Arnold, 1995). Genetic adaptation to captivity has been demonstrated in fish, insects and amphibians (Frankham and Loebel, 1992; Lewis and Thomas, 2001; Woodworth et al., 2002; Heath et al., 2003; Kraaijeveld-Smit et al., 2006). For example, female Chinook salmon (*Oncorhynchus tshawytscha*) from a hatchery had smaller eggs and reduced reproductive success relative to wild populations (Heath et al., 2003). In contrast, in a population of large white butterflies (*Pieris brassicae*) bred in captivity for 100–150 generations, fecundity in captivity was higher compared to that of a wild strain bred in the same conditions for one generation (Lewis and Thomas, 2001). Although the authors did not compare the strains in the natural environment, the results show how fecundity in a captive environment can change over many generations, a length of time that many species are expected to stay in captivity. However, adaptation to captivity can occur rapidly. In only eight generations, an experimental population of *Drosophila melanogaster* doubled its relative fitness in captivity compared to a wild population (Frankham and Loebel, 1992). Similarly, after nine to twelve generations of captivity, the predator-induced defenses of the Mallorcan midwife toad (*Alytes muletensis*) began to develop at a slower rate and toads demonstrated an overall reduction in trait response (Kraaijeveld-Smit et al., 2006).

As threatened species have small population sizes, there has been little replication and control in studies examining genetic adaptation to captivity other than those using model organisms (Woodworth et al., 2002; Margan et al., 1998; Frankham and Loebel, 1992). Based on a series of studies involving *Drosophila spp.* and other models of captive species, Richard Frankham (2008) modeled the effects of genetic adaptation on populations in captive situations. Frankham (2008) constructed the following equation that could be used to predict the genetic change in reproductive fitness over time in captivity (GA_t) based on the breeder's equation for quantitative genetic response to selection:

$$GA_t \sim Sh^2 \Sigma \left(1 - \frac{1}{2N_e}\right)^{t-1} \tag{1}$$

where S is the selection differential, h^2 is heritability, which is dependent on genetic diversity for reproductive fitness, N_e is the effective population size and t the number of generations in captivity (Margan et al. 1998; Frankham and Loebel, 1992). The response to selection in the first generation is represented by Sh^2 and the expression after sigma (Σ) represents the loss of genetic diversity due to genetic drift in successive generations (Frankham, 2008). The equation predicts that genetic adaptation in captivity will be positively related to the number of generations in captivity, intensity of selection, genetic diversity, and effective population size. Adding new individuals from a wild population will also slow genetic adaptation (Frankham and Loebel, 1992). Theoretically, if two identical populations split and gene flow between them is stopped, they will differentiate (measured by F_{ST}) as described by the equation:

$$F_{ST} = 1 - e^{-t/2N} \tag{2}$$

With N equal to the effective population size and t equal to time in generations (Wright, 1943). To minimize genetic differentiation between captive and wild populations, even limited migration has a homogenizing effect. How migration influences genetic differentiation is described by the equation:

$$f_t = \left[\frac{1}{2N} + \left(1 - \frac{1}{2N}\right)f_{t-1}\right](1 - m)^2 \tag{3}$$

with f_t equal to F_{ST} at time t; fixation is necessarily interrupted by the addition of migrant alleles into the population (Hedrick, 2005). To minimize genetic adaptation to captivity based on the terms of Eq. (1), Frankham (2008) recommends reducing the number of generations spent in captivity (reducing t), minimizing selection (reducing Sh^2), reducing effective population size and genetic diversity by fragmenting and isolating populations, and adding new founder individuals from wild populations (Frankham, 2008). Furthermore, Eq. (3) indicates that slowing adaption will occur with an influx of species from wild populations.

While the direct relationship between reducing genetic adaptation to captivity and the recommendations listed above have only recently been formalized, some of the recommended procedures have been taking place within current captive breeding programs. In this review, we sought to determine the efficacy of these practices in reducing genetic adaptation to captivity with regards to these contemporary captive breeding programs. Specifically, we sought to address three questions: (i) Are these recommendations already being carried out in captive programs? (ii) How practical is each recommendation? and (iii) Which recommendations call for future investigation? Whereas the equations above present the theory behind how many of these recommendations minimize selection, we explored the literature to determine how these recommendations had been applied to actual cases and critically examined each. We performed an extensive search of the published literature for studies of non-domestic, non-model, captive animals in which the investigators used and reported one or more of the recommendations given by Frankham (2008; see above) or introduced immigrants from wild populations to reduce genetic adaptation to captivity. We have excluded bacteria and plants in this review due to a strong bias towards vertebrates in both reintroduction projects and zoological publications (Wemmer et al., 1997; Seddon et al., 2005) although it should be noted that both have demonstrated adaptation to captive situations (Allard, 1988; Korona, 1996).

2. Minimizing number of generations in captivity (t)

Minimizing the number of generations that a population remains in captivity (t) before reintroduction into the wild lessens the number of generations for selection to act upon the population thereby reducing the amount of adaptation possible. Indeed, reducing the amount of time species spend in captivity before

Table 1
Minimizing number of generations: Traits that exhibited changes due to increased numbers of generations in a captive environment. Parentheses indicate the general type of trait.

Class	Order	Species	Number of generations	Trait	Reference
Amphibia	Anura	*Alytes muletensis*	9–12 Generations	Predator defenses (morphology)	Kraaijeveld-Smit et al. (2006)
Aves	Gruiformes	*Eurypyga helias*	Simulation based on pedigree	Founder genome equivalents (degree of genetic change from source population)	Earnhardt (1999)
Insecta	Lepidoptera	*Pieris brassicae*	100–150 Generations	Size and number of eggs (reproductive success)	Lewis and Thomas (2001)
Mammalia	Carnivora	*Chrysocyon brachyurus*	Simulation based on pedigree	Founder genome equivalents (degree of genetic change from source population)	Earnhardt (1999)
		Canis lupus baileyi	Simulation based on pedigree	Founder genome equivalents (degree of genetic change from source population)	Earnhardt (1999)
	Rodentia	*Peromyscus polionotus subgriseus*	2–35 Generations	Overall response to predators (behavioral)	McPhee (2003)

reintroduction is the most direct and best method for ensuring survival of founded captive populations (Eq. (1); Derrickson and Snyder, 1992; Miller et al., 1996). We found only three studies that examined the direct effect of reducing the number of generations in captivity by reducing the amount of time spent in captivity (Table 1). The oldfield mouse (*Peromyscus polionotus subgriseus*), Mallorcan midwife toad and large white butterfly all demonstrate greater changes in physical or behavioral traits or fecundity as a result of more generations in captivity than those that have been in captivity for fewer generations (Lewis and Thomas, 2001; McPhee, 2003; Kraaijeveld-Smit et al., 2006). An additional study simulated actual pedigrees and concluded that releasing individuals that had a history of the fewest generations in captivity had the greatest success upon reintroduction (Earnhardt, 1999). However, reintroduction is only practical for species in which the issues that created a need for a captive breeding program have been resolved (Kleiman et al., 1994). For species that must remain in captivity, minimizing generations may take on two different approaches – delayed reproduction of live animals and cryopreservation.

2.1. Delayed reproduction

Delayed reproduction of live captive animals can occur by simply separating male and female individuals into separate groups. However, the separation of males and females can have disadvantages owing to the greater space requirement and the lack of such space in zoos (Soule et al., 1986). This grouping may also be socially atypical for some species and lead to aggression and stress (Monfort et al., 1993; Sainsbury, 1997). A possible solution to the difficulties associated with separation of the sexes may be found through a number of reversible contraceptive methods available to captive breeding programs: steroidal and non-steroidal hormones, immunological methods and physical barriers (Dutton and Allchurch, 1998). Members of the American Zoo and Aquarium Association (AZA) Wildlife Contraception Center recently published a book containing an extensive review of contraceptive methods using data from the AZA Contraceptive Advisory Group database (Asa and Porton, 2005). They reported 261 species and more than 4800 individuals in which contraceptive methods were used.

In our search of peer-reviewed literature, we found 31 studies documenting effective contraceptive methods within 55 captive bred mammals (Table 2). One common conclusion concerning the utility of contraception is that the practical use of contraceptives depends upon the species in question (Asa and Porton, 2005). We found that among Carnivora, side effects of steroidal contraceptives included behavioral and reproductive pathologies. Ungulates, however, including the artiodactylids and equids, tend to respond well to reversible contraceptives with no major side effects found in studies that used the two most common immunocontraceptives: porcine zona pellucida (PZP) or deslorelin, a gonadotropin-releasing hormone agonist (Table 2).

The use of contraceptives for genetically important individuals in rare and endangered species has made reversibility an essential factor in their use as a method of delaying reproduction. Reversibility following contraception is typically determined by regaining normal hormone concentrations, restoration of ovulation or pregnancy and birth (Asa, 2005). In the literature, reversibility has only been documented in 19 species (Table 2). In an additional 33 species, reversibility was not clearly examined due to restrictions on the length of the study (Kirkpatrick et al., 1996; Bertschinger et al., 2002) or lack of the desire to reverse contraception on the part of the authors (Gould and Johnson-Ward, 2000); Table 2).

One problem associated with delayed reproduction is that behavioral and physiological abnormalities may arise in some species that are reared under abnormal conditions. Reproductive difficulties have been reported in the genus *Eulemur* as a result of delaying reproduction. However, whether the cause is physiological or behavioral is unclear (Tamara Bettinger, AZA SSP Species Coordinator, personal communication). For white rhinoceros (*Ceratotherium simum*) and African elephants (*Loxodonta africana*), physiological effects of nulliparity have been reported. These effects tend to appear as reproductive pathologies and shorter reproductive life-spans regardless of whether contraception was used (Hermes et al., 2004, 2006). Behaviorally, delayed reproduction can prevent proper sociosexual development and impede future reproductive success as shown in Callitrichids, chimps (*Pan troglodytes*) and mouse lemurs (*Microcebus murinus*) (Tardif et al., 1984; King and Mellen, 1994; Radespiel and Zimmermann, 2003).

While delaying reproduction is currently practiced, it may only be practical for species with long life spans or high reproductive output because fecundity can decrease with age (Ballou and Foose, 1996; Ricklefs et al., 2003; Swanson, 2006). For example, delayed reproduction is not considered practical for small cats as they have relatively short life spans, few offspring per litter and a quick drop-off in fecundity (Swanson, 2006). Theoretically, however, delaying reproduction until a later age should give a high payoff, despite a high cost, as the number of generations has an exponential effect on genetic adaptation (see Eq. (1)). As population control in breeding programs becomes crucial, captive breeding programs will likely continue to utilize both management practices and reversible contraceptives as a means of delaying reproduction (Soule et al., 1986; Asa and Porton, 2005) because the potential payoff of this method is high. Moreover, enlarging the generation interval will reduce the effects of genetic drift, including the reduction in the loss of genetic diversity which will enhance the probability of survival of the individuals when reintroduced to the wild. Because of the relative paucity of studies that directly investigate the effects of delayed reproduction of live animals we suggest that population monitoring should continue in non-mammal species

Table 2
Delaying reproduction: reversible contraceptives used in mammalian population control and delayed reproduction. Possible side effects of reversible contraceptives were also examined. NE denotes that reversibility was not examined in a particular study. Where more than one contraceptive was studied, footnote designates which contraceptive used in each species.

Order	Species	Contraceptive	Reversible?	Side effects	Reference
Artiodactyla	*Antilope cervicapra*[1] *Cervus dama*[1] *C. elaphus nelsoni*[2] *C. nippon taiwanaus*[1] *C. unicolor*[1] *C. axis*[1] *Naemorhedus goral arnouxianus*[1] *Odocoileus hemionus*[2]	MGA in feed[1]; Leuprolide[2]	Yes	No	Raphael et al. (2003), Deigert et al. (2003), Kirkpatrick et al. (1996), Patton et al. (2000), Baker et al. (2004, 2002)
	Addax nasomaculatus *Alces alces* *Bison bison* *Bos javanicus* *Capra ibex* *Cervus axis* *C. elaphus roosevelti* *C. nippon taiwanaus* *C. unicolor* *Giraffa camelopardalis* *Hemitragus jemlahicus* *Muntiacus reevesi* *Oreamnos americanus* *Dama dama* *Ovis canadensis* *Rangifer tarandus* *Tragelaphus angasii* *Tragelaphus euryceros* *Litocranius walleri*	PZP	NE	No	Kirkpatrick et al. (1996, 1995), Frank et al. (2005)
	Addax nasomaculatus *Oryx leucoryx*	MGA implant	Yes	Build up of fluid in uterus	Hall-Woods et al. (2007)
	Cervus duvauceli	MGA in feed	Low	Low fecundity following removal	Raphael et al. (2003)
Carnivora	*Panthera tigris altaica* *P. t. sumatrae*	MGA implant	Yes	Lower probability of breeding than nonimplanted females after removal	Chuei et al. (2007)
	Panthera leo	MGA implant	Yes	Loss of secondary sexual characteristics	Seal et al. (1976)
	Pteropus rodricensis	MGA implant	NE	Weight gain, hair loss	Hayes et al. (1996)
	Felis chaus[2] *F. concolor*[2] *F. geoffroyi*[2] *F. serval*[2] *Nasua nasua*[2] *Panthera leo*[2] *P. onca*[2] *P. onca*[1] *P. pardus*[2] *P. tigris*[2] *P. uncial*[2]	MGA oral[1]; MGA implant[2]	NE	Higher prevalence of reproductive pathology in treated individuals	Munson et al. (2002), Chittick et al. (2001), Linnehan and Edwards (1991), Harrenstien et al. (1996), Kollias et al. (1984)
	Canis lupus *Panthera leo* *P. onca* *P. pardus*	Mibolerone	NE	Aggression	Gardner et al. (1985)
	Panthera pardus	Mibolerone	Yes	Food refusal	Gardner et al. (1985)
	Panthera leo	Mibolerone	Yes	Weight loss; Masculinization	Gardner et al. (1985)
	Acinonyx jubatus[2] *Helarctos malayanus*[3] *Panthera leo*[2] *P. onca*[1] *P. pardus*[2] *Ursus americanus*[3] *U. arcto*[3] *Zalophus californian*[3]	PZP[3], Mibolerone[1], Deslorelin[2]	NE	No	Frank et al. (2005), Gardner et al. (1985), Bertschinger et al. (2002)

(continued on next page)

Table 2 (*continued*)

Order	Species	Contraceptive	Reversible?	Side effects	Reference
Diprotodontia	*Macropus giganteus*	Levonorgestrel implant	NE	No	Nave et al. (2002)
	Macropus eugenii	Deslorelin implant	NE	Weduced uterine weight	Herbert et al. (2004)
	Macropus eugenii	Deslorelin implant	Yes	No	Herbert et al. (2005)
	Trichosurus vulpecula	Deslorelin implant	Yes	Extreme variation in reversibility	Eymann et al. (2007)
Perissodactyla	*Ceratotherium simum cottoni* *C. s. simum*	Reproductive delay	Low	Higher prevalence of reproductive pathologies in older, non-reproductive animals	Hermes et al., 2004; Hermes et al. (2006)
	Equus przewalskii	PZP	NE	Temporary abscesses at injection site	Kirkpatrick et al., 1995
	Equus burchelli *E. grevyi* *E. przewalskii* *E. zebra*	PZP	NE	No	Frank et al. (2005)
Primates	*Callithrix jacchus*	MGA implant	Yes	No	Mohle et al. (1999)
	Leontopithecus rosalia	MGA implant	Yes	High number of stillbirths and low infant survival	Wood et al. (2001)
	Leontopithecus chrysomelas	MGA implant	Low	High number of stillbirths	DeVleeschouwer et al. (2000)
	Pan troglodytes	IUD; MGA implant	NE	No	Gould and Johnson-Ward (2000), Bourry et al. (2005)
	Callithrix goeldii *Saimiri sciureus*	MGA implant	NE	Higher prevalence of reproductive pathology in MGA treated animals	Murnane et al. (1996)

such as reptiles that may also be long-lived to more fully characterize the potential costs associated with reproductive delay.

2.2. Cryopreservation

Long-term preservation of genetic material through germplasm resource banks (GRBs) is also used as a means of maintaining biodiversity (Ballou, 1992; Johnston and Lacy, 1995; Bennett, 2001). Although much of the research on this preservation mechanism has been summarized in recent books and reviews [e.g. 50–200 aquatic species; Rana and Gilmour (1996)], here we further synthesize these data (241 species). One general conclusion from the literature is that studies of spermatozoa cryopreservation are overrepresented (Table 3). Moreover, comparatively little progress has been made in the cryopreservation of oocytes (Table 3). However, studies tend to find oocytes much less hardy than spermatozoa because the sensitivity to any small changes in structure can be extremely disruptive (Watson and Fuller, 2001; Leibo and Songsasen, 2002). Nevertheless, maternal germplasm can be preserved through embryo cryopreservation. Recent progress has been made in embryo cryopreservation (Table 3), particularly in the felids and primates. For example, Morrell and Hodges (2001) reported five species of primates born from frozen embryos and Swanson and Brown (2004) reported the successful cryopreservation of the embryos of three species of exotic cat and the birth of an ocelot (*Leopardus pardalis*) from a frozen embryo transfer.

One general drawback to this technique is that a high amount of inter-species variation exists in the preservation methodologies employed (Howard et al., 1981; Saint Jalme et al., 2003). In order to find the optimal conditions for maximum survival of gametes, it is necessary to develop unique protocols for each species. Moreover, there must either be an extant population or a practical domestic surrogate available to give birth using the frozen germplasm (Frankham et al., 2002). Although progress is being made with embryo cryopreservation, the use of spermatozoa is currently the most practical method as it is used for translocations, artificial inseminations and can alleviate space issues (Fickel et al., 2007). Future investigations in embryo cryopreservation are needed to increase the potential number of individuals that can be included in a GRB program (Harnal et al., 2002).

3. Minimizing selection (Sh^2)

The literature discusses three types of selection that are typically guarded against in captive bred populations. Directed artificial selection is relatively easy to guard against in controlled environments, whereas unconscious artificial selection can often be an issue for species in captive breeding programs (Arnold, 1995). Unconscious selection may occur unintentionally in zoos when only the individuals that reproduce well in captivity or are easy to handle are able to pass their genes on to the next generation (Flesness and Cronquist-Jones, 1987). The third type of selection, described by Arnold (1995), is a result of the captive environment such as the lack of predators, abundant water, and a lack of parasites. This inadvertent selection for adaptation to the captive environment, labeled incidental selection, can be difficult to separate from natural selection (Arnold, 1995). The literature indicates two strategies to reduce the influence of selection on captive bred species (Frankham, 2008). First, the use of particular breeding strategies can minimize the effect of unconscious selection. Second, to reduce incidental selection a strategy of creating an environment similar to the natural habitat can reduce incidental selection.

3.1. Breeding strategies

Equalization of family sizes (EFS), or culling the offspring of overrepresented adults, is the primary breeding strategy recommended to reduce selection in captive populations (Allendorf, 1993; Frankham, 2008). Making all family sizes equal eliminates the reproductive variance between families so that selection is limited to within families, usually full siblings. However, under certain scenarios EFS may be impractical (e.g. in threatened species with lower fecundity and long generation time; Zheng et al., 2005). In this case, a breeding strategy of minimizing mean kinship (MK), as proposed by Ballou and Lacy (1995), is recommended. In a MK strategy, unconscious selection is reduced by choosing pairings based on coancestry rather than those individuals which reproduce well in captivity.

Here we identified nine studies that employed one of these two breeding strategies within a captive breeding program to minimize selection (Table 4). In addition to reducing selection, these

Table 3
Cryopreservation of germplasm in non-domestic and captive animals. (S) Spermatozoa, (O) Oocyte, (E) Embryo, (B) Blastomere.

Class	Order	Number of species	Type of germplasm	Reference
Actinopterygii	Acipenseriformes, Beloniformes, Characiformes, Perciformes, Pleuronectiformes, Gadiformes, Mugilliformes, Tetradontiformes, Cyrpriniformes, Salmoniformes, Siluriformes, Gonorhynchiformes	52 species	S	Suquet et al. (2000)[b] Chao and Liao (2001)[b]; Billard and Zhang (2001)[a]
Amphibia	Anura	3 species	S	Millar and Watson (2001)[a]
Asteroidea	Clypeasteroidea, Forcipulatida	2 species	S	Gwo (2000)[b]
Aves	Anseriformes, Falconiformes, Psittaciformes, Gruiiformes, Accipitriformes, Sphenisciformes, Galliformes,	16 species	S	Gee et al. (2004)[b]; Wishart (2001)[a]
Bivalvia	Ostreoida, Veneroida	6 species	S	Gwo (2000)[b]; Chao and Liao (2001)[b]
Echinoidea	Echinoida, Arbacoida	6 species	S	Gwo (2000)[b]
Gastropoda	Vetigastropoda	3 species	S	Gwo (2000)[b]; Chao and Liao (2001)[b]
Malacostraca	Decapoda	4 species	S	Gwo (2000)[b]
Mammalia	Artiodactyla	54 species	S	Leibo and Songsasen (2002)[b]; Stover and Westrom (1984), Holt (2001)[a]; Fickel et al. (2007)[b]; Rott (1995)[b]; Dott and Skinner (1989)
	Carnivora	47 species	S	Leibo and Songsasen (2002)[b]; Stover and Westrom (1984), Fickel et al. (2007)[b]; Hewitt et al. (2001)[a]; Holt and Watson (2001)[a]; Swanson and Brown (2004)[b]; Rott (1995)[b]
	Cetacea	1 species	S	Fickel et al., 2007[b]
	Chiroptera	4 species	S	Fickel et al. (2007)[b]; Rott (1995)[b]
	Diprodontia, Dasyuromorphia, Peramelemorphia	14 species	S	Rott (1995)[b]; Johnston and Holt (2001)[a]
	Lagomorpha	2 species	S	Fickel et al., 2007[b]
	Perissodactyla	9 species	S	Leibo and Songsasen, 2002[b]; Stover and Westrom (1984), Holt (2001)[a]; Fickel et al., 2007[b]; Rott (1995)[b]
	Primates	22 species	S	Rott (1995)[b]; Fickel et al. (2007)[b]; Leibo and Songsasen (2002)[b]; Morrell and Hodges (2001)[a]; Stover and Westrom (1984)
	Proboscidea	2 species	S	Leibo and Songsasen (2002)[b]; Stover and Westrom (1984), Holt (2001)[a] Fickel et al. (2007)[b]; Rott (1995)[b]
	Rodentia	3 species	S	Fickel et al. (2007)[b]; Rott (1995)[b]
Merostomata	Xiphosura	1 species	S	Gwo (2000)[b]
Polychaeta	Capitellida, Aciculata	2 species	S	Gwo (2000)[b]
Mammalia	Primates	2 species	0	Morrell and Hodges (2001)[a]
Bivalvia	Ostreoida, Veneroida	2 species	E	Chao and Liao, 2001[b]
Gastropoda	Vetigastropoda	1 species	E	Chao and Liao (2001)[b]
Mammalia	Artiodactyla	5 species	E	Stover and Westrom (1984); Woolf (1986); Leibo and Songsasen (2002)[b]
	Carnivora	12 species	E	Amstislavsky et al. (2006), Crichton et al. (2003), Miller et al. (2002), Pope et al. (2006), Swanson and Brown (2004)[b]
	Primates	7 species	E	Morrell and Hodges (2001)[a]; Pope et al. (1997), Pope et al. (1984)
	Dasyuromorphia	1 species	E	Johnston and Holt (2001)[a]
Actinopterygii	Salmonidae	1 species	B	Kusuda et al. (2002)

[a] Denotes chapters from (Watson and Holt 2001).
[b] Data from other review sources.

breeding strategies are currently recommended in captive management to achieve other genetic benefits such as increasing N_e and reducing loss of genetic diversity (Ballou and Foose, 1996; Frankham et al., 2002). However, these procedures may be in conflict with other recommendations (see Fragmentation below). Reducing the variance in family sizes through EFS will also act to increase N_e (Allendorf, 1993; Ballou and Foose, 1996; Waples, 1999). Alternatively, MK is recommended for all species that are part of the Species Survival Plans or Population Management Plans within the American Zoo and Aquarium Association (AZA) to preserve species genetic diversity and reduce inbreeding (Ballou and Lacy, 1995; Cronin et al., 2006). With regard to the effect that these strategies have on directly influencing selection to the captive environment, EFS has been demonstrated to halve genetic adaptation, but there is little direct evidence to support an increase in relative fitness upon reintroduction after employing either EFS or MK (Loebel et al., 1992; Montgomery et al., 1997; Frankham et al., 2000; Frankham, 2008). However, both strategies have been shown to be effective in computer simulations. Fernandez and Caballero (2001) found higher fitness as a result of EFS after 50 generations in captivity. Saura et al. (2008) ran a MK simulation study for 14 generations that resulted in reduced adaptation to captivity.

We identified only one study in which EFS was specifically described as a method of minimizing genetic adaptation (Table 4). EFS was used in a supplementation hatchery study that compared N_e estimates from both genetic and demographic data. Unfortunately, culling of surplus offspring can be expensive (Allendorf, 1993; Harada et al., 1998) and viewed by some as unethical

Table 4
Minimizing selection: Studies that employ the strategies of equalization of family sizes (EFS), minimizing mean kinship (MK) or creating a natural environment to minimize selection on a captive species (NE).

Class	Order	Species	Strategy to minimize selection	Reference
Actinopterygii	Salmoniformes	*Oncorhynchus tshawytscha*	EFS	Eldridge and Killebrew (2008)
	Perciformes	*Pagrus major*	MK[a]	Doyle et al. (2001)
	Pleuronectiformes	*Paralichthys olivaceus*	MK[a]	Sekino et al. (2004)
	Siluriformes	*Pangasianodon gigas*	MK[a]	Sriphairoj et al. (2007)
Aves	Ciconiiformes	*Gymnogyps californianus*	MK[a]	Miller (1995)
		Gymnogyps californianus	MK	Ralls and Ballou (2004)
	Galliformes	*Gallus gallus*	NE	Hakansson et al. (2007)
Crustacea	Isopoda	*Thermosphaeroma thermophilum*	NE	Shuster et al. (2005)
Mammalia	Carnivora	*Canis rufus baileyi*	MK	Hedrick and Fredrickson (2008)
		Mustela nigripes	MK	Wisely et al. (2003)
		Canis rufus	MK	Hedrick and Fredrickson (2008)
	Primates	*Callimico goeldii*	MK	Vasarhelyi (2002)
	Perissodactyla	*Equus przewalskii*	MK[a]	Miller (1995)

[a] Denotes that a simulation was run on a pedigree but actual individuals were not used in a MK strategy.

making this method impractical, particularly for larger, charismatic species. Additionally, we found eight studies that explicitly stated that a MK strategy was used as part of species management or experimental design (Table 4). Five of these studies reported an equalization of founder contribution or reduction in allelic founder variance as predicted (Table 4; Montgomery et al., 1997). It is likely that more species are managed using MK than those reported here. However, we found little published analysis of the influence of this management strategy. The cost for EFS is high and the resulting increase in N_e can potentially increase selection. In addition, there is very little evidence to demonstrate that breeding strategies increase fitness upon reintroduction, even in model species (Loebel et al., 1992; Montgomery et al., 1997; Wisely et al., 2003). Overall, these strategies do not seem to be practical for minimizing selection. However, as MK becomes a standard management strategy, future investigations should focus to determine the effect of this breeding strategy on genetic adaptation by closely monitoring pedigrees and reintroductions.

3.2. Creating an environment similar to the wild habitat

Frankham (2008) suggests providing an environment that is similar to the wild habitat to reduce inadvertent selection in captivity. Many zoos have begun to house animals in more natural exhibits that allow animals to perform innate behaviors (Maple and Finlay, 1989; Ogden et al., 1990; Mellen and Sevenich MacPhee, 2001). A few institutions even provide large, free-range exhibits in which some species are able to live in more natural social groups (Spevak et al., 1993; Stafford et al., 1994). Providing environmental enrichment for captive species in the form of naturalistic environments has become a high priority in zoos (Britt, 1998; Mellen and Sevenich MacPhee, 2001; Cummings et al., 2007; Moreira et al., 2007). A great deal of work has been done to encourage animals in captivity to preserve natural behaviors, yet the focus is often on the welfare of animals rather than any changes in genetic adaptability to captive breeding. For these reasons, studies of environmental enrichment concerning only short-term changes in behavior or physiology have been excluded from this review as we determined that these studies were concerned mainly with reducing levels of stress rather than changes in allelic frequencies. We did identify two studies that focused on how changes in the environment showed possible evidence of genetic change (Table 4). First, Red junglefowl (*Gallus gallus*) that had been reared for almost 10 years in a setting in which they were familiar with being handled by humans were much less fearful than a group that had been raised for more than 40 years in a more natural environment away from human contact (Hakansson et al., 2007). Unfortunately, it is difficult to be certain that the divergence in the junglefowl populations was genetic in nature and not a learned behavior. Second, Socorro isopod (*Thermosphaeroma thermophilum*) populations that had an environment most similar to the wild habitat showed the least divergence from the original population both genetically and morphologically (Shuster et al., 2005).

While natural environments are beginning to be used more in captivity, it is usually for a reason other than to minimize selection. However, because of the correlative effects of reducing stress and minimizing selection in a captive bred environment, zoos are achieving the desired effect, even if only incidentally. Although the monetary expense might be prohibitive to attempt to create completely natural environments for larger animals, maintaining natural environments should be the aim of all captive bred populations of smaller animals.

4. Fragmentation of populations and Immigration

The recommendation to fragment populations may seem at first contradictory to preserving the genetic health of a threatened species. Dividing a single large population into several smaller populations will result in the reduction of both N_e and genetic diversity caused by genetic drift (Lacy, 1987; Frankham et al., 2002). However, selection, the driving force behind genetic adaptation in captivity, is not as effective in populations with lower N_e (Frankham et al., 2002). As N_e decreases, genetic diversity also diminishes due to genetic drift and alleles are more likely to become fixed in smaller populations and individuals will be more likely to inbreed (Hartl and Clark, 1997).

Should inbreeding become a dilemma within smaller subpopulations, migration between populations may be necessary (Lacy, 1987). As many as 10 migrants per generation have been suggested for very small populations to alleviate the problems associate with inbreeding (Vucetich and Waite, 2000). Unfortunately, this number may not be realistic for some species due to transportation or disease transmission issues as well as sheer number of available specimens (Wilson et al., 1994). A more practical figure promoted by theory and model species to reduce inbreeding is 1 migrant every 1–2 generations (Allendorf, 1983; Lacy, 1987; Lande and Barrowclough, 1987; Backus et al., 1995). This figure has been suggested because it allows limited gene flow but does not disrupt genetic distinctiveness among population fragments (Allendorf, 1983). Another benefit associated with minimal animal transport is that the direct costs associated with shipping animals among zoological centers will be held to a minimum increasing the likelihood that such transportation, if needed, might take place.

In the literature, population fragmentation takes two forms: fragmentation of captive breeding populations, which we simply refer to as fragmentation, and fragmentation of captive bred populations from wild populations with limited gene flow, which we refer to as immigration but is also known as supplementation when offspring reared under controlled settings are released back into the wild. In the case of fragmentation, the migrants are passing between several small populations. In the case of immigration, the movement is one-way, from the wild into captivity.

4.1. Fragmentation

Genetic diversity can be reduced at the population level and maintained at the species level through fragmentation. In a model by Lacy (1987), completely isolated subpopulations maintained higher total genetic diversity, measured over 100 generations within and between subdivided populations, over a single, panmictic population. Similarly, Margan et al. (1998) demonstrated that small, isolated populations of *D. melanogaster* had higher relative fitness after being pooled together than single, large populations of equal numbers. In addition, crossbreeding between regional strains of domestically bred rhesus monkeys (*Macaca mulatta*) resulted in higher values of fitness related traits (Smith and Scott, 1989). This suggests that a strategy of maintaining isolated, subpopulations and then pooling them immediately before reintroduction is a better method than maintaining a single large population (Margan et al., 1998).

Evidence for fragmentation of populations of captive bred organisms for the purpose of minimizing genetic adaptation to captivity is somewhat scarce. We only identified seven studies showing fragmentation as a strategy for maintaining diversity of captive bred populations (Table 5). These studies are epitomized by the Lake Victoria cichlid *Haplochromis* (*Prognathochromis*) *perrieri* which has been carefully managed during its five generations in captivity (Fiumera et al., 2000). The founding population was subdivided into several subpopulations each experiencing an overall decrease in genetic diversity. However, the combined heterozygosity of the subpopulations was not significantly different from the founding population (Fiumera et al., 2000).

4.2. Immigration

Immigration of wild animals into captive bred populations has been shown to play an important role in minimizing maladaptation associated with captivity (Frankham and Loebel, 1992). However, immigration possesses an interesting situation with regards to minimizing adaptation to the captive environment. While closely linked to fragmentation, the effect of immigration does not have a direct parameter linked with Eq. (1). The direct effect of immigration on population genetic differentiation is described in Eq. (3). The greater the immigration rate of wild individuals into a captive bred population, the slower the rate of genetic adaptation to that captive environment (Haldane, 1930; Frankham et al., 2002). In modeling the effect of immigration on supplementation programs, Ford (2002) used a single trait model to show that captive and wild populations have optimal values that may be different from each other. Although a captive population with immigration from the wild did have reduced fitness upon reintroduction, the loss of fitness was much greater when there was no gene flow at all (Ford, 2002).

Due to the number of restrictions placed on the importation of endangered species, this recommendation may be most practical for animals that are used mainly for commercial purposes such as fish that are bred in hatcheries (Frankham, 2008). Research on these fishes often incorporates fish hatcheries and their utility as a conservation tool. Traditional hatcheries tend to focus on increasing abundance of species for harvest, yet issues such as long-term sustainability and genetic health are sometimes overlooked. Conservation hatcheries strive to combine commercial and conservation practices by attempting to reduce genetic effects by supplementing broodstock with local wild fish, rearing the offspring in captivity and allowing the smolt to return to the wild (Reisenbichler and Rubin, 1999; Heggenes et al., 2006; Araki et al., 2007a). Fraser (2008) offers a comprehensive review of salmonid breeding programs including 20 laboratory studies and 15 field studies that found fitness or genetic changes between hatchery- and wild-born fish.

How important is supplementation? After one year in a conservation hatchery, Steelhead trout (*Oncorhynchus mykiss*) had similar relative fitness as individuals from a wild population, while the relative fitness of those in a traditional hatchery was significantly lower (Araki et al., 2007a). In a declining population, a conservation hatchery could increase the population for the short-term. However, there is also the possibility of a negative interaction since reproductive success of crosses between conservation hatchery individuals was less than expected (Araki et al., 2007a). This reduction in fitness after multiple crosses can occur in a matter of only a few generations (Araki et al., 2007b). Even a Chinook salmon (*O. tshawytscha*) supplementation hatchery program that used only natural-origin broodstock in an attempt to minimize adaptation resulted in a decrease in body size and shifts in the timing of maturation (Knudsen et al., 2006). Unfortunately, the authors were unable to definitively distinguish genetic and environmental effects.

One problem associated with immigration into captive bred populations is that immigration from rare wild populations takes individuals away from a population that is already in danger of extinction. Import or export of many endangered species is extremely restricted by international agreement [Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)]. A recent compilation of studbooks of rare captive species showed that only 4 out of 148 species had individuals imported from the wild between 2005 and 2006 (Fisken, 2007, 2008). Most immigration usually occurs early in captive programs with importations slowly dwindling with time (Marker and O'Brien, 1989; Marker-Kraus and Grisham, 1993). Unfortunately, immigration is more efficient at slowing selection when a larger number of mi-

Table 5
Fragmentation and isolation of populations.

Class	Order	Species	References
Actinopterygii	Perciformes	*Haplochromis* (*Prognathochromis*) *perrieri*	Fiumera et al. (2000)
Aves	Ciconiiformes	*Gymnogyps californianus*	Ralls and Ballou (2004)
Mammalia	Artiodactyla	*Oryx leucoryx*	Price (1989)
	Carnivora	*Canis lupus baileyi*	Hedrick and Fredrickson (2008)
		Lycaon pictus	Frantzen et al. (2001)
		Tremarctos ornatus	Rodriguez-Clark and Sanchez-Mercado (2006)
	Primates	*Microcebus murinus*	Neveu et al. (1998)

grants enter the new population after a greater number of generations have passed (Frankham and Loebel, 1992).

With regards to fragmentation and immigration, we draw two main conclusions. First, studies investigating the long-term effects of fragmenting populations indicate that fragmentation should be employed when possible in captivity (Lacy, 1987; Margan et al., 1998). The advantages of maintaining separate (even if genetically depauperate) populations outweigh the costs associated with the maintenance of a single captive population. Complete isolation of subpopulations results in both short- and long-term non-genetic benefits (such as protection from disease or catastrophic events) and long-term genetic advantages [such as retention of among-fragment diversity results in the retention of species-wide genetic diversity (Fernandez et al,, 2008)]. These benefits occur at the cost of short-term detrimental effects (such as severe inbreeding depression). However, a small amount of gene flow between populations (approximately 1 migrant every 1–2 generations) would be sufficient to minimize inbreeding (Allendorf, 1983; Lacy, 1987; Lande and Barrowclough, 1987; Backus et al., 1995). Fernandez and colleagues (2008) recently developed a "dynamic management method" incorporating pedigree, fragment sizes and migration rates to increase overall species genetic diversity while subpopulation diversity is reduced. Further work with this and other types of modeling strategies may help determine if fragmentation is the best choice for a population as well as to obtain optimal fragment sizes and migration rates.

Second, immigration from the wild is recommended if the size of the natural population will allow for supplementation on a regular basis. While initial studies suggest a large benefit of supplementation there are surprisingly few studies outside of salmonids that have investigated the role that immigration may play in captive bred populations. In a study of laboratory bred deer mice (*Peromyscus maniculatus*), Schwartz and Mills (2005) compared the survival of inbred, out crossed and randomly bred lines with the out crossed line resulting in the highest survival estimates. The authors argue that the one migrant per generation minimum will also hold true for immigration from the wild but must be consistent for a large number of generations to be effective to reduce inbreeding. In contrast, Lynch and O'Hely (2001) argue that supplementation programs are useful only in the short-term to increase the size of the natural population. Programs in which half of the breeders are wild-born versus all of the breeders are wild-born have similar declines in wild fitness. This is because the large amount of relaxation of selection causes a supplementation load on the population. Certainly, the controversy associated with the costs and benefits of fragmentation and even the role of immigration with regard to adaptation in the captive environment highlight the need to further investigate these measures if they are to have a further role in conservation programs.

5. Conclusions

In this review we addressed the fundamental question of how to best maintain captive bred populations in order to increase their chances of survival upon reintroduction by minimizing genetic adaptation to captivity. In order to minimize genetic adaptation, we first recommend reducing the number of generations that a species spends in captivity. The term t in Eq. (1) has an exponential effect and, therefore, the greatest effect on GA_t. Returning species to the wild in as few generations as possible would be optimal; however, this often is not possible. In fact, for some species reintroduction may not be an option owing to the state of their natural environment. In this case, goals of keeping a species in zoos for perpetuity rather than future reintroduction may alter management strategies. What if a species must be maintained in captivity for an extended period of time before reintroduction to the natural environment? Is it still possible for genetic adaptation to the captive environment to be minimized? In such a scenario, we make the following recommendations. We suggest attempting to minimize generations first by delaying reproduction and then by cryopreservation of germplasm. While neither delaying reproduction nor cryopreservation is as effective as directly reducing t, delaying reproduction is the more practical in regards to time and effort. Presently, cryopreservation is more costly and time-consuming as unique protocols must be developed for each species. We suggest delaying reproduction using contraception rather than behavioral or physical barriers. However, the biology of the species plays an important role in whether delaying reproduction through contraception is a safe option at this time. Furthermore, when a founding population is large, we recommend that the population be fragmented in captivity even at the risk of loss of genetic diversity within subpopulations. This is because studies have shown that within species diversity is maintained in the face of loss of diversity within subpopulations. The crossing of individuals from different populations during reintroduction will then increase species genetic diversity. If there is a risk of inbreeding within subpopulations, we advise the immigration of individuals from the wild at a rate of 1 migrant per 1–2 generations to decrease inbreeding as well as minimize adaptation to captivity. However, this recommendation is based on the ability to remove individuals from the wild without further harming the wild population. We do not recommend the immigration of individuals from highly endangered wild populations as this may cause further detriment to the remaining wildlife. A small amount of migration between subpopulations, preferably no more than 1 migrant per 1–2 generations can act to minimize inbreeding when wild individuals can not be used. Moreover, recent computer modeling can help determine the fragment sizes and the optimal number of migrants which should be moved between fragments. Even if there is no anticipated reintroduction, it is practical to maintain multiple populations to insure against extinction in case of catastrophe and disease. Finally, for smaller species, we suggest a strategy to minimize selection by creating an artificial, yet ideal, environment with natural elements such as natural light cycles and temperature regimes but without predators or drought that might be experienced in the natural habitat. For larger animals, creating and maintaining this ideal habitat is much more restrictive with regards to space and funding. Any creation of a natural environment for larger animals is largely practical for the welfare of the animals and the enjoyment of the zoo visitors and less so for minimizing adaptation to the captive environment. In contrast to the above recommendations, we do not see a role of breeding strategies in reducing genetic adaptation to captivity. While both EFS and MK play important roles in maintaining the evolutionary potential of managed populations, there is little direct evidence to demonstrate that breeding strategies increase fitness upon reintroduction. Again, this is not to say that minimizing coancestry through EFS and MK are not worthwhile for conservation purposes; simply, we did not find any evidence of the ability of either breeding strategy to minimize adaptation to the captivity.

Another conclusion that can be drawn from this review is that future research on the benefits of these conservation strategies needs to be continued. There is still too little information available to know the extent that all of these strategies can be completely effective. For example, investigations in cryopreservation should continue since delaying reproduction has been demonstrated to be deleterious in some species and overall, little is known about oocyte preservation. Moreover, unique preservation techniques need to be optimized for species groups. In addition, the costs and benefits of some strategies should be examined in greater detail. For example, our conclusions with regards to breeding strategies are that MK does not appear to confer added fitness benefits during reintroduction and EFS does so only in a simulation. However, other benefits (e.g. increasing N_e or increasing genetic diversity) may make these strategies worthwhile, despite their expense. Furthermore, the effects of delaying reproduction, or other species-specific management problems, are often known only to species managers working with the species or by being passed along through management plans (Tamara Bettinger, AZA SSP Species Coordinator, personal communication). It is important that more information concerning species management continues to be published in peer-reviewed literature. Finally, all of the studies we reviewed here involved strategies that were analyzed independently; perhaps an interactive effect among strategies will lead to an improved outcome in future captive breeding programs.

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