

The Use of Capture-Recapture Methods for Estimating, Monitoring, and Conserving Island Fox Populations

Gary W. Roemer,^{1,2} David K. Garcelon,¹ Timothy J. Coonan,³ and Catherine Schwemm³

¹Institute for Wildlife Studies, P.O. Box 1104, Arcata, CA 95521
Tel. (707) 822-4258; Fax (707) 822-6300

²Department of Biology, University of California, Los Angeles, CA 90024
Tel. (310) 825-5014; Fax (310) 206-3987

³Channel Islands National Park, 1901 Spinnaker Dr., Ventura, CA 93001
Tel. (805) 658-5700; Fax (805) 658-5799

Abstract. Island foxes (*Urocyon littoralis*), the smallest North American canid, are endemic to 6 of the 8 California Channel Islands. We estimated the size of island fox populations on 4 islands by first estimating densities and then extrapolating these estimates to the percent habitat composition on each island. Density estimates were made using the capture-recapture computer program CAPTURE and Chapman's modification of the Lincoln-Peterson estimator. Densities ranged from 2.4 to 14.3 foxes/km². Estimates of population size ranged from 342 foxes on the smallest island (San Miguel) to 1,465 foxes on the largest island (Santa Cruz). Effective population size ranged from 68 to 493 foxes. The total number of individuals composing the species was estimated to be 6,000. Small population sizes, coupled with a lack of genetic variation and a high risk of exposure to virulent canine diseases, suggest that this species is in need of conservation measures.

Keywords: Island fox; *Urocyon littoralis*; California Channel Islands; capture-recapture methods; density estimation; population size; effective population size; conservation.

Introduction

Species conservation is largely dependent upon understanding demographic processes that govern population growth and genetic processes that affect population change (Soulé 1987a; Lande 1988). This information is not always easily obtained, however, and frequently populations become jeopardized, or species become extinct, before even the most basic information can be amassed. Indeed, most conservation efforts start when the species (e.g., California condor, *Gymnogyps californianus*) or population (e.g., San Clemente Island loggerhead shrike, *Lanius ludovicianus mearnsi*) is on the verge of extinction. The problems inherent in designing a conservation plan that ensures the preservation of a species are further

exacerbated by the fact that individual populations may require unique conservation strategies (Soulé 1987b; Wayne et al. 1991a). Developing a sound conservation strategy then depends upon gaining demographic and genetic information for all populations of concern prior to the onset of any irreversible population declines.

The case of the island fox (*Urocyon littoralis*) provides an ideal opportunity to develop such a population-based conservation strategy. This species is endemic to the California Channel Islands where it is distributed as 6 small island populations. Successful species conservation is possible in this case because all islands are managed by resource agencies committed to preserving and restoring their insular ecosystems. Additionally, information on genetic variation (Gilbert et al. 1990; Wayne et al. 1991a, 1991b) and disease exposure (Garcelon et al. 1992), factors important for determining extinction probabilities (Soulé 1987a), have already been gathered. However, few efforts have been made to estimate the size of island fox populations (Laughrin 1980; Kovach and Dow 1981, 1985) or to monitor population dynamics, factors also important for determining population-specific extinction probabilities. No long-term quantitative population studies have been conducted and estimates of population size for each island, based on a standardized methodology, are not available for this species. This lack of information contributed to the state of California listing the species as threatened (California Department of Fish and Game 1987), and to the federal government designating the species a candidate for listing as threatened or endangered (U.S. Fish and Wildlife Service 1989).

In this paper we present a capture-recapture methodology that can be used to monitor and estimate the size of island fox populations. We present estimates of population size for 4 islands, refine earlier estimates of effective population size based on 6 yr of demographic data, and advocate the establishment of a long-term, interagency monitoring program aimed at species conservation.

Methods

Trapping

Field work was conducted in the summer months from 1988 through 1993 on San Clemente Island, in 1989 and 1990 on Santa Catalina Island, and in 1993 on both Santa Cruz and San Miguel islands. Trapping was initiated no earlier than 26 May and finished no later than 9 September. Most trapping was conducted from late June till mid-August.

Three trapping grids were established on San Clemente and Santa Catalina islands while 2 grids were established on the remaining islands (Fig. 1). Trapping grids were arranged in a variety of configurations and comprised several different habitat types (Table 1). Grid locations were chosen subjectively, but arranged so that dominant habitats were represented while severely altered habitats (explosive shell impact sites and human inhabited areas) and topographically inaccessible regions were avoided. Live traps (23 x 23 x 66 cm, Tomahawk

WI) were spaced approximately 250 m apart and were baited with dry cat food and a fruit scent (Nick Wyshinski, Berwick, PA). Traps were covered with burlap and placed to provide protection from sun, precipitation, and wind. Traps were checked once in a 24-hr period, and trapping continued for 5–7 consecutive days on each grid.

Marking and handling

At their first capture, foxes were weighed (± 25 g), with sex, age, reproductive condition, presence of ectoparasites, and injuries also recorded. Foxes were placed into 1 of 4 age classes based on wear patterns of the first upper molar (Wood 1958). A colored ear tag (Rototag, Nasco-West, Stockton, CA) labeled with a unique alphanumeric combination was placed in the pinna of each animal. On San Miguel Island each animal was also tagged with a passive integrated transponder (Destron/IDI, Boulder, CO) implanted between and just anterior to the scapulae.

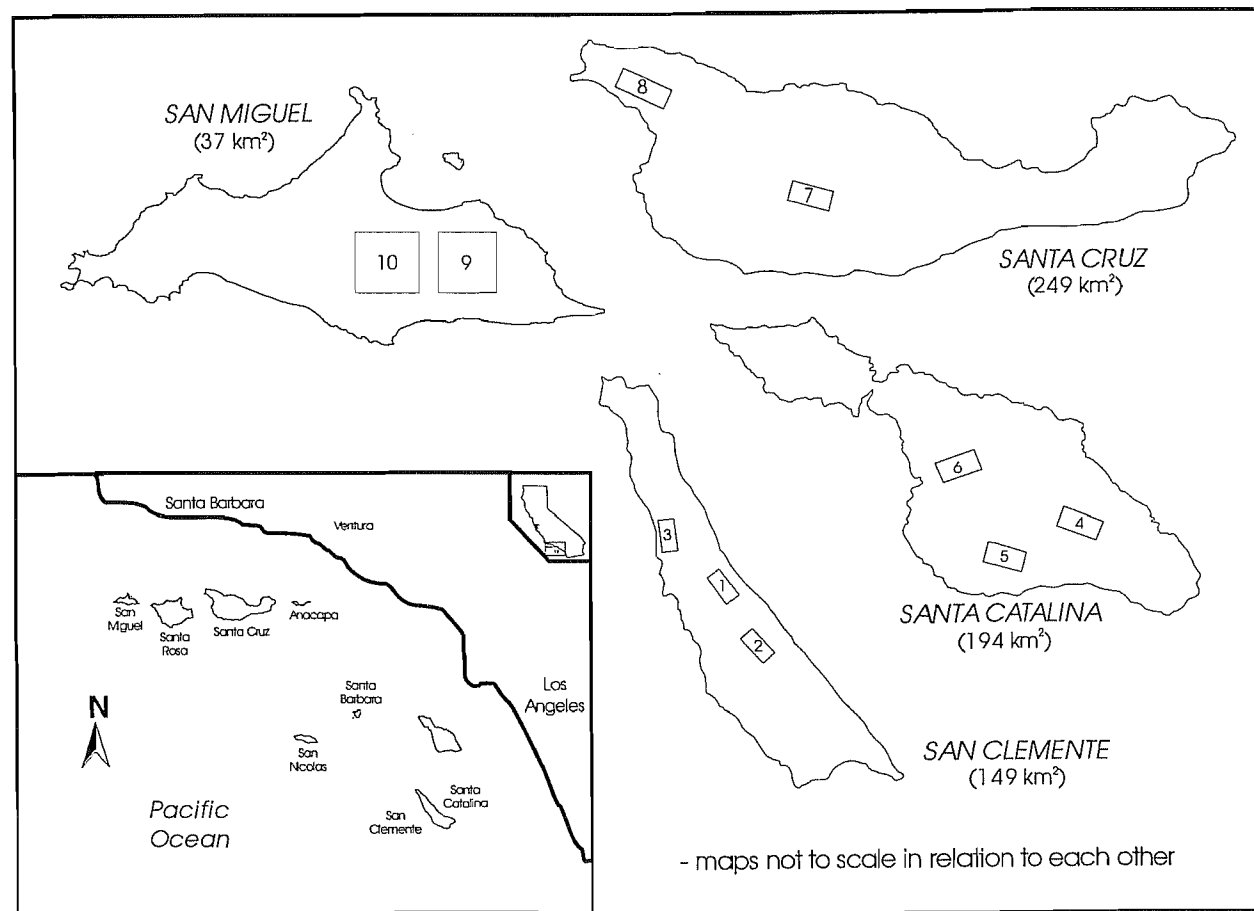


Figure 1. Distribution of island fox trapping grids on the California Channel Islands. Numbers within grids correspond to numbers defining grids in Table 1.

Table 1. Island/Grid¹, grid configuration, area (km²), and number of habitats² (in descending order of area covered) for each of the 10 island fox trapping grids established on 4 California Channel Islands.

Grid	Island	Configuration	Area	Habitat
San Clemente				
1	Grass I	8 x 10	3.94	GR
2	Grass II	8 x 10	3.94	GR
3	MDS	6 x 11	3.1	MDS, GR
Santa Catalina				
4	Mixed I	6 x 11	3.1	GR, CSS, CH, OW, R
5	Mixed II	6 x 11	3.1	CH, OW, GR, R
6	Mixed III	6 X 11	3.1	CSS, OW, R
Santa Cruz				
7	Mixed	5 x 10	2.25	GR, CH, OW, CSS, R
8	Grass	5 x 13	3.0	GR, CDS
San Miguel				
9	Mixed I	6 x 7	1.88	GR, HS, CSS, CDS
10	Mixed II	7 x 7	2.25	GR, HS, CSS, CDS

¹ Grid numbers define grid locations in Figure 1.

² Habitats: GR = grassland OW = oak woodland
MDS = maritime desert scrub R = riparian
CSS = coastal sage scrub CDS = coastal dune scrub
CH = chaparral HS = *Happlopappus* scrub

Density estimation

The computer program CAPTURE (version 2; White et al. 1982) or Chapman's modification of the Lincoln-Peterson (LP) estimator was used to estimate population size on each grid. CAPTURE's model selection procedure may not perform effectively with small population sizes and may be severely biased depending on the true capture probabilities of the population (Otis et al. 1978; Menkins and Anderson 1988). Therefore, we used the estimate generated by CAPTURE only if a behavioral response and/or heterogeneous capture probabilities were

evident; if these factors were not evident we then used the modified LP estimator (Menkins and Anderson 1988).

The naive density estimator, $D = N/A$ (where N is the estimate of population size and A is the area of the trapping grid), was modified due to the bias caused by the lack of a barrier to animals residing on the periphery of the grid (Dice 1938). The area influenced by the trap grid (i.e., the effective trap area $A(W)$, where W is the boundary strip around the trap grid) was determined using the mean maximum distance moved (MMDM) between traps (Wilson and Anderson 1985). MMDM is a measure of the maximum distance a fox moves between successive cap-

Table 2. Total number of adults captured, total captures, population estimate (s.e.), model used¹, and effective trap area [A(W)] for each of 3 island fox trapping grids on San Clemente Island, California.

Grid/Yr	Num of adults	Num of captures	Population estimate	Model ¹	A(W) km ²
Grass I					
1988	43	119	53 (8.3)	Mb	7.1
1989	56	130	61 (12.0)	LP	6.4
1990	58	199	59 (1.9)	Mbh	6.8
1991	52	210	57 (6.3)	Mbh	7.5
1992	49	103	55 (3.4)	LP	6.5
1993	33	98	60 (32.2)	Mb	7.4
Grass II					
1988	28	99	29 (1.5)	Mb	7.3
1989	33	118	36 (3.9)	Mh	8.0
1990	46	196	48 (2.0)	Mb	7.8
1991	35	133	36 (1.6)	Mbh	7.8
1992	32	93	36 (3.6)	Mh	7.2
1993	31	95	34 (3.5)	Mbh	7.0
MDS					
1988	31	129	31 (1.0)	Mh	4.8
1989	33	113	41 (7.5)	Mh	5.2
1990	31	92	55 (20.2)	Mh	5.4
1991	29	128	29 (0.9)	Mb	5.2
1992	40	92	43 (2.2)	LP	4.7
1993	19	57	22 (2.7)	Mh	4.7

¹ Capture-recapture models selected by program CAPTURE were: behavior model (Mb), heterogeneous capture probability model (Mh), and a combination of the two models (Mbh). Chapman's modification of the Lincoln-Peterson estimator (LP) was used if behavioral response or heterogenous capture probabilities were not evident.

tures averaged over all foxes that were captured at least twice. CAPTURE provides an estimate of MMDM and A(W) is then calculated by adding 1/2 MMDM to all sides of a grid. Density estimates for each grid were determined by dividing the estimate of population size by A(W). Pups were excluded from the population estimate due to their close association with adults and their potential biasing effect on MMDM.

Island-wide population estimates

Island fox population size for each island was estimated by extrapolating density estimates. Habitat distributions for each island were determined from the literature (Raven 1963; Thorne 1967; Hochberg et al. 1979; Minnich 1980) and compared to the distribution on each grid. The fox density from each grid was then multiplied

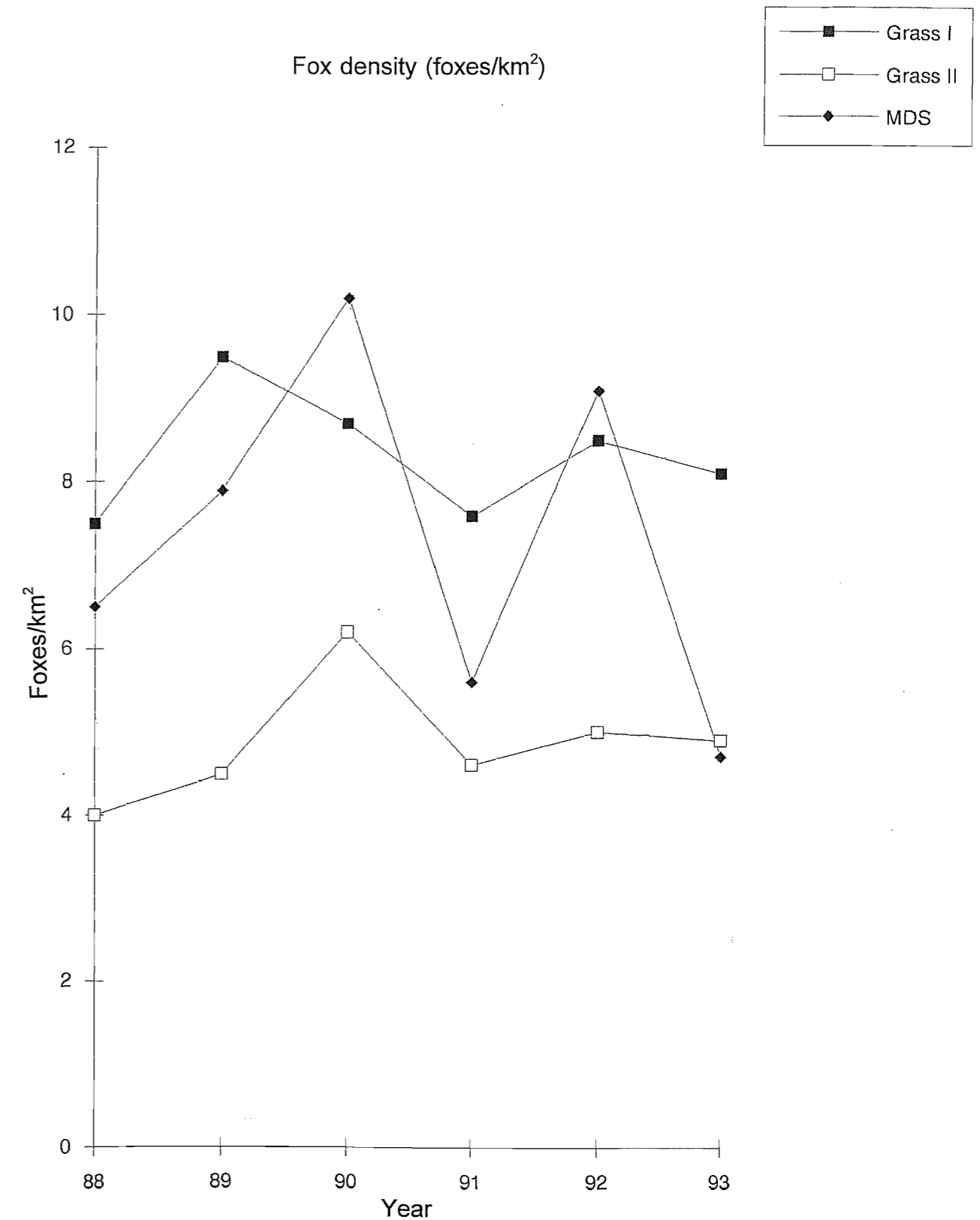


Figure 2. Island fox density estimates for 3 trapping grids on San Clemente Island, California, 1988–1993.

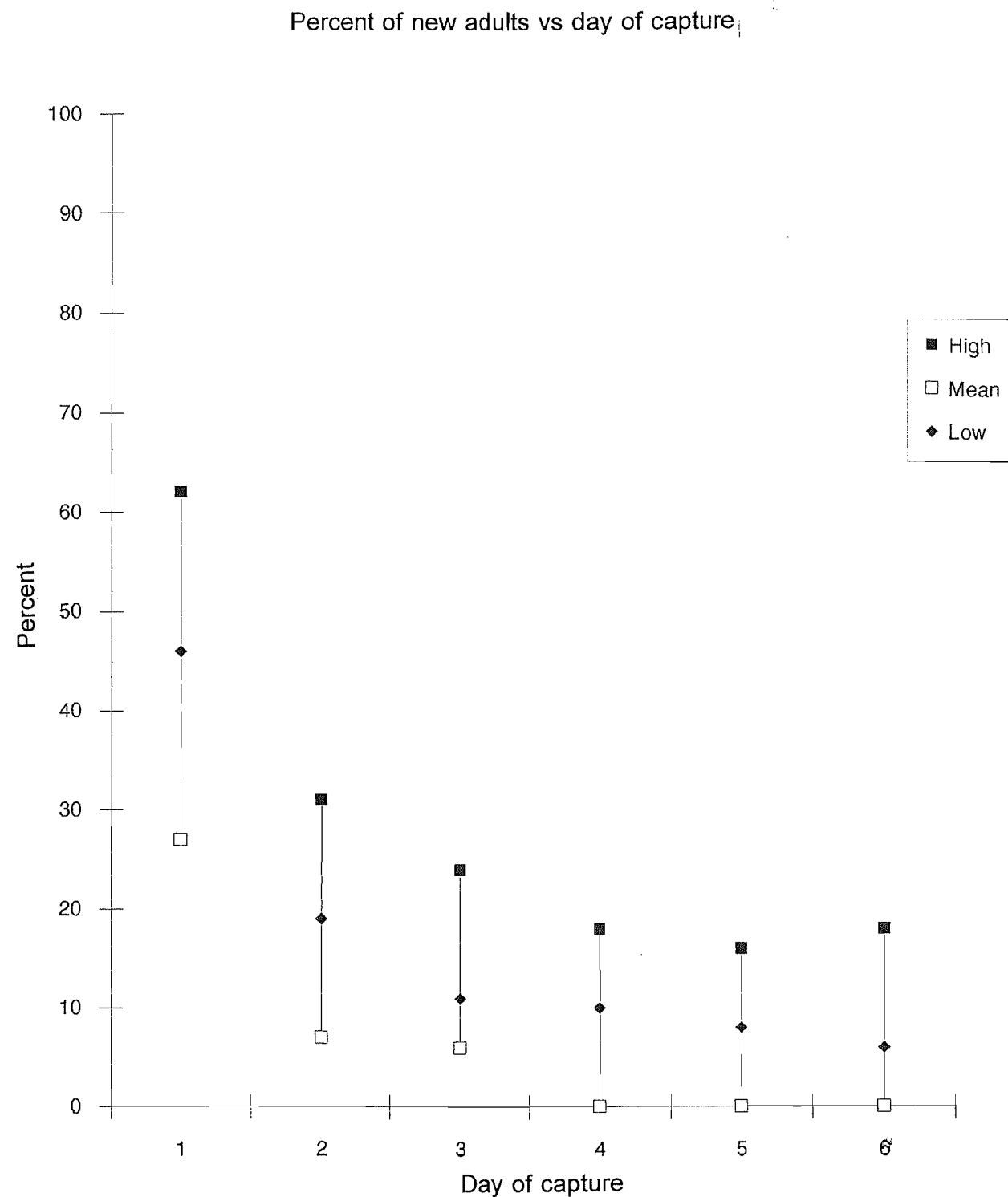


Figure 3. The percent of new adult island foxes captured each day, as a percentage of the total number of individual adults captured over a 6-dy period, for the 3 trapping grids on San Clemente Island, California. Percentages represent averages over all years (1988–1993).

by the appropriate habitat area for each island, yielding an estimate of the number of adults. Areas not likely to harbor foxes (urban, bare, and cultivated) were omitted from the calculations.

Effective population size

Effective population size (N_e) is a measure of the number of individuals contributing genes to the next generation and can be used to estimate the rate of loss of selectively neutral variation (Nunney and Campbell 1993). N_e was estimated using the model of Reed et al. (1986). Although this model has been shown to overestimate N_e by approximately 60% (Harris and Allendorf 1989), other less biased models require an estimate of the variance in lifetime reproductive success of newborns, a parameter for which we have no data. A rigid dependence on an estimate of N_e is probably not warranted for management purposes, because of the uncertainties in the data needed to estimate N_e , and because these estimates provide only an approximation of the amount of genetic loss that is likely to occur (Harris and Allendorf 1989).

Results

Density estimates

San Clemente Island. Over the past 6 yr we trapped 384 individuals, including pups, a combined 3,145 times on the 3 trapping grids. Population estimates for each grid varied among years (Table 2), and density estimates ranged from 4.0–9.5 foxes/km² (Fig. 2). After an initial increase in density during the first 2–3 yr for each grid, the grassland grids reached a period of relative stability while the maritime desert scrub (MDS) grid varied over the last 3 yr. These temporal differences are also reflected in the coefficient of variation for each grid (Grass 1 = 9.0%, Grass 2 = 15.1%, MDS = 28.9%). Because CAPTURE's model selection procedure may be biased, and therefore provide inaccurate population estimates, we also looked at the total number of individuals captured on each grid under the premise that we were capturing most of the resident adults (see Fig. 3). The total number of individuals captured on each grid showed a slightly different pattern than did density (Fig. 4). In general, the number of individuals captured on the 2 grassland grids increased during the second and third years of the study and then decreased over the last 3 yr with the trend exhibited by the Grass II grid mimicking that of density; this last result was due to the similarity between the population estimates and the total number of individuals captured (Table 2). The MDS grid exhibited a pattern of 4 yr of relative stability followed by an increase in 1992 and then a sharp decrease during the last year, a trend also exhibited by the density estimates. Pup production on

each grid was also variable with the Grass II and MDS grids exhibiting similar patterns over all 6 yr, and each grid displaying a sharp decline in 1993 (Fig. 5). These data suggest that both density-dependent and density-independent factors may be influencing this island population, and that island fox populations may be moderately cyclic.

Trends in density and in the total number of individuals captured were similar, and the average population estimate was similar to the average number of individuals captured for each grid (Grass 1, 58 vs 49; Grass 2, 37 vs 34; MDS, 37 vs 31). This suggests that the population estimate derived from either CAPTURE or the LP estimator, and the subsequent density estimate, can be used to estimate the size of island fox populations.

Santa Catalina Island. The spatial variation in density was much greater for grids on Santa Catalina Island than on San Clemente Island grids. Density estimates ranged from 2.4 to 14.3 foxes/km² with the Mixed I grid having the highest number of individuals captured followed by Mixed II and Mixed III (Table 3). Density estimates within each grid were similar over the 2 yr that trapping occurred (Table 3).

Santa Cruz Island. Density estimates for the 2 grids on Santa Cruz Island were very similar (Mixed—7.3 foxes/km²; Grass—7.0 foxes/km²). A total of 19 adults captured on the Mixed grid yielded a population estimate of 24 (s.e. = 2.8) while a total of 27 adults captured on the larger Grass grid yielded a population estimate of 31 (s.e. = 2.5). [CAPTURE selected model Mh in both cases.]

San Miguel Island. Similarly, density estimates for the 2 grids on San Miguel Island varied little (Mixed I—8.9 foxes/km²; Mixed II—9.6 foxes/km²). A total of 29 adults captured on the Mixed I grid yielded a population estimate of 32 (s.e. = 3.6) while a total of 30 adults captured on the slightly larger Mixed II grid also yielded a population estimate of 32 (s.e. = 2.3). [Model Mbh was selected in both cases.]

Island-wide population estimates

Island-wide population estimates varied for the 4 islands as follows: San Clemente, 1003; Santa Catalina, 1,342; Santa Cruz, 1,465; and San Miguel, 342. We used the most recent estimate for San Nicolas Island of 520 individuals (Kovach and Dow 1985). There were no density estimates available for Santa Rosa Island; therefore, we took the average density from Santa Cruz and San Miguel islands (8.2 foxes/km²) and multiplied this value times the area of the island to obtain an estimate of 1,780. This brings the total number of adult foxes composing the species to 6,452 individuals. Because the population estimate for Santa Rosa Island (217 km²) is larger than the estimate for Santa Cruz Island (249 km²), it is probably positively biased. The number of individuals composing the species is probably closer to 6,000.

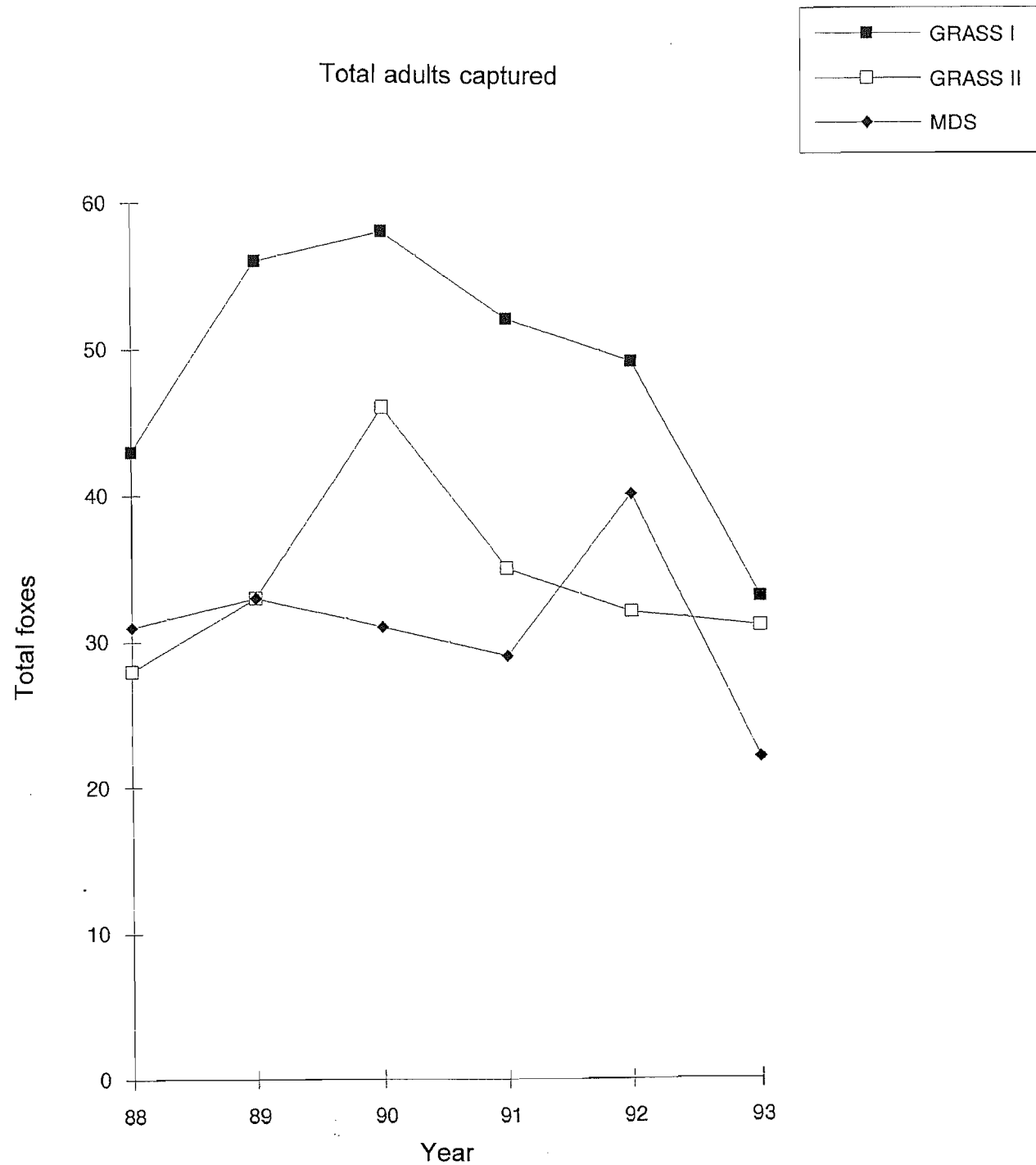


Figure 4. The total number of adult island foxes captured on each of 3 trapping grids on San Clemente Island, California, 1988–1993.

Effective population size

Using the 2 different estimates of pup survivorship, effective population size varied from only 68 individuals on the smallest island to 493 individuals on the largest (Table 4). These estimates are 29–73% smaller than previous estimates employing the same model (Wayne et al. 1991b).

Discussion

Density and island-wide population estimates

Based on a standard methodology, island fox density estimates varied among islands, among different habitats on the same island, and within a given area over time. Because of the small standard errors associated with most

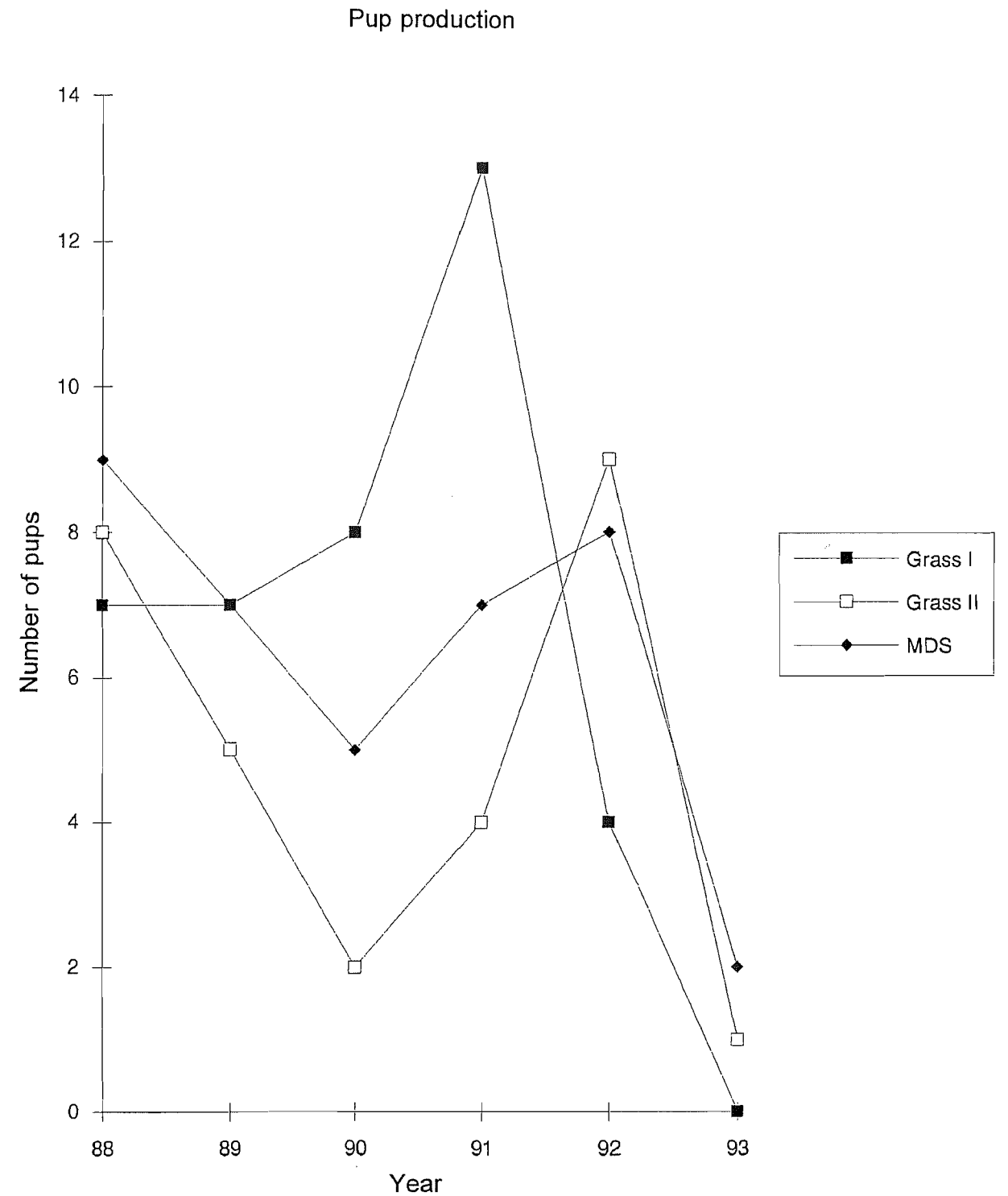


Figure 5. Total number of island fox pups captured on each of 3 trapping grids on San Clemente Island, California, 1988–1993.

of the population estimates for each grid, and the similarity between the estimates and the total number of individuals captured, we feel this methodology works well for estimating densities and subsequently the size of island fox populations. However, certain improvements

can be made to increase the accuracy of both density and island-wide population estimates.

First, CAPTURE's model selection procedure can be improved based on an examination of the capture data and the overall experience of the researcher (Menkins and

Table 3. Total number of adults captured, total captures, population estimate (s.e.), model used¹, effective trap area [A(W)], and density estimate for the 3 island fox trapping grids on Santa Catalina Island, California.

Grid/Yr	Num of adults	Num of captures	Population estimate	Model ¹	A(W) km ²	Density foxes/km ²
Mixed I						
1989	42	95	67 (7.6)	Mh	4.7	14.3
1990	47	123	55 (3.7)	Mh	3.8	11.4
Mixed II						
1989	31	51	32 (1.4)	Mb	5.4	5.9
1990	20	49	42 (9.3)	Mh	5.7	7.4
Mixed III						
1989	11	41	11 (0.5)	LP	4.5	2.4
1990	13	43	13 (0.1)	Mbh	4.4	2.9

¹ Capture-recapture models selected by program CAPTURE were: behavior model (Mb), heterogenous capture probability model (Mh), and a combination of the two models (Mbh). Chapman's modification of the Lincoln-Peterson estimator (LP) was used if behavioral response or heterogenous capture probabilities were not evident.

Anderson 1988). Island foxes exhibit high capture probabilities (0.24–0.60) and recapture probabilities (0.31–0.87). These data suggest that island foxes exhibit a behavioral response whereby many individuals become “trap-happy.” However, because individuals reside on the periphery of the grids, and few traps are encompassed by their home ranges, these individuals are captured a fewer number of times than individuals residing more centrally. This situation may result in a heterogeneous capture response even if foxes are “trap-happy.” The most appropriate models may be those that account for a behavioral response or a combination of behavior and heterogeneous capture probabilities. But, even if these models are selected, aberrant estimates can still occur (see Table 2: Grass I grid, 1993). Estimates derived from inappropriate models might be avoided by comparing the capture and recapture probabilities of individuals caught on the periphery of the grid with those caught in the grid center. We are currently developing a set of guidelines, based on these probabilities in conjunction with capture location, which can be used to select a more appropriate model estimator.

Second, density estimates have 2 basic sources of variation. The first is the error associated with the popu-

lation estimate, discussed above, and the second is error in estimating A(W). Recent telemetric studies of red foxes (*Vulpes vulpes*, Doncaster and Macdonald 1991), crab-eating foxes (*Cerdocyon thous*, D. Macdonald 1993, pers. comm.) and Blandford's foxes (*V. cana*, Geffen and Macdonald 1992) have shown that in undisturbed habitats fox home ranges can be highly stable over an individual's life span and even between successive generations. Our estimates of A(W) varied little over time (see Table 2), suggesting that island fox home ranges are stable, and probably contributed little to temporal variance in the density estimates.

Estimates of island population size could be improved by running more trapping grids per season, thereby increasing spatial sampling. However, it is logistically difficult to operate more than 3 or 4 grids in a summer trapping season. Each grid takes a minimum of 8 consecutive days to complete (6 dy of trapping, 2 dy for set-up/take down), and if it is desirable to estimate pup production, there is a narrow window of time when pups are large enough to forage away from the den, and thus be captured, yet young enough to be distinguished from yearlings. Moreover, some islands are so topographically diverse, and

Table 4. Comparison of estimates of effective population size based on a model by Reed et al. (1986). The first 2 estimates were derived from data collected in this study using 2 methods of calculation¹, the last estimates are from Wayne et al. (1991b).

Population estimates				Study/method
San Clemente	Santa Catalina	Santa Cruz	San Miguel	
199	266	290	68	This study—Method 1
338	451	493	115	This study—Method 2
551	979	984	163	Wayne et al. (1991b)

¹ The model parameters are as follows:

$$1/N_e = 1/(4 L_m M_b K_m l_m) + 1/(4 L_f F_b K_f l_f)$$

where L_m and L_f = age at first breeding for males and females, respectively—defined as 2 yr. M_b and F_b equal the number of breeding males and females, respectively—defined as $1/2 * N * 0.45$. N = the population estimate for a given island which is then halved (our data suggests an equal sex ratio [Garcelon et al. 1991]) and 0.45 is the average proportion of females which showed signs of lactation. This value was determined from 12 grid-years of data from San Clemente Island. We assumed the mating system to be monogamous, with the number of breeding males equalling the number of breeding females (Laughrin 1977). K_m and K_f = the number of young born to each sex each year—defined as 1. Finally, l_m and l_f = the proportion of newborn males and females which survive and reproduce. These latter values were estimated in 2 ways (Method 1 and 2). Both methods used data only from San Clemente Island. In method 1, we calculated the proportion of pups which survived and remained on a trapping grid after the year they were born (0.49) and multiplied this value by the probability of breeding (0.45) to yield a value of 0.22 for l_m and l_f . This value underestimates the actual number of surviving pups, because pups which disperse from the grids are counted as dead. In method 2, we attempted to account for successful dispersers by assuming an equilibrium flux among immigrating and emigrating foxes. In other words, the percentage of new foxes captured on a grid that were age class 1 (67%, immigrants) was assumed to equal the percentage of pups born the previous year that had not been captured the ensuing year, but that had dispersed and survived (emigrants). Thus, an average of 67% of all pups which were absent from the grid the year after they were born were assumed to be alive. The proportion of surviving dispersers ($0.67 * 0.51 = 0.34$) was then added to the proportion of pups remaining philopatric (0.49) to yield an estimate of 0.83 for all surviving pups. This value was then multiplied by the probability of breeding to yield 0.37—the probability of a newborn surviving and reproducing regardless of dispersal.

some habitats so dense, that there are few areas where grids of this size can be established and then checked every 24 hr. Correlating density estimates from trapping grids, with relative estimates obtained by transect trapping could be used to determine densities in areas where grid trapping is not conducted. However, it may take several years to accumulate enough data to correlate these estimates. Finally, estimates of the number of adult foxes occupying certain habitats may be inaccurate either because these habitats

were not represented by the trapping grids (e.g., conifer forest on Santa Cruz Island) or because habitat distributions reported in the literature differ from current distributions as a result of recent invasions by nonnative plants (e.g., fennel, *Foeniculum vulgare*) or because of recent restoration efforts. These methodological problems could be overcome by placing trapping grids in very different habitats (e.g., as on Santa Catalina Island), assuming that similar habitats in different areas have similar fox densities

(average fox density across all grids that were at least 50% grassland ($n = 5$) was 8.2 foxes/km², s.e. = 1.1), and then utilizing geographical information systems (GIS) to quantify habitat composition for each island. Density estimates could then be extrapolated by habitat yielding more accurate estimates of island population size. This was the general approach taken here, but it was nonetheless crude compared to what could be accomplished using GIS. Since many island resource agencies are currently creating GIS databases, this will be a viable alternative in the near future.

Effective population size and loss of heterozygosity

Estimates of N_e were lower than previous estimates (Wayne et al. 1991b) and probably realistic because of more accurate estimates of both population size and of the other parameters needed for the model (see Table 4). Nevertheless, our current estimates could be improved by using demographic parameters specific to each population and by collecting the data needed to use more accurate estimators (Lande and Barrowclough 1987; Harris and Allendorf 1989). However, all of our estimates are within an order of magnitude of each other, and all are relatively small (< 500). For management purposes these estimates yield the same prediction: current levels of heterozygosity will continue to be eroded over time, and for some populations the loss will be relatively rapid because N_e is small. Two of the 6 island fox populations are already homozygous for allozymic variability, and of the remaining 4 populations only the 2 largest (Santa Rosa and Santa Cruz) have appreciable levels of allozyme heterozygosity (Wayne et al. 1991b). Using our larger estimates of N_e , and the following equation ($H_t = H_0(1-1/[2N_e])^t$) (Falconer 1981), estimates of allozyme heterozygosity for the San Miguel and San Clemente populations will be 11% and 46%, respectively, of their currently low levels, in only 500 generations. Heterozygosity in the Santa Cruz Island population is predicted to be 37% of the current level in 1,000 generations. Although higher levels of variation may be maintained than this simple exercise predicts (Wayne et al. 1991b), levels of genetic variation in island fox populations are low compared with outbred populations (Gilbert et al. 1990; Wayne et al. 1991b). Genetic variation has been correlated with a population's ability to resist disease (O'Brien and Evermann 1988), and because island fox populations appear to have had no previous exposure to some infectious canine diseases (Wayne et al. 1991a; Garcelon et al. 1992) they may be exceptionally vulnerable. A potential source of disease transmission exists from domestic dogs that reside on at least 3 islands. In addition, working dogs have been used on various islands in feral animal management programs, and dogs are illegally brought ashore by recreational boaters (Garcelon et al. 1992; G. Roemer, pers. obs.). The recent decline in a pop-

ulation of black-footed ferrets (*Mustela nigripes*) resulting from the introduction of canine distemper virus (Thorne and Williams 1988) is a contemporary example of such a concern.

Conclusions and management recommendations

Island fox populations are small, have low effective population sizes, low levels of genetic variation and have probably not been exposed to some virulent canine diseases. These factors underscore the need for a sound conservation strategy for this species. The design presented here can be used to estimate the size of island fox populations, to estimate N_e and, in addition, to estimate survival rates and recruitment by employing open-population models (Pollock 1982; Pollock et al. 1990; Nichols 1992). Thus island fox populations can be monitored over time, and an understanding of the dynamics of each population can be achieved. Further, estimates of growth rate (r), and its variance, can be obtained and used to determine persistence times for each population (Goodman 1987; Shaffer 1987). We recommend that this design be implemented on all islands harboring fox populations, integrated with other measures of genetic variation (Lande and Barrowclough 1987), including analyses of more rapidly evolving loci (e.g., simple sequence repeats and/or the major histocompatibility complex), and coupled with a continued surveillance of disease exposure. A viability analysis incorporating both demographic and genetic information could be used to identify populations under the greatest risk of extinction, and management guidelines aimed at ensuring a high probability of population persistence (Shaffer 1987) could then be developed. For such an effort to reach fruition, it would require cooperation among all resource agencies involved in managing the California Channel Islands. This species represents a unique opportunity to gain information on proximate causes influencing population growth and evolutionary processes governing population change that, in turn, may be used to improve theoretical models in population biology (Soulé 1987c; Wayne et al. 1991b). It should be a paramount concern of resource managers of the California Channel Islands to ensure the preservation of a biological resource of such scientific importance.

Acknowledgments. We thank the following organizations and agencies for logistical support and permission to trap foxes: The Nature Conservancy, Santa Cruz Island Preserve, Santa Catalina Island Conservancy, California Department of Fish and Game, and the U.S. Department of the Navy.

We thank the following individuals for providing assistance in the field: G. Brundige, H. David, M. Deisch, D. Delaney, G. Frederick, D. Haney, R. Long, T. Roemer,

C. Starbird, and E. Steinberg. Funding for this study was provided by the California Department of Fish and Game, Southern California Edison Company, Los Angeles County Fish and Game Commission, Newman's Own, Inc., Institute for Wildlife Studies, the National Park Service/ Channel Islands National Park, the Theodore Roosevelt Memorial Fund, and Sigma-Xi Grants-in-Aid of Research.

Helpful comments were provided on earlier drafts of this manuscript by L. Laughrin, P. White, K. Crooks, and R. Klinger. H. David assisted in preparing figures.

Literature Cited

- California Department of Fish and Game. 1987. Five-year status report on the island fox (*Urocyon littoralis*). Unpublished report, California Department of Fish and Game, Sacramento, California. 7 pp.
- Dice, L. R. 1938. Some census methods for mammals. *Journal of Wildlife Management* 2:119-130.
- Doncaster, C. P., and D. W. Macdonald. 1991. Drifting territoriality in the red fox *Vulpes vulpes*. *Journal of Animal Ecology* 60:432-439.
- Falconer, D. S. 1981. Introduction to quantitative genetics. Longman, New York.
- Garcelon, D. K., G. W. Roemer, and G. C. Brundige. 1991. The biology of the island fox on San Clemente and Santa Catalina Islands, California. Draft final report, Institute for Wildlife Studies, Arcata, California. 59 pp.
- Garcelon, D. K., R. K. Wayne, and B. J. Gonzales. 1992. A serologic survey of the island fox (*Urocyon littoralis*) on the Channel Islands, California. *Journal of Wildlife Diseases* 28(2):223-229.
- Geffen, E., and D. W. Macdonald. 1992. Small size and monogamy: spatial organization of Blanford's foxes, *Vulpes cana*. *Animal Behaviour* 44:1123-1130.
- Gilbert, D. A., N. Lehman, S. J. O'Brien, and R. K. Wayne. 1990. Genetic fingerprinting reflects population differentiation in the Channel Island fox. *Nature* 344:764-767.
- Goodman, D. 1987. The demography of chance extinction. In: *Viable Populations for Conservation* (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 11-34.
- Harris, R. B., and F. W. Allendorf. 1989. Genetically effective population size of large mammals: an assessment of estimators. *Conservation Biology* 3(2):181-191.
- Hochberg, M., S. Junak, R. Philbrick, and S. Timbrook. 1979. Botany. In: *Natural Resources Study of the Channel Islands National Monument, California* (edited by D. M. Power), Final report to the National Park Service, CX-2000-8-0040, Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 5.1-5.84.
- Kovach, S. D., and R. J. Dow. 1981. Status and ecology of the island fox on San Nicolas Island, 1980. Technical Memorandum TM-81-28. Pacific Missile Test Center, Point Mugu, California. 33+ pp.
- Kovach, S. D., and R. J. Dow. 1985. Island fox research on San Nicolas Island. Annual Report, Department of the Navy, Pacific Missile Test Center, San Diego, California.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.
- Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. In: *Viable Populations for Conservation* (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 87-123.
- Laughrin, L. 1977. The island fox: a field study of its behavior and ecology. Ph.D. dissertation, University of California, Santa Barbara, California. 83 pp.
- Laughrin, L. 1980. Population and status of the island fox. In: *The California Islands: Proceedings of a Multidisciplinary Symposium* (edited by D. M. Power), Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 745-750.
- Menkins, G. E., and S. H. Anderson. 1988. Estimation of small-mammal population size. *Ecology* 69:1952-1959.
- Minnich, R. A. 1980. Vegetation of Santa Cruz and Santa Catalina Islands. In: *The California Islands: Proceedings of a Multidisciplinary Symposium* (edited by D. M. Power), Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 123-137.
- Nichols, J. D. 1992. Capture-recapture models. *Bioscience* 42(2):94-102.
- Nunney, L., and K. A. Campbell. 1993. Assessing minimum viable population size: demography meets genetics. *Trends in Ecology and Evolution* 8:234-239.
- O'Brien, S. J., and J. F. Evermann. 1988. Interactive influence of infectious disease and genetic diversity of natural populations. *Trends in Ecology and Evolution* 3:254-259.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1-135.
- Pollack, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:757-760.
- Pollack, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:1-97.
- Raven, P. H. 1963. A flora of San Clemente Island, California. *Aliso* 5:289-347.
- Reed, J. M., P. D. Doerr, and J. R. Walters. 1986. Determining minimum population sizes for birds and mammals. *Wildlife Society Bulletin* 14:255-261.

- Shaffer, M. 1987. Minimum viable populations: coping with uncertainty. In: *Viable Populations for Conservation* (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 69–86.
- Soulé, M. E. (editor). 1987a. *Viable populations for conservation*. Cambridge University Press, Cambridge, Great Britain. 189 pp.
- Soulé, M. E. 1987b. Introduction. In: *Viable Populations for Conservation* (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 1–10.
- Soulé, M. E. 1987c. Where do we go from here? In: *Viable Populations for Conservation* (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 175–183.
- Thorne, R. F. 1967. A flora of Santa Catalina Island, California. *Aliso* 6:1–77.
- Thorne, E. T., and E. S. Williams. 1988. Disease and endangered species: the black-footed ferret as a recent example. *Conservation Biology* 2:66–74.
- U.S. Fish and Wildlife Service. 1989. Endangered and threatened wildlife and plants; animal notice of review. *Federal Register* 54(4):554–579.
- Wayne, R. K., S. B. George, D. Gilbert, and P. W. Collins. 1991a. The Channel Island fox (*Urocyon littoralis*) as a model of genetic change in small populations. In: *The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology, Volume II* (edited by E. C. Dudley), Dioscorides Press, Portland, Oregon, pp. 639–649.
- Wayne, R. K., S. B. George, D. Gilbert, P. W. Collins, S. D. Kovach, D. Girman, and N. Lehman. 1991b. A morphologic and genetic study of the island fox, (*Urocyon littoralis*). *Evolution* 45(8):1849–1868.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico. 235 pp.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.
- Wood, J. E. 1958. Age structure and productivity of a gray fox population. *Journal of Mammalogy* 39:74–86.

Effects of Precipitation and Density on the Abundance of California Quail on Santa Cruz Island

Louis W. Botsford,¹ Dale F. Lott,¹ John G. Brittnacher,¹ and Sonke Mastrup²

¹*Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616
 Tel. (916) 752-6169; Fax (916) 752-4154*

²*California Department of Fish and Game, 1416 Ninth St., Sacramento, CA 95814
 Tel. (916) 653-4673; Fax (916) 653-1019*

Abstract. Lack of a detectable dependence of recruitment on density in hunted populations of California quail (*Callipepla californica*) led us to examine an unhunted population on Santa Cruz Island for this characteristic. We have estimated juvenile-to-adult ratios and an index of abundance near the beginning of August annually for the past 7 yr (1987–1993). Our sampling consists of 2 observers in each of 2 vehicles driving fixed transects and counting quail by age and sex for 3 dy. The juvenile-to-adult ratio depends positively and significantly on precipitation from January through March ($R = 0.87$, $p < 0.05$). With the effect of precipitation removed, the juvenile-to-adult ratio declines with adult density ($R = 0.69$, $p < 0.1$). Although sample size is low, these data indicate reproduction in California quail may be density-dependent.

Keywords: California quail; population dynamics; density-dependence; Santa Cruz Island.

Introduction

Although reproduction in California quail (*Callipepla californica*) has been shown to depend on physical environmental conditions in a variety of ways, no dependence on density has been demonstrated. From an analysis of the factors controlling quail population dynamics over 23 yr at a semi-arid site in central California, Botsford et al. showed in their 1988 study that reproduction did not depend on density. They proposed that the absence of density-dependence could be due to the fact that virtually all populations of California quail in California are hunted; hunting could maintain these populations below an abundance at which density-dependence would occur. We therefore sought an unhunted population of California quail to determine the nature of density-dependence in quail reproduction. The only viable candidate population in terms of both a current lack of hunting and future prospects for not being hunted was the population on Santa Cruz Island. This population had the added advantages that it was in a semi-arid climate zone, similar to

other populations we had studied, and it was on an island, hence was a closed population.

Reproduction in California quail is affected by weather; however different populations are affected in different ways. Early summer rains destroyed California quail nests and chicks on the Modoc Plateau (Savage 1974) and wetting from rain and fog led to the deaths of chicks near Berkeley on the California coast (Raitt and Genelly 1964). Populations in semi-arid regions usually produce more chicks in seasons with higher rainfall. McMillan (1964), Francis (1967), and Erwin (1975) all reported that a population near Shandon, California, had higher production of juveniles in years with higher rainfall. Francis (1967) reported that the strongest correlate of juvenile production was soil moisture in April. For the years from which his model was developed this single variable accounted for 83% of the variance. However, it accounted for less of the variance in other years (Francis 1970; Leopold 1977). In our earlier study (Botsford et al. 1988) we found that soil moisture accounted for 38.4% of the variance, while total rainfall from December through April accounted for 74.1% of the variance.

Although California quail reproduction has been demonstrated to be both positively and negatively related to atmospheric and soil moisture, there has never been clear evidence that it is negatively related to population density, i.e., that it is density-dependent. Leopold (1977) reviewed the existing evidence for density-dependence. He noted that reproduction per individual was the same in the high density population on the McMillan ranch as in the adjacent lower density populations. However, densities were high on the McMillan ranch only during winter, when the quail were attracted by habitat enhancements and supplementary food. Barclay and Bergerud (1975) reported that recruitment was inversely correlated with spring density; but they did not report spring density, and there was no significant inverse correlation in September. Botsford, et al. (1988) showed that the relationship between juveniles and adults indicated a linear increase of juveniles with adults (i.e., no density-dependence).