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ESTIMATING COYOTE DENSITY FROM MARK-RESIGHT SURVEYS

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Abstract: Because studies of coyote (*Canis latrans*) density have lacked standardization and estimates of variance, we conducted a mark-resight study of 17 coyotes on the Rocky Mountain Arsenal (RMA), Colorado, to provide the basis for recommending survey design. Radiolocations of some coyotes on and off the study area verified that geographic closure of the population was violated. Thus, we estimated coyote population size with an estimator that allows for immigration and emigration. Using program NOREMARK (a mark-resight program; Neal et al. 1993), we estimated that a daily population of 50 (95% CI = 34–81, 0.71/km²) coyotes and a total population of 73 (95% CI = 50–121) coyotes used the study area during December 1990–January 1991. With Monte Carlo simulations in program NOREMARK, we demonstrated that if $\geq 20\%$ of the population is marked and observed during each survey, it is more cost effective to decrease bias and improve precision by conducting additional surveys rather than capturing and marking more coyotes. We recommend conducting simulations with program NOREMARK to determine the best way to decrease bias and improve precision while minimizing cost of a coyote mark-resight study.

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Key words: bias, *Canis latrans*, closure, Colorado, coyote, density, emigration, immigration, NOREMARK, precision, radio telemetry, Rocky Mountain Arsenal, survey.

Although coyote populations have been widely studied, densities have rarely been estimated with mark-resight methods. Indices such as scent station surveys (Linhart and Knowlton 1975), scat deposition rates (Clark 1972), responses to sirens (Okoniewski and Chambers 1984), den counts (Pyrah 1984), and coyote sightings per day (Dekker 1989) might provide information on population trends but may not be appropriate for comparisons among areas. Researchers have estimated coyote density from a modified Lincoln-Petersen mark-recapture (Clark 1972) or mark-recapture estimator using radioisotope fecal tagging (Knowlton et al. 1985, Crabtree 1989), but these and other studies (Pyrah 1984, Andelt 1985, Babb and Kennedy 1989, Gese et al. 1989), with the exception of Camenzind (1978), have not included measures of variance. Only Todd et al. (1981) observed coyotes by conducting mark-resight surveys along transects. Many coyote density estimates (Pyrah 1984, Andelt 1985, Babb and Kennedy 1989, Gese et al. 1989) also were derived with estimators that were not based on testable assumptions (Otis et al. 1978), and therefore, were ad-hoc estimators with unknown statistical properties (White et al. 1982).

To estimate population size with precision and without bias, population closure must be determined. Population closure is defined as no births, deaths, immigration, or emigration from the study area. Radio telemetry may be used to determine if the study area contains all marked animals during all sighting occasions (Kufeld et al. 1987, Eberhardt 1990, Neal et al. 1993) and can aid in selecting an open or closed population estimator. No studies of coyotes have attempted to verify the closure assumption using radio telemetry, although a relative measure of the closure violation from radioisotope fecal-tagging and a possible correction has been suggested (Crabtree et al. 1989).

Program NOREMARK (Neal et al. 1993) was developed to estimate population size from mark-resight data. NOREMARK estimators are based on mark-recapture assumptions including the population is closed, animals do not lose their marks, all marked animals are correctly identified, recorded, and counted, and all animals (both marked and unmarked) have a similar probability of being captured (sighted) on a particular occasion (Otis et al. 1978). NOREMARK also has precise and unbiased estimators for determining a population estimate where immigration and emigration commonly occur (Neal et al. 1993). We present a density estimate for coyotes on the RMA and make recommendations for future coyote mark-resight studies.

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STUDY AREA

The RMA was 70 km² at the northern boundary of Stapleton International Airport near Commerce City, Colorado. Average elevation was 1,600 m with maximum topographical relief of approximately 60 m. Climate was characterized by low humidity, and temperatures averaged -1 C in January and 23 C in July (Natl. Oceanic and Atmos. Adm. 1990). Precipitation averaged 37 cm annually with the majority falling between April and July.

The RMA was primarily a grassland dominated by cheatgrass (*Bromus tectorum*), crested wheatgrass (*Agropyron cristatum*), blue grama (*Bouteloua gracilis*), perennial summercypress (*Kochia americana*), silvery wormwood (*Artemisia filifolia*), and rubber rabbitbrush (*Chrysothamnus nauseosus*) (Weber 1976). Trees such as plains cottonwood (*Populus sargentii*), New Mexican locust (*Robinia neomexicana*), peach-leaved willow (*Salix amygdaloides*), and Russian-olive (*Elaeagnus angustifolia*) occurred in localized stands.

METHODS

We captured 17 coyotes (3 ad F, 4 ad M, 9 juv F, and 1 juv M), using Softcatch® traps (Woodstream Corp., Lititz, Pa.) (Linhart et al. 1986) (3,920 trap nights) with attached tranquilizer tabs (Balsler 1965, Linhart et al. 1981) and snares (Nellis 1968) (100 snare nights) from 7 July 1990 to 21 January 1991. Trap sets and capture locations were relatively uniform throughout the RMA. We marked coyotes with standard Roto-tags® (Nasco, Fort Atkinson, Wis.) and 167 mHz radio-telemetry collars wrapped with brightly colored vinyl plastic electrical tape to enhance visual identification.

We systematically surveyed coyotes from a vehicle on the RMA during 7 snow-covered mornings in December 1990–January 1991 (Table 1). We do not believe that the presence of

snow biased population estimates by altering the proportion of marked to unmarked coyotes observed, but rather facilitated our ability to see coyotes. All surveys were conducted by the same observer. Each survey began shortly after sunrise and continued for 3.0–3.5 hours. We drove section roads (each 1.6 km) at speeds averaging 29 km/hour during each survey. We started in the southeast corner of the RMA and traveled to its northern boundary, west 1.6 km, then to the southern boundary of the RMA, and continued by alternating the direction of travel from north to south until the entire site was surveyed. We alternated routes from north-south (59 km/survey) to east-west (62 km/survey) during surveys on subsequent days.

We refined our ability to differentiate marked and unmarked coyotes by observing coyotes ($n = 34$ marked and 10 unmarked) with a spotting scope or binoculars while radiotracking from July to December 1990, before our surveys began. Using a spotting scope or binoculars during our surveys, we also identified marked and unmarked coyotes. We recorded number of coyotes, direction of travel, and distance from observer. Estimated sighting distances averaged 170 m, although we believe that we could accurately differentiate between marked and unmarked coyotes at ≤ 600 m. After the number of marked and unmarked coyotes was recorded, we verified the status (radiocollared, uncollared) of each coyote and identified marked animals by scanning all coyote frequencies with a radio-telemetry receiver. We found no discrepancies between visual identification and telemetry verification of coyotes during 46 observations of ≥ 1 marked or unmarked coyotes/group. Immediately after each survey, we used radio telemetry to determine the number of marked coyotes on the RMA but not observed, which coyotes were off the area during the survey, and to verify that all marked coyotes were still alive.

We used the immigration/emigration estimator in program NOREMARK (Neal et al. 1993:440) to generate a population estimate. We chose this estimator because geographic closure was violated; some individual coyotes were located on and off the study area during subsequent surveys. In addition, as we captured and marked more coyotes, the number of marked coyotes on or near the RMA remained constant (Table 1). We calculated density by dividing the population estimate by the area of the RMA.

NOREMARK uses the Joint Hypergeometric

Table 1. Coyote survey data collected on Rocky Mountain Arsenal (RMA), Commerce City, Colorado, during December 1990–January 1991.

Date	No. marked coyotes	No. marked coyotes on or near RMA	No. marked coyotes on RMA	No. coyotes observed		Chapman corrected Lincoln/Petersen daily population estimate ^a (95% CI) ^b
				Marked	Unmarked	
23 Dec	14	12	10	3	8	32.0 (13.2–50.8)
24 Dec	14	12	9	0	10	
29 Dec	14	12	10	2	1	13.7 (7.5–19.8)
30 Dec	14	12	10	2	13	57.7 (13.5–101.9)
16 Jan	16	12	10	3	5	23.8 (10.9–36.6)
21 Jan	17	12	12	2	11	59.7 (13.4–105.9)
23 Jan	17	12	11	2	5	31.0 (9.5–52.5)
\bar{x} daily population estimate						49.7 (34.4–80.7)
Total population estimate						73.0 (49.9–120.8)

^a Calculated with program NOREMARK (Neal et al. 1993).^b Calculated with program NOREMARK using a profile likelihood confidence interval (Neal et al. 1993).

Maximum Likelihood Estimator (JHMLE) because the lower confidence bound is never lower than the minimum number alive and it generates smaller confidence intervals than either a mean or median Lincoln-Petersen estimate by incorporating all point estimates into 1 estimate (White and Garrott 1990). The JHMLE has performed well in evaluations (Bartmann et al. 1987, White and Garrott 1990, Neal et al. 1993). NOREMARK calculates a 95% profile likelihood confidence interval on the basis of the mean of the population size estimates from each survey (Neal et al. 1993).

We conducted Monte Carlo simulations with program NOREMARK using an immigration/emigration model (Neal et al. 1993) to investigate the potential effects of varying the proportion (0.20–0.50) of coyotes marked, number (7–15) of surveys, and the proportion (0.10–0.50) of the population observed on percent bias (the difference of the \bar{x} of the simulated estimates and the true population size divided by the true population size $\times 100$) of the population estimate and to estimate percent confidence interval length (difference of the upper and lower confidence interval endpoints divided by the population size $\times 100$). We conducted 1,000 replications for each scenario. We used a simulated total population size of 75 coyotes with 70% present on the study area.

RESULTS

Radio telemetry confirmed geographic closure was violated. Three coyotes (1 ad M and 2 juv F) were regularly located on and off the RMA. One adult male was marked on the RMA

but was seldom located in the area. Three coyotes (1 ad F, 1 ad M, and 1 juv F) were captured on the RMA, located off the area shortly after release, and could not be subsequently located. One juvenile female was located for approximately 10 days on the RMA but could not be subsequently located. Nine coyotes (2 ad F, 1 ad M, 5 juv F, and 1 juv M) were always located on the RMA. We marked 14 coyotes prior to the 23 December 1990 survey and 17 coyotes prior to the 21 January 1991 survey. We located or observed 12 marked coyotes on or near the RMA during each survey (Table 1).

Using the immigration/emigration estimator in program NOREMARK, we estimated a mean daily population of 50 (95% CI = 34–81) coyotes and a total population of 73 (95% CI = 50–121) coyotes that used the RMA at various times (Table 1). An average of 10.3 (SE = 0.36) marked coyotes were found on the RMA and were subject to resighting during each of the 7 surveys (Table 1). We observed 19% (14 of 72) of the marked coyotes that were present on the RMA during the 7 surveys (Table 1). Sighting probabilities for individual marked coyotes averaged 15% (range 0–43%). The minimum number of coyotes known alive on the RMA was 23, with 10 marked and 13 unmarked and 12 marked and 11 unmarked animals located or observed on 30 December 1990 and 21 January 1991, respectively. Observed group sizes ($n = 46$) averaged 1.5 animals.

Monte Carlo simulations using an immigration/emigration model demonstrated that percent bias and percent confidence interval length decreased by increasing the proportion of individuals marked in the population or increas-

Table 2. Percent bias (PB) and percent confidence interval length (PCIL) for 1,000 Monte Carlo simulations of each scenario using the immigration/emigration model in NOREMARK (Neal et al. 1993) with 20% of the population observed and 70% of the total population of 75 present in the study area.

Proportion marked	No. sighting occasions							
	7		10		12		15	
	PB	PCIL ^a	PB	PCIL	PB	PCIL	PB	PCIL
0.20	5.43 ^b	61.39	3.18	43.50	2.45	37.81	3.25	33.76
	4.90 ^c	58.78	2.74	41.52	2.44	36.28	2.85	32.28
0.30	3.16	39.09	1.81	30.88	1.26	27.65	1.28	24.56
	2.87	37.17	1.73	29.43	1.11	26.35	0.96	23.37
0.40	1.05	29.49	0.45	24.01	0.43	21.74	0.43	19.15
	1.03	27.96	0.28	22.72	0.33	20.59	0.23	18.10
0.50	-0.24	23.29	0.45	19.60	0.16	17.70	-0.68	15.36
	-0.41	21.89	0.08	18.33	0.06	16.60	-0.94	14.36

^a PCIL = ([95% upper - 95% lower confidence interval endpoints]/population size × 100).

^b Represents the total population.

^c Represents the daily population.

ing the number of surveys (Table 2). Percent bias and percent confidence interval length also decreased by increasing the proportion the population observed (Table 3).

DISCUSSION

Radio telemetry verified that population closure was violated for the RMA coyote population. We used an open population estimator because a closed estimator would have underestimated the coyote population. We estimated that 73 coyotes used the RMA, but an average of 50 coyotes were there at any particular time. These findings further substantiate that density estimates are less than the number of coyotes using an area (Windberg and Knowlton 1988). Because of the presence of transient coyotes that range over large areas (Andelt 1985, Roy and Dorrance 1985, Gese et al. 1989), clo-

sure is likely violated in all coyote population studies.

Comparing coyote densities among areas is difficult because of lack of standardized estimation techniques (Babb and Kennedy 1989) and measures of variance. Therefore, we are hesitant to compare our density of 0.71 (95% CI = 0.49–1.16) coyotes/km² on the RMA with other studies. We believe the assumptions of mark-recapture (mark-resight) models (Otis et al. 1978) have been met in this study because no coyotes lost their radio collars and we correctly identified all marked coyotes as marked. We assumed marked coyotes were not affected by capture or handling and had similar resighting probabilities as unmarked animals. However, if the assumption of homogeneous sighting probabilities among animals is violated for smaller populations, estimates will be biased (Neal et al. 1993). If all mark-resight assumptions are met, the immigration/emigration estimator should have low bias and good precision (Neal et al. 1993).

Problems in estimating coyote density include a small proportion of individuals marked, low sighting probabilities, and possible violation of closure with immigration and emigration or uncertainty of the presence of marked coyotes (Clark 1972, Todd et al. 1981). With Monte Carlo simulations, we demonstrated that percent bias and percent confidence interval length decreased by conducting more surveys, increasing the proportion of individuals marked, or increasing the proportion of the population observed.

Percent bias and percent confidence interval length also will be affected by study area size

Table 3. Percent bias (PB) and percent confidence interval length (PCIL) for 1,000 Monte Carlo simulations of each scenario using the immigration/emigration model in NOREMARK (Neal et al. 1993) with 20% of the population marked, 7 surveys, and 70% of the total population of 75 present on the study area.

Proportion of population observed	PB		PCIL ^c	
	Total ^a	Daily ^b	Total	Daily
0.10	15.18	14.62	144.87	135.43
0.20	5.43	4.90	61.39	58.78
0.30	3.74	2.96	40.91	37.81
0.40	2.37	1.40	32.18	28.61
0.50	0.82	0.19	26.16	22.20

^a Represents the total population.

^b Represents the daily population.

^c PCIL = ([95% upper - 95% lower confidence interval endpoints]/population size × 100).

and the associated population size and number of animals observed (Neal et al. 1993). If the proportion of animals marked, sighting probabilities, number of surveys, and proportion of the total population found in another study area at a given time are the same as the RMA, but if the total population size is <75, then percent bias and percent confidence interval length will be larger. To compensate for this decrease in precision, given that the other parameters remain the same as at RMA, a larger study area and/or longer surveys would be required. We observed 9.6 coyotes/survey. Thus, to obtain precision similar to that in this study, assuming the above parameters will be similar to RMA, we suggest conducting pre-study surveys to determine the study area size or length of surveys that will be needed to observe about 9.6 coyotes and then marking a similar proportion of the coyotes. If 9.6 coyotes are observed but if sighting probabilities are lower than at the RMA, more coyotes will need to be marked to achieve a similar proportion of marked coyotes and similar precision. The number of animals observed per km is not a useful index of coyote abundance unless sighting probabilities are constant.

MANAGEMENT IMPLICATIONS

Trade-offs between costs and benefits (i.e., having a less biased and more precise estimate) of capturing and marking a larger proportion of the population, conducting additional surveys, or increasing the proportion of animals observed should be evaluated along with study objectives when designing a coyote mark-resight study. We estimate that each survey on the RMA cost \$29.00 (3.5 hr [\$6.25/hr] + 60 km/survey [\$0.12/km]). Eight additional surveys (total of 15 surveys) would decrease percent bias from 5.43 to 3.25%, decrease percent confidence interval length from 61.39 to 33.76% (Table 2), and cost approximately \$233.00. To achieve a similar decrease in percent confidence interval length, we would need to increase the proportion of coyotes marked from 0.20 to about 0.35 (Table 2), which would require capturing and collaring about 13 ($0.35/0.20 \times 17$) additional coyotes. This would be more expensive than increasing the number of surveys. Andelt (1980) estimated aerial darting and a transmitter cost \$305.00/coyote captured, and trapping and a transmitter cost \$266.00 (\$383.00 - \$117.00)/coyote captured. These costs would have been higher on the RMA because of an increase in

helicopter rental costs, and we averaged 1 coyote/236 trap nights, whereas Andelt (1980) averaged 1 coyote/54 trap nights.

We believe aerial surveys would improve coyote mark-resight estimates by increasing the proportion of the population observed. To decrease percent bias and improve percent confidence interval length similar to that achieved by increasing automobile surveys from 7 to 15 (above) or increasing the proportion of the population marked from 0.20 to 0.35 (above), we would need to increase the proportion of the population observed from 0.20 to about 0.40 if 20% of the population is marked and if 7 surveys are conducted (Table 3). We estimate that 7 surveys in our study area using a helicopter would have cost about \$6,530.00 (2 hr [\$6.25/hr]/survey + 2 flight hr/survey [\$460.00/hr]), whereas an airplane would have cost about \$1,200.00 (2 hr [\$6.25/hr]/survey + 2 flight hr/survey [\$80.00/hr]). Although we are uncertain how much we could increase the proportion of the population observed with aerial surveys, it is likely that a helicopter and 7 surveys (\$6,530.00) would be much more expensive than conducting 15 surveys (\$435.00) from an automobile. In conclusion, we recommend conducting simulations with program NOREMARK (Neal et al. 1993) to determine the best parameters for decreasing bias and improving precision while minimizing cost of a mark-resight study.

LITERATURE CITED

- ANDELT, W. F. 1980. Capturing coyotes for studies of their social organization. *Wildl. Soc. Bull.* 8:252-254.
- . 1985. Behavioral ecology of coyotes in South Texas. *Wildl. Monogr.* 94. 45pp.
- BABB, J. G., AND M. L. KENNEDY. 1989. An estimate of minimum density for coyotes in western Tennessee. *J. Wildl. Manage.* 53:186-188.
- BALSER, D. S. 1965. Tranquilizer tabs for capturing wild carnivores. *J. Wildl. Manage.* 29:438-442.
- BARTMANN, R. M., G. C. WHITE, L. H. CARPENTER, AND R. A. GARROTT. 1987. Aerial mark-recapture estimates of confined mule deer in pinyon-juniper woodland. *J. Wildl. Manage.* 51:41-46.
- CAMENZIND, F. J. 1978. Behavioral ecology of coyotes on the National Elk Wildlife Refuge, Jackson, Wyoming. Pages 267-294 in M. Bekoff, ed. *Coyotes: biology, behavior, and management*. Academic Press, New York, N.Y.
- CLARK, F. W. 1972. Influence of jackrabbit density on coyote population change. *J. Wildl. Manage.* 36:343-356.
- CRABTREE, R. L. 1989. Socio-demography of an unexploited coyote population. Ph.D. Diss., Univ. Idaho, Moscow. 80pp.

- , F. G. BURTON, T. R. GARLAND, D. A. CATALDO, AND W. H. RICKARD. 1989. Slow-release radioisotope implants as individual markers for carnivores. *J. Wildl. Manage.* 53:949–954.
- DEKKER, D. 1989. Population fluctuations and spatial relationships among wolves, *Canis lupus*, coyotes, *Canis latrans*, and red foxes, *Vulpes vulpes*, in Jasper National Park, Alberta. *Can. Field-Nat.* 103:261–264.
- EBERHARDT, L. L. 1990. Using radio-telemetry for mark-recapture studies with edge effects. *J. Appl. Ecol.* 27:259–271.
- GESE, E. M., O. J. RONGSTAD, AND W. R. MYTTON. 1989. Population dynamics of coyotes in south-eastern Colorado. *J. Wildl. Manage.* 53:174–181.
- KNOWLTON, F. F., L. A. WINDBERG, AND C. E. WAHLGREN. 1985. Coyote vulnerability to several management techniques. *Proc. Great Plains Wildl. Damage Control Workshop.* 7:165–176.
- KUFELD, R. C., D. C. BOWDEN, AND D. L. SCHRUPP. 1987. Estimating mule deer density by combining mark-recapture and telemetry data. *J. Mammal.* 68:818–825.
- LINHART, S. B., G. J. DASCH, C. B. MALE, AND R. M. ENGEMAN. 1986. Efficiency of unpadded and padded steel foothold traps for capturing coyotes. *Wildl. Soc. Bull.* 14:212–218.
- , ———, AND F. J. TURKOWSKI. 1981. The steel leghold trap: techniques for reducing foot injury and increasing selectivity. Pages 1560–1578 in J. A. Chapman and D. Pursley, eds. *Worldwide Furbearer Conf., Worldwide Furbearer Conf., Inc., Frostburg, Md.*
- , AND F. F. KNOWLTON. 1975. Determining the relative abundance of coyotes by scent station lines. *Wildl. Soc. Bull.* 3:119–124.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1990. Local climatological data annual summary-Denver, Colorado. *Natl. Clim. Data Cent., Asheville, N.C.* 8pp.
- NEAL, A. K., G. C. WHITE, R. B. GILL, D. F. REED, AND J. H. OLTERMAN. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. *J. Wildl. Manage.* 57:436–450.
- NELLIS, C. H. 1968. Some methods for capturing coyotes alive. *J. Wildl. Manage.* 32:402–405.
- OKONIEWSKI, J. C., AND R. E. CHAMBERS. 1984. Coyote vocal response to an electronic siren and human howling. *J. Wildl. Manage.* 48:217–222.
- OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* 62. 135pp.
- PYRAH, D. 1984. Social distribution and population estimates of coyotes of north-central Montana. *J. Wildl. Manage.* 48:679–690.
- ROY, L. D., AND M. J. DORRANCE. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. *J. Wildl. Manage.* 49:307–313.
- TODD, A. W., L. B. KEITH, AND C. A. FISCHER. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. *J. Wildl. Manage.* 45:629–640.
- WEBER, W. A. 1976. *Rocky Mountain flora.* Colorado Assoc. Univ. Press, Boulder. 479pp.
- 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 Natl. Lab. LA-8787-NERP, Los Alamos, N.M.* 235pp.
- , AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data.* Academic Press, New York, N.Y. 383pp.
- WINDBERG, L. A., AND F. F. KNOWLTON. 1988. Management implications of coyote spacing patterns in southern Texas. *J. Wildl. Manage.* 52:632–640.

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