DEMOGRAPHY OF DESERT MULE DEER
IN SOUTHEASTERN CALIFORNIA

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Desert mule deer, *Odocoileus hemionus eremicus*, occur at low densities in the Sonoran Desert of southeastern California and consequently are difficult to monitor using standard wildlife techniques. We used radiocollared deer, remote photography at wildlife water developments (i.e., catchments), and mark-recapture techniques to estimate population abundance and sex and age ratios. Abundance estimates for 1999-2004 ranged from 40 to 106 deer, resulting in density estimates of 0.05-0.13 deer/km^2. Ranges in herd composition were 41-74% (females), 6-31% (males), and 6-34% (young). There was a positive correlation (R = 0.73, P = 0.051) between abundance estimates and number of deer photographed/catchment-day, and that relationship may be useful as an index of abundance in the absence of marked deer for mark-recapture methods. Because of the variable nature of desert wildlife populations, implementing

strategies that recognize that variability and conserving the habitat that allow populations to fluctuate naturally will be necessary for long-term conservation.

INTRODUCTION

Desert mule deer, *Odocoileus hemionus eremicus*, occur in the Sonoran Desert of southeastern California (Bowyer and Bleich 1984) at low densities (Thompson and Bleich 1993) and in a scattered distribution (Celentano and Garcia[1] 1984). Efforts to quantify deer population parameters in that area have been difficult because of low densities and low detection probabilities (Thompson and Bleich 1993). Celentano and Garcia[1] (1984) estimated sex and age ratios using aerial and ground telemetry, and Thompson and Bleich (1993) evaluated methods (aerial and ground surveys, hunter interviews) to estimate deer herd composition. The methods of Thompson and Bleich (1993) produced proportions of adult males, adult females, and young-of-the-year, but not estimates of abundance. Annual deer harvest records for this region may also provide useful information about the general trend of this deer population (Marshal et al. 2002). However, further efforts to quantify this deer herd should move beyond indices of abundance and trend, and toward more rigorous population estimates.

Recent efforts to quantify the demographics of this deer population have used remote photography (Kucera and Barrett 1993) of deer visiting wildlife water developments (i.e., catchments) to estimate population parameters. Remote photography, in combination with marked animals, allows for use of mark-recapture methods to estimate population abundance (Martorello et al. 2001, Heilbrun et al. 2003). Our objectives were to develop remote photography methods for population studies of desert ungulates and to use those methods to estimate abundance and composition of mule deer in a region of the Sonoran Desert in southeastern California.

STUDY AREA

We monitored the deer population from 1999 to 2004 in a region of the Lower Colorado River subdivision of the Sonoran Desert (Brown 1994) in eastern Imperial County near the East Chocolate and Cargo Muchacho Mountains (1,681 km^2, Fig. 1). Temperatures ranged from 0°C in winter to >45°C in summer. Annual rainfall was low, but highly variable (mean = 74 mm, range = 4-216 mm; 1914-2003, Imperial Irrigation District, unpublished data). The study area contained three major landforms: mountain, piedmont, and flat (Andrew et al. 1999). Vegetation was most dense in xeroriparian zones around washes (Marshal et al. 2005) and consisted largely of desert ironwood, *Olneya tesota*, creosote bush, *Larrea tridentata*, and palo verde, *Cercidium floridum* (Andrew[2] 1994). Outside of xeroriparian zones, creosote bush, and cholla and prickly

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[1] Celentano, R. R. and J. R. Garcia. 1984. The burro deer herd management plan. California Department of Fish and Game, Sacramento, California, USA.

[2] Andrew, N. G. 1994. Demography and habitat use by desert-dwelling mountain sheep in the East Chocolate Mountains, Imperial County, California. Thesis, University of Rhode Island, Kingston, Rhode Island, USA.
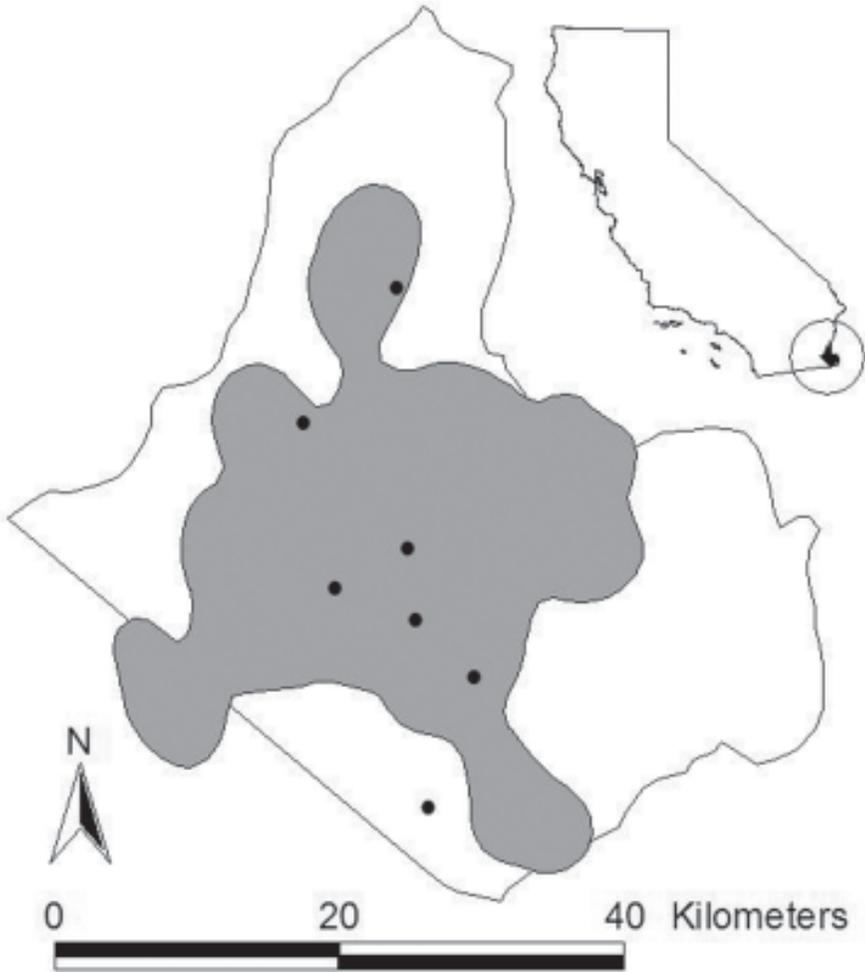
Fig.1. East Chocolate-Cargo Muchacho study area showing locations of the seven catchments at which radiocollared deer were photographed (circles), and the population range polygon for estimating density (grey area), Imperial County, California.

pear, *Opuntia* spp., were common (Andrew[2] 1994). Plant nomenclature follows Munz (1974). Other large- and medium-sized herbivores in the area were bighorn sheep, *Ovis canadensis*, feral ass, *Equus asinus*, black-tailed jackrabbit, *Lepus californicus*, desert cottontail, *Sylvilagus audubonii*, and desert tortoise, *Gopherus agassizii*. Potential predators of mule deer included mountain lion, *Puma concolor*, coyote, *Canis latrans*, bobcat, *Felis rufus*, and golden eagle, *Aquila chrysaetos* (Andrew et al. 1997). Hunting season for mule deer occurred in October and November. Since 1990, approximately

15-60 deer have been harvested each year from the hunting zone that contains our study area (Marshal et al. 2002).

There were several sources of free water available to deer. The Colorado River and the All-American Canal were at the eastern and southeastern boundaries of the study area. Seventeen catchments occurred in the study area, at an average density of 1/35 km^2; these provided water in all seasons. Natural rock basins and springs also occurred, but many were dry for part of the year. We defined seasons according to patterns of rainfall and temperature (Marshal et al. 2005). Generally, winter (January-March) was cool-rainy, spring (April-June) was hot-dry, summer (July-September) was hot-rainy, and autumn (October-December) was cool-dry. Radio-collared mule deer moved to catchments (within approximately 5 km) during spring, where they remained until the first rains of the hot-rainy season (Marshal et al., unpublished data). Timing of movements varied between years, and depended on forage conditions the previous winter and timing of the first summer precipitation.

METHODS

Capture and handling of mule deer occurred in accordance with protocols approved by the California Department of Fish and Game (Jessup et al. 1986). We captured deer with a net-gun (Krausman et al. 1985) fired from a helicopter, with chase times limited to ≤5 minutes. Upon capture, we blind-folded and hobbled deer to facilitate handling and to protect the animal (Jessup et al. 1986). We fitted each deer with a VHF radio collar with 6-hour delay mortality signal (Telonics MOD-500, Mesa, Arizona, USA) prior to release. To establish when deer moved to catchments, we located radio-collared deer approximately weekly from a fixed-wing aircraft.

Once deer moved to the catchments, we used infrared remote triggers (TrailMaster 1500; Goodson and Associates, Inc., Lenexa, Kansas, USA) and automatic film cameras to photograph them at the catchments. We placed the emitter and receiver on either side of the access point for a catchment. The triggers were connected to a camera via a cable, and the camera was positioned to facilitate identification of deer at the catchment as adult male, adult female, or young-of-the-year (10-12 months of age at the time of photographic sampling). This distance was typically 3 m, but varied with the surrounding terrain and vegetation. Sensitivity of the infrared units was set low (setting = 5) to trigger a photograph only if a large object broke the infrared beam, and the timer was set to take photographs >20 minutes apart. Photographic sampling occurred at 2-7 catchments (Fig. 1), depending on the number visited by radio-collared deer, and continued until deer moved away from the catchments in early summer.

We used radio-collared deer and two-sample Lincoln-Peterson mark-recapture methods to estimate population abundance in the study area. We estimated abundance from observations of collared and uncollared deer at visited catchments. We estimated abundance with Chapman's (1951) bias-adjusted mark-recapture estimator:

$$\tilde{N} = [(n_1 + 1)(n_2 + 1) / (m_2 + 1)] - 1,$$

where $\tilde{N}$ was the population estimate, n_1 was the number of collared deer in the population, n_2 was the number of deer photographed, and m_2 was the number of collared deer photographed. We determined n_1 from the number of collared deer observed near catchments after they had moved to them in the spring. After 2001, we estimated the number of collared deer in the study area because of transmitter failures. To determine a number of marked deer during 2002, 2003, and 2004, we calculated annual average survival rate for transmitting deer using the Kaplan-Meier estimator (Pollock et al. 1989). From survival rate, we estimated the number of nontransmitting deer that would have been alive to be seen during photographic sampling (Appendix 1). We assumed that nontransmitting deer had the same survival rates as transmitting deer, that transmitter failure and not emigration was occurring, and that transmitter failure was independent of the fate of the animal.

Values for n_2 and m_2 came from direct counts of deer in photographs; we did not identify individual deer (i.e., we sampled with replacement). As a consequence, $m_2 > n_1$, which produced a negative value for the estimate of var($\tilde{N}$), based on Seber's (1970) formula for variance. Therefore, we estimated 95% confidence intervals using bootstrap methods (Manly 1997). We selected, at random and with replacement, a number of week-long sampling periods and their associated deer counts equal to the total number of sampling periods for one year. From each random sample of periods, we calculated a population estimate. We repeated this procedure 1,000 times to produce a bootstrapped population estimate ($\tilde{N}_{bs}$, the average of the 1,000 estimates), and 95% confidence intervals. We calculated density by dividing $\tilde{N}_{bs}$ by the area occupied by the population. We calculated this area by estimating a home range polygon around all locations for all collared deer with a 95% adaptive-kernel home range estimator (Worton 1989).

Males were identified by presence of antlers. Females were distinguished from young by face and body proportions; young had smaller, thinner bodies, and their faces were narrower and smaller relative to the size of ears. We combined all young into a single category. In cases where distinguishing characteristics of deer could not be identified in photographs, we categorized those deer as undetermined. We calculated annual proportion of deer in each age and sex category using counts of deer from photographs (excluding deer classified as undetermined), and we calculated ratios of males:100 females and young:100 females. Because we were unable to identify individual deer when classifying them, we could not determine a number of independent trials to use when estimating variance based on the binomial distribution. Consequently, we used bootstrap methods similar to those described earlier for abundance estimation to calculate 95% confidence intervals for age and sex ratios.

To develop an index of abundance that would not rely upon a sample of collared deer in the population, we compared population abundance estimates to total observations of photographed deer/catchment-day. We tested for a positive association by using Pearson's product-moment correlation.

RESULTS

Over 5 years, we captured 47 female and 7 male deer. The population home-range size was 817 km^2 (Fig. 1), based on 4,013 deer locations. Estimated abundance of deer was variable among years, ranging from 40 deer (95% CI: 36-46) in 2001 to 106 deer (95% CI: 77-138) in 2002 (Table 1). Average abundance over the 6 years was 79 deer, and the coefficient of variation was 32%. Based on the estimated population range size, density was 0.05-0.13 deer/km^2 (Table 1). There was evidence for a positive association between $\tilde{N}_{bs}$ and number of observed deer photographed/catchment-day (R = 0.73, 1-tailed P = 0.051). Deer herd composition was also variable. Males:100 females ranged from 9 to 61 in 1999 and 2004, respectively (Table 2). Young:100 females ranged from 10 in 2001 to 85 in 2004 (Table 2). Ranges in percent of females, males, and young were 41-74, 6-31, and 6-34, respectively (Table 2).

Table 1. Population abundance ($\tilde{N}_{bs}$) for desert mule deer in the East Chocolate-Cargo Muchacho area of Imperial County, California 1999-2004.

Year	$\tilde{N}_{bs}$	95% LCL	95% UCL	Density (deer/km^2)	Deer/catchment-day
1999	56	38	68	0.07	15.6
2000	90	76	108	0.11	11.6
2001	40	36	46	0.05	6.2
2002	106	77	138	0.13	27.4
2003	87	70	111	0.11	26.4
2004	95	70	134	0.12	17.5

Table 2. Bootstrap-estimated sex and age composition of mule deer in the East Chocolate-Cargo Muchacho Area, Imperial County, California, 1999-2004.

Year	Catchment-days	No. deer classified	Males: 100 females (95% CIs)	Young: 100 females (95% CIs)	% Females (95% CIs)	% Males (95% CIs)	% Young (95% CIs)
1999	20	312	9 (5-11)	28 (19-31)	74 (71-80)	6 (4-8)	20 (15-22)
2000	66	766	33 (15-59)	17 (10-27)	67 (54-78)	22 (12-33)	11 (7-16)
2001	95	589	55 (30-85)	10 (2-24)	62 (50-72)	31 (21-43)	6 (1-13)
2002	39	1070	38 (16-69)	71 (55-93)	48 (40-55)	18 (9-29)	34 (28-41)
2003	23	608	40 (21-68)	43 (32-54)	55 (48-60)	21 (13-34)	24 (16-30)
2004	28	491	61 (35-102)	85 (56-113)	41 (33-48)	24 (16-36)	34 (25-42)

DISCUSSION

Our findings confirm the conclusions of Celentano and Garcia[1] (1984) and Thompson and Bleich (1993) that this is a low-density mule deer population. Comparisons to other parts of desert mule deer range support this conclusion. For example, density of mule

deer in the Belmont Mountains, Arizona, was 0.5/km² (Albert and Krausman 1993). Densities of desert mule deer ranged from 0.7 to 4.2/km² in the Chihuahuan Desert, Durango, Mexico (Sánchez-Rojas and Gallina 2000). Densities of desert mule deer in Buenos Aires National Wildlife Refuge, Arizona, ranged seasonally between 0.9 and 2.5 deer/km² (Koenen et al. 2002). Martinez-Muñoz et al. (2003), however, reported a desert mule deer density as high as 13.3/km² in Coahuila, Mexico. Historical information on the number of deer in our study area is scarce. McLean (1940) reported a herd size of 920 deer that occupied an area of approximately 11,900 km² (0.08 deer/km²) covering eastern Imperial and Riverside counties next to the Colorado River. Longhurst et al. (1952) reported that the deer population in a similar region contained 2,000 individuals (0.11 deer/km²). These historical numbers fell within our range of densities over the 6 years of our study (0.05-0.12 deer/km²).

Low density of deer in this region is likely the result of low rainfall, and its consequences for production of deer forage (Marshal et al. 2005). However, a low average rainfall masks the highly unpredictable and dynamic nature of this arid system. In arid environments, variation in rainfall leads to variation in plant biomass, and each is rarely near the long-term average (Noy-Meir 1973). Forage conditions in this arid region of California match this scenario (Marshal et al. 2005). Deer populations likely responded demographically in a manner that produced a similarly variable trend in abundance. As a result, the range in deer abundance estimates appeared wide and the coefficient of variation for abundance large. This would not be unexpected in a plant-herbivore system driven by stochastic rainfall events (Caughley 1987). Such fluctuations may have contributed to the relatively high and low population estimates observed during this study (Table 1). Movements of deer into or out of the study area probably contributed little to this variation; evidence from the radio-collared deer indicated little movement of deer to areas neighboring the study area (Marshal et al., unpublished data).

Using our methods, we were unable to estimate seasonal changes in deer density. Such changes could occur because of movements of deer into or out of the study area, or when the same number of deer use a larger or smaller area. Some studies of desert mule deer have reported fairly large changes in density across seasons. Densities estimated by Koenen et al. (2002) show a marked change between summer (0.9 deer/km²) and winter (2.5 deer/km²) over a single year. Desert mule deer densities in Durango, Mexico varied considerably across seasons, but not consistently by season. Sánchez-Rojas and Gallina (2000) estimated June densities of 3.6, 0.7, and 2.1 deer/km² during their 3-year study. Because arid environments are highly variable (Noy-Meir 1973), describing seasonal variation in deer density may be less useful for understanding population ecology of this species than describing density responses to specific environmental conditions. In our study area, density may increase during hot, dry conditions because of a decrease in the area used as animals moved toward water sources and, consequently, ranged less widely, rather than because of a change in the number of animals in the area. We considered this possibility and estimated a 95% adaptive-kernel home range polygon for locations during spring. The difference between home range sizes was not substantial (annual: 817 km²; spring only [1,031

locations]: 811 km^2).

Age ratios involving young-of-the-year or yearlings:100 females are frequently used as indices of reproduction or juvenile recruitment, respectively. At the time that photographic sampling occurred, young were nearing their first birthday. A measure of the proportion of these "near-yearlings" would provide a reasonable estimate of the rate at which young animals are becoming adults, assuming no variation in the rest of the population (McCullough 1994). Biologists should exercise caution when using age ratios as a measure of recruitment to a population. Using simulations to investigate the use of age ratios in evaluating the dynamics of wildlife populations, Caughley (1974) reported that populations exhibiting the same rates of increase could have very different age ratios, depending on what was occurring in the adult part of the population. Further, populations with the same age ratios could be exhibiting very different dynamics. For example, a population may have an increasing proportion of young because of an increase in the number of young animals, as might occur in an increasing population. But such a ratio also may be due to a large mortality event among adults that results in a decreasing population. While the use of age ratios may provide some information about population trend, they are unreliable in the absence of supporting data, such as rate of change estimates (Caughley 1974, McCullough 1994). In the absence of such data, use of age ratios requires the assumption of low variability in adult mortality (McCullough 1994). There is evidence that, for ungulate populations, most mortality occurs in the few months following birth (White and Bartmann 1998, Gaillard et al. 2000, Bleich et al. in press); in our study area, early fawn mortality also likely fluctuates considerably, and may do so in response to rainfall and forage conditions.

Despite the shortcomings associated with use of age ratios, our study had the support of estimates of abundance, and from abundance, estimates of rate of change were possible. Further, additional information on the survival of adults is available from telemetry data that may assist in interpreting the dynamics of the adult portion of the population. However, in the absence of survival data and if monitoring of this population occurs entirely by remote photography (i.e., without the assistance of radio collars or marked animals), use of age ratios alone may not allow for an adequate understanding of the dynamics of this deer population.

One alternative to age ratios may be to rely upon predictable relationships between rainfall and deer abundance to understand current deer dynamics and to predict future dynamics. Indeed, Marshal et al. (2002) used deer harvest as an index to deer abundance and reported a positive linear association between harvest in any year and rainfall the previous year. That relationship included a large amount of variation, so efforts to predict deer abundance may require relationships between more closely related variables, such as between browse biomass and deer abundance rather than between rainfall and reported harvest. Another alternative may take advantage of the positive correlation between estimated deer abundance and number of deer observed in photographs/catchment-day. A longer-term study with a larger sample size would be necessary to produce a relationship that could predict deer abundance simply from photograph counts. Nonetheless, it does suggest a means to evaluate density and rate

of change of this deer population without the need for marked animals or the use of age ratios to evaluate dynamics.

The two-sample Lincoln-Peterson method has three assumptions: the population is closed to births, deaths, immigration, or emigration during sampling; all animals have an equal probability of capture or sighting in each sample; and marks are not lost, overlooked, or misinterpreted by the investigator (Otis et al. 1978). This population likely met the assumption of closure during photographic sampling. Observations from telemetry flights confirmed that collared deer moved little during spring and stayed relatively close to water sources (Marshal et al. unpublished data). During that time of limited resources, it was unlikely that animals would choose to leave a familiar area. For similar reasons, it was probably unlikely for new immigrants to enter the study area. Further, births did not generally occur in this area until after rains in summer, after which deer stopped visiting catchments and photographic sampling ended. Deaths among uncollared deer probably occurred over the sampling period; indeed, we lost some radiocollared deer during spring. But because of the short photographic sampling period, losses were probably minimal, and so the effect on bias was minimal.

Probability of detection in a photograph was a function of how frequently animals visited catchments to drink. We had no reason to expect a difference in frequency of drinking between collared and uncollared deer. However, a violation of this assumptions may have resulted in a population estimate for 2001 that appeared relatively low and precise, compared to the other estimates during the study (Table 1). If, by chance, the number of marked deer in photographs was greater than would be expected from their proportion in the population, or if the number of unmarked deer was less than would be expected, population estimates would be biased low, but would also have relatively narrow confidence intervals, as observed for the 2001 estimate.

There may have been sex differences in drinking frequency that could influence sex ratios calculated from these data. Females in the Belmont and Picacho Mountains, Arizona, visited catchments to drink on average once/day, whereas males visited catchments once/1-4 days (Hervert and Krasuman 1986). Hazam and Krausman (1988), however, reported a drinking frequency of 1.1 times/day for males in the Picacho Mountains. If males did visit catchments less frequently than females, the result would be an underestimate of their proportion in the population.

The reliability of our herd composition estimates depended on the accuracy with which we identified adult females from young females. Factors that affect this ability include head or body position of deer when photographed (identifying features obscured), distance from the camera (further deer appear smaller and thus younger), and whether a young deer is standing next to an adult (identification by size comparison). Forage conditions may also affect the accuracy of identification, because in years with abundant forage, young grow more rapidly and by their first birthday appear to be similar in size to adults. When we were unsure about the classification of a deer, we categorized it as undetermined and removed it from subsequent analysis. Nonetheless, there exists the possibility of misclassification, which was a weakness of this method. For the cost and logistics, however, more accurate methods were not available.

An assumption that potentially was violated was that of no loss of marks. After

2001, transmitters began to fail, and we approximated the number of marked animals in the population. Our method involved estimating number of nontransmitting deer that survived to be photographed and was based on the assumptions that nontransmitting deer had the same survival rates as transmitting deer, that transmitter failure and not emigration was occurring, and that transmitter failure was independent of the fate of the animal. Because we could not monitor nontransmitting deer, we could not evaluate these assumptions. Nevertheless, there is some support for our method of estimating number of marked deer in the positive correlation between number of deer observations/ catchment-day, which was not based on number of collared deer, and estimates of population abundance, which were. Overall, we believe these methods were useful for monitoring a low-density population of cryptic animals, and has allowed a level of statistical rigor that had not before been applied to this deer population.

Although it is clear that deer populations in California's Sonoran Desert are at low density, our results more importantly have demonstrated the highly variable nature of a population occupying an arid environment. Management of such populations is difficult, particularly where harvest is a management objective. Efforts to reduce variability and increase predictability in arid system are not likely to succeed, because they require management of factors outside the control of wildlife biologists (e.g., rainfall and forage availability). A more likely possibility is to implement a management strategy that recognizes the inherent variability of wildlife populations in arid environments and to conserve the natural systems (i.e., habitat) that allow those populations to fluctuate.

ACKNOWLEDGMENTS

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Appendix 1. Information used to calculate population estimates in East Chocolate-Cargo Muchacho Area, California, 1999-2004.

Year	Catchments	Catchment -days	No. nontransmitting deer	Survival rate estimate	n_1[a]	n_2[b]	m_2[c]
1999	2	20	0	-	14	312	79
2000	4	66	0	-	23	776	201
2001	4	95	0	-	21	587	314
2002	4	39	3	0.962	21[d]	1070	221
2003	7	23	7	0.958	21[d]	608	154
2004	4	28	14	0.788	20[d]	491	108

[a] No. collared deer in the population

[b] No. deer observed in photographs

[c] No. collared deer in photographs

[d] No. marked deer in population estimated from number of nontransmitting deer and survival rate