The Journal of Wildlife Management 77(2):346–351; 2013; DOI: 10.1002/jwmg.492

Population Ecology

Factors Influencing Reproductive Success and Litter Size in Captive Island Foxes

ELIZABETH S. CALKINS,[1] *Department of Environmental Conservation, 160 Holdsworth Way, University of Massachusetts, Amherst, MA 01003, USA*

TODD K. FULLER, *Department of Environmental Conservation, 160 Holdsworth Way, University of Massachusetts, Amherst, MA 01003, USA*

CHERYL S. ASA, *Research Department, Saint Louis Zoo, St. Louis, MO 63110, USA*

PAUL R. SIEVERT, *U.S. Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts, Amherst, MA 01003, USA*

TIMOTHY J. COONAN, *National Park Service, Channel Islands National Park, Ventura, CA 93001, USA*

ABSTRACT A severe decline of island foxes (*Urocyon littoralis*) on the northern Channel Islands in the 1990s prompted the National Park Service to begin a captive breeding program to increase their numbers. Using detailed records of all the fox pairs ($N = 267$) that were part of the program on San Miguel, Santa Rosa, and Santa Cruz Islands from its inception in 2000 through 2007, we identified factors influencing the breeding success of pairs in captivity in the interest of formulating strategies that could increase captive productivity. We compiled a database of variables including litter size, reproductive success, distance to nearest occupied pen during the breeding season, subspecies, exposure, female age, male age, age difference, female and male origin (wild vs. captive born), same versus different origin, years paired, previous reproductive success by the pair, previous reproductive success by the female, mate aggression-related injuries, male previous involvement in a pair with mate aggression, and female previous involvement in a pair with mate aggression. We used multiple linear regression to identify factors predictive of litter size, and logistic regression to predict the probability of reproductive success. A larger inter-pen distance, older male age, less exposure, and a smaller intra-pair age difference positively affected litter size. The probabilities of reproductive success increased with fewer years paired and less exposure. Comparatively, pairs with wild born females (vs. captive born females), and previously successful pairs (vs. previously unsuccessful and new pairs) were most likely to be successful. These results indicate that the optimal situation was to pair wild-caught females with older males in sheltered pens that were as far from other pens as possible, to maintain successful pairs and repair unsuccessful ones.

KEY WORDS behavior, canid, captive breeding, island fox, reproduction, *Urocyon littoralis*.

The island fox (*Urocyon littoralis*), found solely on the Channel Islands off the coast of southern California, is the largest native terrestrial predator on the islands, and a different subspecies of the island fox inhabits each of the 6 largest Channel Islands (Coonan et al. 2010*a*). The 4 subspecies on San Miguel (*U. l. littoralis*), Santa Rosa (*U. l. santarosae*), Santa Cruz (*U. l. santacruzae*), and Santa Catalina (*U. l. catalinae*) Islands underwent dramatic population declines (up to 95%) from 1995 to 2000, likely due to high levels of predation by historically absent golden eagles (*Aquila chrysaetos*; Roemer et al. 2001, Coonan et al. 2005*a*). For example, in 1994 the Santa Rosa population numbered around 1,500 but declined to 14 animals by 2000 (Coonan and Rutz 2001). As a result of these declines, the United States Fish and Wildlife Service recommended listing these 4 subspecies under the Endangered Species Act (U.S. Fish and Wildlife Service 2004).

Received: 20 June 2011; Accepted: 19 June 2012
Published: 12 January 2013

[1]*E-mail: escalkins@gmail.com*

Because of the precipitous declines in fox numbers, the National Park Service began emergency recovery actions in 1999. This included relocating the golden eagles that were known to be breeding on Santa Cruz and Santa Rosa, eradicating the nonnative feral pigs (*Sus scrofa*) on Santa Cruz that had been providing a prey base for the golden eagles, and restoring bald eagles (*Haliaeetus leucocephalus*), which were thought to have kept golden eagles from inhabiting the islands in the past (Roemer et al. 2001). After construction of captive breeding facilities on each island, all remaining wild foxes on San Miguel and Santa Rosa Islands and a portion of the wild foxes on Santa Cruz Island were captured and brought into captivity for safe keeping while the threats to their survival were being mitigated.

Captive breeding programs for other North American canids have been very successful. Both red (*Canis rufus*) and Mexican gray wolves (*C. lupus baileyi*) were believed extinct in the wild, but a few pairs remaining in zoos became the founders of managed breeding programs that provided animals for reintroductions. However, the 39.5% reproductive rate of the captive foxes in the first few years was less than expected (Coonan et al. 2004; also see Clifford et al. 2007) and was surprising since most canids seem to breed well in captivity. For example, sexually mature captive-born individual gray wolves observed by Mech (1999) always bred when paired in captivity. Even more critical for island foxes was that some of the potential genetic founders consistently failed to reproduce (Coonan et al. 2010*a*).

Information on reproduction and captive breeding is available for larger canids such as gray wolves, red wolves, and coyotes (*Canis latrans*), but considerably less is known for the smaller species (Asa and Valdespino 2003). Closely related mainland gray foxes (*U. cinereoargenteus*) are much more common than island foxes, yet surprisingly little is known about their reproduction beyond life-history information on age of puberty, breeding seasonality, and litter size (Fuller and Cypher 2004). Thus, reasons for low reproductive rates in the captive island foxes were not apparent.

One factor that may have affected reproduction was intra-pair aggression. Through both our preliminary investigations and observations by caretakers, fox pairs seemed to exhibit unusually high levels of aggression, sometimes requiring a fox to be removed for veterinary treatment (Coonan et al. 2005*b*). Serious aggression even occurred in pairs that appeared to be compatible during initial observations, when they spent most of the time resting in contact with each other (E. S. Calkins, University of Massachusetts, personal observation).

Additional variables that may have affected reproductive success were previous experience or success, age or age difference within pairs, and origin of foxes (wild-born vs. captive-born). Coonan et al. (2005*b*) reported that island fox reproductive success in the wild on San Miguel increased with age class. Data indicated that reproductive rates were greater for wild-caught than for captive-born foxes, but those results were confounded by age, since all wild-caught foxes were older than those born in captivity. The objective of this project was to use the data from every fox pair that was part of the captive breeding program on San Miguel, Santa Rosa, and Santa Cruz Islands since its inception in 2000 through 2007 to analyze life-history factors influencing reproductive success and, more specifically, to determine whether failure to breed might be related to intra-pair aggression. Such aggression could influence every stage of reproduction, such as failure to enter estrus, mate, ovulate, conceive, maintain pregnancy, or successfully give birth. In addition, we investigated whether pen site characteristics, pair background and reproductive history, and mate aggression had an effect on litter size and reproductive success. We hypothesized that if increased aggression was deleterious to reproduction, pairs in pens that were farther apart should be more productive, as well. Also, the likelihood of reproducing should decrease among older females, and for pairs with disparate ages and shorter pair histories.

STUDY AREA

We conducted research at the captive breeding facilities on San Miguel, Santa Rosa, and Santa Cruz Islands located off the coast of southern California, the 3 northernmost islands of the 5 that make up Channel Islands National Park (34°N, 120°W). Each island was home to 2 separate (>500 m apart) facilities to minimize the danger of a catastrophic event damaging or destroying both.

San Miguel Island is a small (38.5 km^2), windswept, treeless island dominated by grasslands intermixed in some areas with coyote brush (*Baccharis pilularis*) and giant coreopsis (*Coreopsis gigantea*). San Miguel Island pens were in the brushy Willow Canyon site, which was relatively sheltered from wind on the south side of the island and the Brooks site, which had pens positioned along a ridge top surrounded by very little vegetation and was subject to very high winds on the north side. Willow Canyon pens mostly varied between 1.5 m and 2 m apart with 1 pen that was 14 m from the next nearest pen. The Brooks pens by contrast were between 6 m and 56 m apart.

Santa Rosa Island is a predominantly low-lying island bisected by a high central mountain range, the majority of which is covered by grasslands. Pens on Santa Rosa Island were in the relatively windy Caballo Del Muerto site on a slope face and the sheltered Windmill Canyon site in the bottom of a valley. Pens in the Caballo Del Muerto site were spaced between 20 m and 35 m with 1 pen isolated 100 m away, whereas the Windmill Canyon pens ranged between 4 m and 14 m apart. Santa Rosa Island is the second largest island off the coast of California (214.5 km^2), second in size only to Santa Cruz Island (249 km^2).

Santa Cruz Island is characterized by 2 mountain ranges and a large central valley. The Central Valley breeding site on Santa Cruz was situated on the slope face of the valley where the pens were relatively sheltered from wind, whereas the Navy site was positioned along a ridge top subject to much greater wind exposure. The pens were spaced between 25 m and 257 m apart at the Navy site and were spaced between 5 m and 19 m in the Central Valley (Coonan et al. 2004).

METHODS

All pens were constructed of 2-m × 3-m chain-link panel walls, 3-m × 3-m chain-link panel ceilings of 3.12-cm mesh with a skirt buried about 1 m underground, and a natural dirt floor. All pens were between 45 m^2 and 60 m^2 in size, and had a variety of shelters including at least 2 den boxes, climbing structures, and perches.

We collected detailed records of all the fox pairs that were part of the captive breeding program on San Miguel, Santa Rosa, and Santa Cruz Islands since its inception in 2000 ($N = 267$ pairs). We treated every pairing in every year as a separate observation unit, each with a separate set of characteristics.

We recorded the following parameters: litter size, reproductive success, distance to nearest occupied pen during the breeding season, subspecies, exposure, female age, male age, age difference for the pair, female origin (wild vs. captive born), male origin, same versus different origin for the pair, years paired, previous reproductive success by the pair, previous reproductive success by the female, mate aggression related injuries, male previous involvement in a pair with mate aggression, and female previous involvement in a pair with mate aggression.

We calculated inter-pen distances using a combination of pen maps and aerial photos, and recorded the distance to the closest pen that was occupied in that breeding season. We then grouped the distances into the following ranges: 0–2.9 m, 3–5.9 m, 6–8.9 m, 9–11.9 m, 12–14.9 m, 15–17.9 m, 18–20.9 m, 21–23.9 m, 24–26.9 m, 27–29.9 m, and >30 m. We rated pen site exposure on a scale from 0 (least exposed, such as a valley) to 1 (most exposed, such as a ridge top). We recognize that a relationship between inter-pen distance and reproductive success would not likely follow a linear trend, but space between pens could not be maximized because each grouping of pens had to be fenced to keep wild foxes from interacting with captive foxes.

We recorded male and female age as the age they would be at the end of the current breeding season (so this is also a record of possible breeding seasons). For example, a fox born in April 2004 would be recorded as 1-year-old during the 2005 breeding season. We calculated years paired starting with 1 indicating their first year paired. We considered litter size to be the number of offspring raised to 3 weeks of age, and reproductive success to be that the pair raised 1 or more pups to 3 weeks of age. Pair previous success was a measure of the previous success of that specific pairing of foxes. We entered 3 possibilities for pair previous success as 0 (they were not previously paired and therefore did not have the opportunity), 1 (they were reproductively unsuccessful previously), and 2 (they were successful previously). We used this same method for female previous success, recording her history regardless of mate. We examined a comprehensive collection of the handling records for all foxes to obtain a record of mate aggression related injuries. Injuries were discovered either during veterinary exams or during routine feeding and pen cleaning. We judged an injury to be a result of mate aggression if it could not have been self-inflicted, such as a bite wound to the ears, back, neck, nose, and head.

We used multiple linear regression analysis (Systat 12; Systat Software Inc., Chicago, IL) to identify factors predictive of litter size and selected the best model based on Akaike's Information Criterion (AIC; Akaike 1981, Gelfand and Dey 1994). In the best model, one that had an AIC value 2 points less than the next best competing model, we considered predictors to be either statistically significant where $P < 0.05$, or indicative of possible trends where $P < 0.10$. We evaluated the entire population of captive fox breeding attempts, not a sample, with an aim of informing potential future captive breeding efforts.

Because reproductive success is a binary variable (success equaling 1 and failure equaling 0), we used a binary logit (logistic regression; Hosmer and Lemeshow 2000) to predict the probability of success by inputting the following categorical and continuous predictor variables: distance to the nearest occupied pen, subspecies, exposure, female age, male age, age difference, female origin, male origin, same or different origin, years paired, pair previous success, female previous success, mate aggression injuries, female and male previous involvement in a pair with mate aggression. Because we were interested in the potential role of all predictors, we examined a full model and report those predictors that were statistically significant ($P < 0.05$). We also examined the odds ratios, the ratio of the probability of success to the probability of failure, as these are more readily interpreted (Brant 1996).

RESULTS

In 10 years of captive breeding, 226 pups were produced in captivity on San Miguel, Santa Rosa, and Santa Cruz Islands, and 254 foxes were released. High reproduction and survival in reintroduced populations allowed captive breeding to cease by 2008 (Coonan et al. 2010*a*). Eight of 15 potential San Miguel founders bred in captivity, as did 13 of 15 potential Santa Rosa founders. This met our goal of sampling >95% of the source population heterozygosity. By the end of captive breeding, both subspecies were estimated to have retained >90% of founder gene diversity (Coonan et al. 2010*b*).

In assessing factors predictive of captive fox litter size, a multiple linear regression model containing the variables distance to the nearest occupied pen, exposure, male age, and age difference provided the best fit (Table 1), as judged by an AIC value that was 2 points less than the next best model. Based on the partial regression coefficients from the final model, litter size was predicted to increase by 0.66 for every additional 3 m of distance to the nearest occupied pen, and by 0.148 for every additional year in the male's age (Table 1; Fig. 1). Litter size was predicted to decrease by 0.065 for every additional year in the pair's age difference (Table 1; Fig. 2), and by 0.561 for every incremental increase in exposure. The correlation between litter size and age difference was weaker in pairs where the male was of the same age or older than the female compared to pairs where the female was as old or older than the male ($P < 0.001$).

To assess the significance of predictor variables related to reproductive success, we used a logistic regression approach, and report the significant predictors from a full model (Table 2). Based on odds ratio tests, success was 50% less

Table 1. Parameter estimates for pair parameters in the model receiving the most support from a multiple linear regression analysis of litter size for 267 pairings of captive Channel Island foxes monitored during 2001–2007.

Effect	Coefficient	SE	Standard coefficient	Tolerance	*t*	*P*-value
Constant (intercept)	−2.811	1.829	0.000		−1.536	0.126
Distance to nearest occupied pen	0.660	0.279	0.217	0.386	2.364	0.019
Exposure	−0.561	0.268	−0.220	0.291	−2.090	0.038
Male age	0.148	0.046	0.265	0.481	3.224	0.001
Age difference	−0.065	0.038	−0.102	0.936	−1.739	0.083

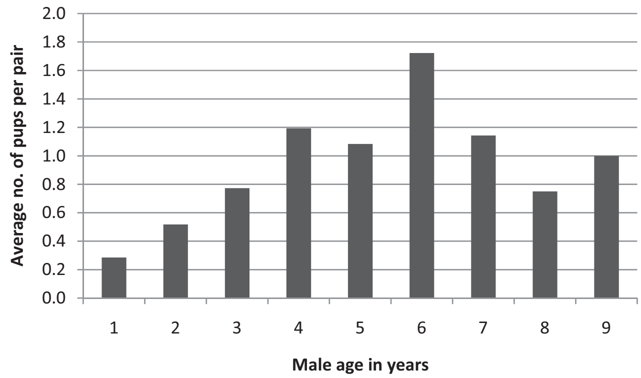

Figure 1. Average litter size as a function of male fox age for 267 pairings of captive Channel Island foxes monitored during 2001–2007.

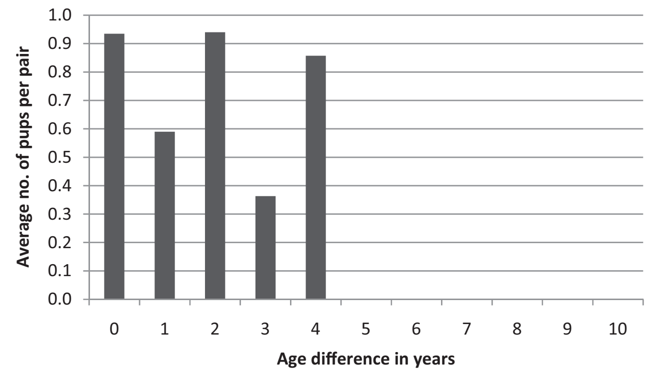

Figure 2. Average litter size as a function of intra-pair age difference for 267 pairings of captive Channel Island foxes monitored during 2001–2007.

likely (odds ratio = 0.503, 95% CI = 0.27–0.93) for every additional year a pair was together and 9.5 times more likely (odds ratio = 9.523, 95% CI = 0.01–0.606) for each incremental decrease in exposure.

Pairs involving females from a wild-born background were 12.1 times more likely (odds ratio = 12.124, 95% CI = 3.1–47.6) to reproduce successfully than those with a captive-born female ($P < 0.001$). In the captive population, 74 of 144 pairs with wild-born females were successful (51.3%), whereas only 18 of 123 pairs with captive-born females were successful (14.6%). Pairs that were previously successful as a unit, however, were 111 times more likely than new pairs (odds ratio = 0.009, 95% CI = 0.001–0.109, $P < 0.001$), and 100 times more likely than previously unsuccessful pairs (odds ratio = 0.010, 95% CI = 0.001–0.127, $P < 0.001$) to reproduce successfully (Table 2).

Although reproductive rates between the islands differed, we did not find that subspecies had an effect on reproductive success. Also, the model did not support that presence of, or previous involvement in, mate aggression was correlated with reproductive success.

DISCUSSION

We included in the analyses as many variables as we could, given the limitations of the data set, but include speculation here to provide additional potential considerations for future breeding efforts. Our results identified factors associated with reproductive success that included environmental variables, such as pen exposure, as well as attributes of the individual animals, such as breeding experience and whether they were wild-caught or captive-born. Some of the factors identified are similar to those reported to affect reproductive performance in other canid species (e.g., age and previous success; Macdonald 1980, Green et al. 2002, Lockyear et al. 2009), but some were unexpected (e.g., greater reproductive rates in wild-caught foxes).

A greater distance to the nearest occupied pen during the breeding season was associated with an increase in the number of pups per litter that survived to at least 3 weeks. In the live observations on San Miguel Island, several foxes were observed pacing the wall of their pen closest to another pair, appearing to respond to and monitor neighboring pairs. Such constant proximity could lead to chronic stress, which may have affected reproduction (Rivier and Rivest 1991, Pottinger 1999, Creel 2005). However, analysis of fecal glucocorticoid levels, as a measure of stress, in foxes on Santa Rosa and Santa Cruz islands revealed no association between stress and reproduction (Asa 2010).

Increased exposure to wind was associated with decreased probability of a pair reproducing and decreased number of pups produced per pair. The environmental parameters related to successful reproduction suggest that relative seclusion from other foxes and protection from exposure to wind may be influential components of den site selection. When pairs were forced, through pen assignment, to den in a less ideal area with greater environmental stressors reproductive success suffered.

Offspring per litter increased with male age. A study on mice found litter size to be highly dependent on the individual male but not affected by male age (Finn 1964), and an increase in mating success between young and intermediate-aged males was found in coyotes (Windberg 1995,

Table 2. Significant predictors of reproductive success of captive Channel Island foxes based on 267 pairings that occurred from 2001 to 2007, and analyzed using a logistic regression model.

Parameter	Estimate	SE	Z	P-value	95% CI Lower	95% CI Upper
Constant (intercept)	10.624	12.018	0.884	0.377	−12.932	34.180
Exposure	−2.257	0.896	−2.520	0.012	−4.012	−0.501
Wild-caught (vs. captive-born) female	2.495	0.698	3.574	0.000	1.127	3.863
Years paired	−0.687	0.314	−2.192	0.028	−1.302	−0.073
New pair	−4.674	1.253	−3.729	0.000	−7.130	−2.217
Previously unsuccessful pair	−4.622	1.307	−3.536	0.000	−7.183	−2.060

Dummond and Villard 2000, Sacks 2005). Sacks (2005) suggested that this could be because only a portion of the first year age class of coyotes reached the level of physical maturity necessary for reproduction. Because no males beyond age 9 occurred in the captive island fox population, our results show that litter size increased between first year and middle-aged males.

Of the pairs with age differences larger than 5 years, only 1 pair involved an older male paired with a younger female. The other 13 were females aged 7–13 paired with males aged 1–5 years, which encompasses the entire female population aged 10 and above, but none of these pairs was successful. The negative correlation between litter size and age difference was weaker when it only included the 150 pairs with a male fox whose age was equal to or greater than that of the female compared with that for the entire population and pairs in which the female's age was equal to or greater than that of the male. This suggests that the greater impediment to breeding occurred when older females were paired with younger males.

An unexpected finding was that the longer a pair was kept together, the less likely they were to be reproductively successful. One possible explanation could be reduction in fecundity with advancing female age; females were older each subsequent breeding attempt. Although we did not identify any age effect, other studies found a decline in productivity among female coyotes starting at ages 6 (Crabtree 1988), 8 (Green et al. 2002), and 10 (Windberg 1995). Alternatively, the likelihood of reproduction in newly assigned pairs may reflect the strategy for pair assignments. Unsuccessful females, who may have failed to reproduce because of inherently lower fertility, were more likely to be assigned a new mate and to be unsuccessful with that male, as well.

Wild-caught females were far more likely to reproduce successfully even though their average age was 5.2 years compared to captive-born females whose average age was 2.3 years. A possible explanation may be the differing methods of pair assignment. Wild-caught females were paired with males captured nearby, suggesting they might have been paired in the wild; these may have been the males they chose. In contrast, captive-born females were assigned partners based on their genetic relationships to avoid inbreeding and maximize heterozygosity of the captive population (Lacy 1994, Ballou et al. 2010). Mate choice is a critical variable in the reproductive success of a broad range of species (Clutton-Brock and Mcauliffe 2009), and the lack of opportunity for mate choice among the captive-born females may have compromised their success. That the predictor variable, wild-caught or captive-born, was only supported for females provides further support for a role of mate choice, since most of the evidence for the influence of choice in other species has been for females (Clutton-Brock and Mcauliffe 2009).

Another factor that may have influenced the disparity between the wild- and captive-born foxes is that the captive-born females were all young when first paired, typically when less than 1-year-old, whereas females captured in the wild were of differing ages. As was shown for this population of captive island foxes, reproductive rates were especially low (10–15%) in young captive-born females (Coonan et al. 2010*a*). In contrast, young wild-caught females reproduced at greater rates (above 50%), which is further evidence of the influence of birthplace. However, which factors associated with growing up in captivity versus the wild influence reproductive success are not known.

Our findings provide insight into the factors affecting reproductive success in this species in captivity, and indicate that the optimal situation was to pair young wild-caught females with older males in sheltered pens that are as far from other pens as possible, while maintaining successful pairs and repairing unsuccessful pairs. Though not all of the results are intuitively or logically obvious, this may result from either the continual efforts to improve reproductive performance during the captive breeding experience, or the inherently variable and complicated mating behavior of island foxes, or both. Fortunately, the captive breeding effort overall resulted in the opportunity to successfully recover each of the subspecies in the wild (Coonan et al. 2010*a*), and one hopes that the future management of the species in the wild will preclude the need for another such captive effort.

MANAGEMENT IMPLICATIONS

The island fox captive breeding program implemented from 1999 to 2008 was born of necessity; populations on San Miguel and Santa Rosa Islands had each declined to 15 individuals by 1999–2000 and the prospects for a natural recovery were slim to none. Because island foxes had not been bred in captivity before, and were not held in mainland zoos, the captive breeding program could not take advantage of previous husbandry work for the species. Our research has filled that gap, as we have identified the individual combinations and environmental conditions associated with island fox reproductive success in captivity. Though the captive breeding program shut its doors in 2008, this information will be valuable in the future, both for island foxes that will always have limited distribution, small population sizes, vulnerability to disease, and thus a good chance of requiring captive breeding again, and for other canid species whose captive breeding is minimally known and thus will be in need of useful insights in the event of their sudden demise and urgent need for conservation action.

ACKNOWLEDGMENTS

The project was supported by the Saint Louis Zoo and a grant from the United States Geological Survey managed by M. Sovada. We thank K. Bauman, for field video equipment installation, troubleshooting from afar, and organization of the endless video review; our island interns P. Charoenpunthong, E. Posthumous, S. Roenfeldt, P. Valcarcel, and J. Carrero for able assistance; and National Park Service fox care technicians, specifically A. Guglielmino, L. Drake, T. Smith, E. Scott, and D. Watson. The use of trade names or products does not constitute endorsement by the U.S. Government.

LITERATURE CITED

Akaike, H. 1981. Likelihood of a model and information criteria. Journal of Econometrics 16:3–14.

Asa, C. S. 2010. Reproductive biology. Pages 115–128 *in* T. J. Coonan, C. A. Schwemm, and D. K. Garcelon, editors. Decline and recovery of the island fox: a case study for population recovery. Cambridge University Press, Cambridge, United Kingdom.

Asa, C. S., and C. Valdespino. 2003. A review of small canid reproduction. Pages 117–123 *in* M. A. Sovada, and L. Carbyn, editors. The swift fox: ecology and conservation of swift foxes in a changing world. Canadian Plains Research Center, Regina, Saskatchewan, Canada.

Ballou, J. D., C. Lees, L. J. Faust, S. Long, C. Lynch, L. Bingaman Lackey, and T. J. Foose. 2010. Demographic and genetic management of captive populations. Pages 219–252 *in* D. Kleiman, K. V. Thompson, and C. K. Baer, editors. Wild mammals in captivity: principles and techniques for zoo management. University of Chicago Press, Chicago, Illinois, USA.

Brant, R. 1996. Digesting logistic regression results. American Statistician 50:117–119.

Clifford, D. L., R. Woodroffe, D. K. Garcelon, S. F. Timm, and J. A. K. Mazet. 2007. Using preganancy rates and perinatal mortality to evaluate the success of recovery strategies for endangered island foxes. Animal Conservation 10:442–451.

Clutton-Brock, T., and K. Mcauliffe. 2009. Female mate choice in mammals. Quarterly Review of Biology 84:3–27.

Coonan, T. J., K. M. McCurdy, K. A. Rutz, M. Dennis, S. Provinsky, and S. Coppelli. 2005*b*. Island fox recovery program 2004 annual report. Technical Report 05-07. National Park Service, Ventura, California, USA.

Coonan, T. J., and K. Rutz. 2001. Island fox captive breeding program, 1990–2000 annual report. National Park Service, Ventura, California, USA.

Coonan, T. J., K. A. Rutz, K. McCurdy, D. K. Garcelon, B. C. Latta, and L. Munson. 2004. Island fox recovery program, 2003 annual report. Technical Report 04-02. National Park Service, Ventura, CA, USA.

Coonan, T. J., C. A. Schwemm, and D. K. Garcelon. 2010*a*. Decline and recovery of the Island fox: a case study for population recovery. Cambridge University Press, Cambridge, United Kingdom.

Coonan, T. J., C. A. Schwemm, G. W. Roemer, D. K. Garcelon, and L. Munson. 2005*a*. Decline of an island fox subspecies to near extinction. Southwestern Naturalist 50:32–41.

Coonan, T. J., A. Varsik, C. Lynch, and C. A. Schwemm. 2010*b*. Cooperative conservation: zoos and in situ captive breeding for endangered Island fox *Urocyon littoralis* ssp. International Zoo Yearbook 44:165–172.

Crabtree, R. 1988. Sociodemography of an unexploited coyote population. Dissertation, University of Idaho, Moscow, USA.

Creel, S. 2005. Dominance, aggression, and glucocorticoid levels in social carnivores. Journal of Mammalogy 86:255–264.

Dummond, M., and M. A. Villard. 2000. Demography and body condition of coyotes (*Canis latrans*) in eastern New Brunswick. Canadian Journal of Zoology 78:399–406.

Finn, C. A. 1964. Influence of the male on litter size in mice. Journal of Reproduction and Fertility 7:107–111.

Fuller, T. K., and B. Cypher. 2004. Gray fox (*Urocyon c inereoargenteus*). Pages 92–97 *in* C. Sillero-Zubiri, M. Hoffmann, and D. W. Macdonald, editors. Canids: foxes, wolves, jackals, and dogs—status survey and conservation action plan. IUCN/SSP Canid Specialist Group, Gland, Switzerland and Cambridge, United Kingdom.

Gelfand, A., and D. K. Dey. 1994. Bayesian model choice: asymptotics and exact calculations. Journal of the Royal Statistical Society 56:501–514.

Green, J. S., F. F. Knowlton, and W. C. Pitt. 2002. Reproduction in captive wild-caught coyotes (*Canis latrans*). Journal of Mammalogy 83:501–506.

Hosmer, D., and S. Lemeshow. 2000. Applied logistic regression. Wiley, New York, New York, USA.

Lacy, R. C. 1994. Managing genetic diversity in captive populations of animals. Pages 63–89 *in* M. L. Bowles, and C. J. Whelan, editors. Restoration and recovery of endangered plants and animals. Cambridge University Press, Cambridge, United Kingdom.

Lockyear, K. M., W. T. Waddell, K. L. Goodrowe, and S. E. Macdonald. 2009. Retrospective investigation of captive red wolf success in relation to age and inbreeding. Zoo Biology 28:214–229.

Macdonald, D. W. 1980. Ten social factors affecting reproduction amongst red foxes. Biogeographica 18:123–176.

Mech, L. D. 1999. Alpha status, dominance, and division of labor in wolf packs. Canadian Journal of Zoology 77:1196–1203.

Pottinger, T. G. 1999. The impact of stress on animal reproductive activities. Pages 130–177 *in* P. H. M. Baum, editor. Stress physiology in animals. CRC Press, Boca Raton, Florida, USA.

Rivier, C., and S. Rivest. 1991. Effect of stress on the activity of the hypothalmic–pituitary–gonadal axis: peripheral and central mechanisms. Biology of Reproduction 45:523–532.

Roemer, G. W., T. J. Coonan, D. K. Garcelon, J. Bascompte, and L. Laughrin. 2001. Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Animal Conservation 4:307–318.

Sacks, B. N. 2005. Reproduction and body condition of California coyotes (*Canis latrans*). Journal of Mammalogy 86:1036–1041.

United States Fish and Wildlife Service. 2004. Endangered and threatened wildlife and plants; listing the San Miguel Island fox, Santa Rosa Island fox, Santa Cruz Island fox, and Santa Catalina Island fox as endangered. Federal Register 69:10335–10353.

Windberg, L. A. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology 73:942–954.

Associate Editor: Jeff Bowman.