

SOCIODEMOGRAPHY OF AN UNEXPLOITED COYOTE POPULATION

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AUTHORIZATION TO SUBMIT
DISSERTATION

This dissertation of Robert L. Crabtree, submitted for the degree of Ph.D. with a major in Forestry, Wildlife, and Range Sciences and titled "Sociodemography of an unexploited coyote population," has been reviewed in final form, as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

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DEDICATION

Although I considered many appropriate thoughts, from Einstein's writings to the Tao Te Ching, this dissertation is dedicated to the coyotes themselves, the sages of the desert that allowed me the chance to observe and study them.

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PREFACE

This dissertation is written in the form of three independent manuscripts ready for submittal to a professional journal. As such, the format of the manuscripts, each corresponding to a chapter, adheres to the guidelines of the Journal of Wildlife Management. This research was conducted with various other colleagues. Thus, the manuscripts will be submitted with multiple authorship and the personal pronoun "we" is used occasionally.

ABSTRACT

We estimated socio-demographic parameters of a natural, unexploited coyote (Canis latrans) population in the shrubsteppe of southcentral Washington from 1984 to 1988. A large proportion of the population was sampled (145 individual captures). Adult coyotes were categorized by social class based on physical characteristics, space use, site fidelity, movements patterns, and social interactions with other coyotes. Adult coyotes exhibited a high degree of spatial structuring according to well-defined social classes and subclasses. Territorial social groups (67% of the spring prewhelping population) contained an older-aged alpha pair and an average of 1.4 young adult associates. Loners or non-territorial individuals comprised 33% of the spring population and were divided into 2 major social classes: solitary residents (18%) with younger and older subclasses and nomads (15%). The average range size of social group members, solitary residents, and nomads was 14.5, 54, and 220 km², respectively. Territories were contiguous, non-overlapping, and uniform in size. Loners were located on the periphery of and in narrow corridors between territorial ranges. A healthy class of 2 to 4 year-old mature loners form a reservoir of potential territorial replacements, followed by a young group of 1 and 2 year-old nomads. Additional intraspecific "pressure" may result from old-aged solitary residents that were former territorial owners.

Successful breeding occurred at ages 2 through 6 for alpha females ranging in ages 2 through 11 years. Reproductive failure among territorial groups was 27% and

mainly involved breeding adults age 6 years and older. Population productivity was very low at 0.62 pups per female, whereas average litter size was 5.6. Pups weighed 27% below average and incurred a 58% mortality rate during the first 14 weeks following birth. The overall annual survival rate was 0.90 and was strongly a function of social class ($P < 0.001$). Emigration from the population was low (16%) and consisted primarily of pups and associates. Immigration was low (6%) and limited mainly to younger nomads. Density averaged 0.41 and 0.38 coyotes per km^2 for an absolute density estimate and complete enumeration, respectively. The ALE coyote population was stable and appeared to have a high degree of intraspecific strife. We propose a theory of population regulation similar to that described for wolves (Canis lupus) and discuss the possible compensatory responses to exploitation.

CHAPTER I

SLOW-RELEASE RADIOISOTOPE IMPLANTS
AS INDIVIDUAL MARKERS FOR CARNIVORES

SLOW-RELEASE RADIOISOTOPE IMPLANTS AS INDIVIDUAL MARKERS FOR
CARNIVORES

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Abstract: We developed a technique that identifies an individual animal by labeling its excreta. Various gamma-emitting radioisotopes were incorporated into implantable discs made of polylactic acid (PLA), a biodegradable polymer. Laboratory testing and field studies with coyotes (Canis latrans) demonstrated that the 6 radioisotopes evaluated were released from the subcutaneously-implanted polymer at a relatively constant rate after an initial burst phase and allowed a minimum marking period of 6 months. Prototype slow-release implants were used in a field study of coyotes to estimate population abundance, estimate home range, assess individual diets, and examine social and scent-marking behavior. The implant technique has potential widespread application in studies of wild carnivores.

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Carnivores are difficult to study due to secretive behavior, high mobility, low population densities, and tendency to inhabit remote and rugged areas. These

difficulties have prompted biologists to continually evaluate new techniques for studying carnivore behavior and population ecology. Pelton and Marcum (1977) stated that individualized feces tags would provide an excellent means to study carnivore movements and interactions. They discussed the advantages of radioisotope feces-tagging over traditional mark-recapture or mark and reobserve techniques for estimating carnivore populations. Advantages included substantially larger samples sizes and the elimination of the need to recapture animals.

Radioisotope tagging has been conducted on canids (Green 1978, Davison 1980, Knowlton et al. 1986), felids (Conner 1982), bears (Ursus spp.) (Pelton and Marcum 1977), mustelids (Kruuk et al. 1980, Shirley et al. 1988), raccoons (Procyon lotor) (Conner and Labisky 1985), deer (Odocoileus spp.) (Kinningham et al. 1980), rabbits (Nellis et al. 1968, Green and Dunsmore 1978), rodents (Gentry et al. 1971, Tamarin et al. 1983) and game birds (McCabe 1974) to estimate abundance. These studies utilized radioisotopes to aid in the study of population abundance, movements, genetics, and energetics.

Crabtree (1989) individually marked and identified an animal's excreta to estimate population density and examine the social and scent-marking behavior of coyotes in the semi-arid, shrubsteppe region of eastern Washington. In order to meet these objectives the marking system required 15-20 distinguishable marks, marks which produced no significant adverse health effects, and marks that persisted for 6 months.

We chose radioactive markers over non-radioactive markers such as dyes and particles (Evans and Griffith 1973, Sowls and Minnamou 1963) because they were closer to meeting the above requirements. However, only zinc-65 (⁶⁵Zn) and manganese-54 (⁵⁴Mn) satisfied our requirements and the selection criteria described by Pelton and Marcum (1977). Intramuscular

injection of ^{65}Zn and ^{54}Mn chloride solutions have been used successfully in field studies to mark animal feces for ≤ 300 days. Use of many otherwise acceptable radioisotopes for marking feces is limited only by their short body-retention times. Recent developments in human medicine using slow-release drug-delivery devices (Blackshear 1979) offered a way for extending the body-retention times of radioisotopes. By incorporating a radioisotope into an implant that slowly releases the isotope into an animal's body, the body retention time of the isotope could be greatly increased, extending the length of the marking period, and providing an additional number of individualized markers.

We evaluate an individualized, animal marking system that incorporates a radioisotope into an implantable, slow-release polymer. We describe the successful use of the prototype implant in a field study with coyotes and discuss actual and potential applications.

N. R. Gordon and R. T. Webster assisted with laboratory testing and J. W. Blatt and C. J. Perham assisted with field studies. E. D. Ables, R. L. Hartmann, and B. T. Kelly provided helpful suggestions on the manuscript. L. M. Merkle typed and edited revisions. This research was supported by U.S. Department of Energy Contract DE-AC06-76RLO-1830 to Pacific Northwest Laboratory and the Northwest Organization of Colleges and Universities for Science.

METHODS

The implant material used in this study, PLA, is probably the most widely used and well understood slow-release material available. We specifically chose poly (DL-lactide) (Polysciences, Inc., Warrington, Pa). Its properties are well known and it breaks down into lactic acid, a natural metabolite of muscular contraction. In vivo, in vitro, and field tests with wild-captured coyotes were used to evaluate

the slow-release polymer. Commercially available radioisotopes, ^{54}Mn , ^{65}Zn , cobalt-57 (^{57}Co), cadmium-109 (^{109}Cd), antimony-125 (^{125}Sb), and cesium-134 (^{134}Cs) in 0.5 N HCL solution, were each added to individual beakers containing a preweighed amounts of PLA, then mixed thoroughly, and allowed to dry overnight. One-tenth g aliquots of the mixture were loaded into individual 6.0 mm diameter tablet molds. The molds were slowly heated to 80 C or until the PLA mixture melted into a clear solid. The tablets were cooled, removed from the mold, and placed in individually marked plastic bags and stored until used. The PLA tablets, each containing approximately 20 μCi of 1 of 6 different radioisotopes, were implanted subcutaneously in the upper shoulder region of 2 adult coyotes to test their performance. The animals were confined to individual metabolism cages and provided with water and dry dog food. Samples of feces and urine were collected over a 20-week period to determine the detectability period and relative release rates of the isotopes. In addition to the constrained animal study, we approximated the total release period and release rates through in vitro testing. A ^{65}Zn tablet of known radioactivity was suspended in each of 10 flasks containing 200 mL of 23 C physiological saline solution from which an aliquot was taken and counted each week. At the end of 20 weeks the implant itself was recounted to determine its residual radioactivity.

Field testing was conducted on wild-captured coyotes. Twenty-five coyotes were administered individualized feces-tags by implanting them with 1 or 2 PLA implants containing 20 μCi of a single isotope. Each animal was fitted with a radio-transmitter collar, released, and radiotracked for 3 months. At the end of the tracking period, scats were collected from the home-range areas of the radio-collared coyotes. Scats were collected for ≤ 2 years after

implantation to determine the overall detectability period. All feces, urine, and in vitro samples were analyzed by gamma spectrometry using a well-type sodium-iodide crystal connected to a multi-channel, pulse-height analyzer.

RESULTS

Implant Evaluation

The rate of release for radioisotopes in PLA implants using penned coyotes resulted in an initial burst phase that diminished after 80 days (Fig. 1). Radioactivity in feces and urine samples varied over time and was attributable to differences in coyote metabolism, food and water intake, and sampling error. Of the 6 isotopes evaluated, ^{65}Zn and ^{57}Co represent the extreme cases of release behavior. The initial release phase for ^{57}Co was strong whereas the peak for ^{65}Zn was dampened by its long retention time. The in vitro tests indicated similar results. The release rate from start to finish declined about 10-fold. The ^{65}Zn activity remaining at 20 weeks in in vitro implants was 30.6% ($n = 10$) with an estimated 202 day release period.

All radioisotopes appeared acceptable as feces tags (Table 1). The major route of elimination for ^{65}Zn and ^{54}Mn was feces elimination. Although all 6 isotopes were readily detectable in 10 cc samples of urine at 100 days, only ^{57}Co was a strong urine marker. Urine is a major route of elimination for isotopes that are biological analogs to physiological salts and consequently have short biological half-lives (e.g., 10 days for ^{57}Co and sodium-22 (^{22}Na)).

Research Applications

Population and Group Size Estimation.-- Feces-tagging has gained widespread attention as a modified mark-recapture technique to estimate population abundance of carnivores. A major problem plaguing traditional mark-recapture studies is bias associated with unequal recapture probabilities.

However, this bias is eliminated with feces-tagging studies because animals need not be recaptured.

Previous feces-tagging studies have used the Petersen-Lincoln or Schnabel (see Davis and Winstead 1980) estimators. A sample of animals are captured, administered a radioisotope feces-tag, and released. After an accumulation period scats are collected from throughout a pre-defined sampling area to provide an estimate of the ratio of marked to unmarked animals in the population.

A critical assumption of such mark-recapture methods is that the animal population is closed to ingress and egress. This assumption is commonly violated, and can result in severely biased estimates. However, individualized feces-tags can provide a relative measure of closure violation and possible correction.

In our field study, we always identified numerous scats (20-40) from resident animals. Animals that violated closure such as transients, and residents that lived off the edge of the sampling area, had < 15 each in the sample of marked scats. The number of scats found from any particular animal appeared to be a function of its residency time on the sampling area during the scat accumulation period. We found no marked scats from 7 coyotes who dispersed shortly after their initial capture and marking. Thus, animals suspected of violating closure (and their scats) may be identified. Similarly, movement data from animals marked with radio collars and individualized feces tags can enable the identification of feces from animals whose movements generally violate the assumption of closure. In this way, only full-time residents and their marked feces scats are used in the calculation of abundance. Under these conditions the populations can be considered open but the estimate of abundance is a mean during the sampling period.

We had the opportunity to estimate group size for a coyote family. Several times before capturing a 5-year-old radio-collared, territorial female and implanting a ^{65}Zn tablet, we observed her in the company of 2 other coyotes. Six of 19 scats ($p = 0.32$, variance = 0.011) collected from the interior portion of her territory, as determined by radio tracking, were labelled with ^{65}Zn . The estimate of group size, the reciprocal of p (3.17), was significantly different than a group size of 2 ($Z = 1.7$, $P = 0.04$). Later on, nighttime vocalizations also indicated a family group of 3 adults.

Home Range and Diet.-- Individualized feces tags can also provide an alternative to radio tracking as a way to determine home range. In our study, the home range of radio-collared adult coyotes corresponded with the distribution of their feces (Fig. 2). The home range (Mohr 1947) of marked coyotes based on feces locations was always included within (smaller than) the home range based on radio locations. Also, feces locations identified a similar core area of activity as determined by radio locations. Three adults tagged with $^{65}\text{Zn}/^{57}\text{Co}$, $^{54}\text{Mn}/^{109}\text{Cd}$, and $^{125}\text{Sb}/^{57}\text{Co}$ implants all occupied the territory depicted in Figure 2 and their scats were readily distinguishable from one another.

Individualized feces-tags provided information on the diets of individual free-roaming animals. We successfully collected nearly 300 scats from 11 individually-marked resident coyotes. This technique allowed correlation between individual diet and habitat use obtained from radio telemetry. We were also able to identify whether a particular coyote was involved in depredations on adjacent sheep ranches.

Social Behavior.-- Slow-release implants may provide a way to test hypotheses concerning the role of urine, feces, and anal sac secretion in the social and scent-marking behavior of carnivores. To test its feasibility we

artificially transferred 2 mL aliquots of urine labelled with ^{57}Co from a penned coyote onto various objects in the field. We were able to subsequently relocate these artificially-scented positions by using a trained dog as an indicator. The urine spots were then radio-chemically analyzed in the field using a portable germanium detector and multi-channel, pulse-height analyzer with an internal high voltage power supply.

Specially molded PLA implants (1-x 5-mm rods) impregnated with 2 μCi of silver-110 ($^{110\text{m}}\text{Ag}$) were positioned inside the anal sacs of several wild-captured coyotes. Because the animals were not recaptured and the concentration of the isotope was too low to be detected on feces, evaluation was not possible. However, 1 male coyote previously marked with 2 anal sac implants was observed to take a squatting-type position when it was suddenly startled by an approaching person. Radio-chemical analyses of the residual anal discharge (clear, thick fluid) detected the marker isotope, $^{110\text{m}}\text{Ag}$.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Of the 6 isotopes evaluated, 15-20 different and readily detectable feces-tags were identified using single or double isotope marks. Combining 2 isotopes that have similar or otherwise confounding gamma-energies should be avoided with gamma spectrometry using sodium iodide detectors (e.g., ^{54}Mn and ^{134}Cs). This is not a problem when using germanium detectors. When pairing radioisotope marks, we suggest that higher activity levels be assigned to the radioisotope with the lower gamma energy. The Compton edge effect produced by higher gamma-energy isotopes (e.g., ^{65}Zn) can mask the activity and detectability of the lower gamma-energy isotope (e.g., ^{109}Cd). Other isotopes in the 50-150 day physical half-life range that were not evaluated in this investigation should provide additional tagging combinations. Varying the activity

of 1 isotope or the ratio of 2 isotopes to provide additional tags proved futile due to differential metabolism and ingestion rates of nutrients (Pelton and Marcum 1977). However, we suggest using different ratios of 2 isotopes of the same element (e.g., ^{57}Co and ^{60}Co). In this way, differential metabolism and/or ingestion rates of nutrients would not affect their relative proportions.

The PLA implant technique has several advantages over the liquid-injection method, including lower levels of radioactivity required, a more stable form to handle, longer lasting marks, numerous individualized marks, and a relatively constant release rate to the feces. The activity in black bear (*Ursus americanus*) feces from liquid-injected ^{65}Zn varied over 3 orders of magnitude (Pelton and Marcum 1977). Apparently > 90% of the activity is lost in the first few weeks. Labisky and Conner (R. F. Labisky and M. C. Conner, Determination of bobcat (*Lynx rufus*) population abundance by radioisotope tagging. FL. Game and Fresh Water Fish Comm., Tallahassee, unpubl. rep., 11 pp, 1982) reported that a single scat deposited on the fifth day after injection contained 15.6% of the original activity.

Polylactic acid implants have a reported 500 day release period (Brady et al. 1973). This period is characterized by a linear release rate during which the polymer chains undergo hydrolytic backbone cleavage and are solubilized by conversion to small, water-soluble molecules. The shorter release period and the initial release burst of PLA implants in our study suggest that the isotope is bound in the hydrolytically unstable cross links between polymer chains. Consequently, the isotope is leached out through the polymer matrix. Incorporation of isotopes into different polymer compounds and/or with different chemical bonding could provide long-term

markers. The release period in 1 study using solvent-cast PLA encapsulation was estimated at 4.75 years (Heller 1980).

A variety of other potential applications exist. The ability to check an individual's condition from urine collected in snow (Mech et al. 1987, DelGiudice et al. 1988) or the effects of medical treatment on wild-captured animals (W. J. Foreyt, Washington State Univ., pers. commun.) without the necessity of recapture appear feasible. The diet transition from artificial feeding to capturing wild prey is being monitored for newly-released red wolves (Canis rufus) in North Carolina (M. K. Phillips, Alligator River Nat. Wildl. Ref., pers. commun.). Pelton and Marcum (1977) suggest using 1 label/species to build a discriminating model that could classify feces of similar appearance to the proper species. Individual marking would aid in the evaluation and calibration of the scat index to monitor change in population abundance. Pendleton (1956), Pelton and Marcum (1977), and Pelton (1981) provide additional ideas and possible applications.

Use of radioisotopes as a tagging method has the prodigious advantage of being detectable in extremely minute amounts. However, prudent use of radioisotopes in outdoor environments warrants the use of short-lived isotopes in consideration with public and animal health aspects. Although health hazards from radioisotope tagging are believed to be negligible (Nellis et al. 1968, R. F. Labisky and M. C. Conner, Determination of bobcat (Lynx rufus) population abundance by radioisotope tagging. FL. Game and Fresh Water Fish Comm., Tallahassee, unpubl. rep., 11 pp, 1982), the use of radioisotopes may not always be acceptable to the public. Public acceptance and state and federal regulations, concerning the use of radioisotopes in wildlife studies will need to be evaluated on a case by case basis.

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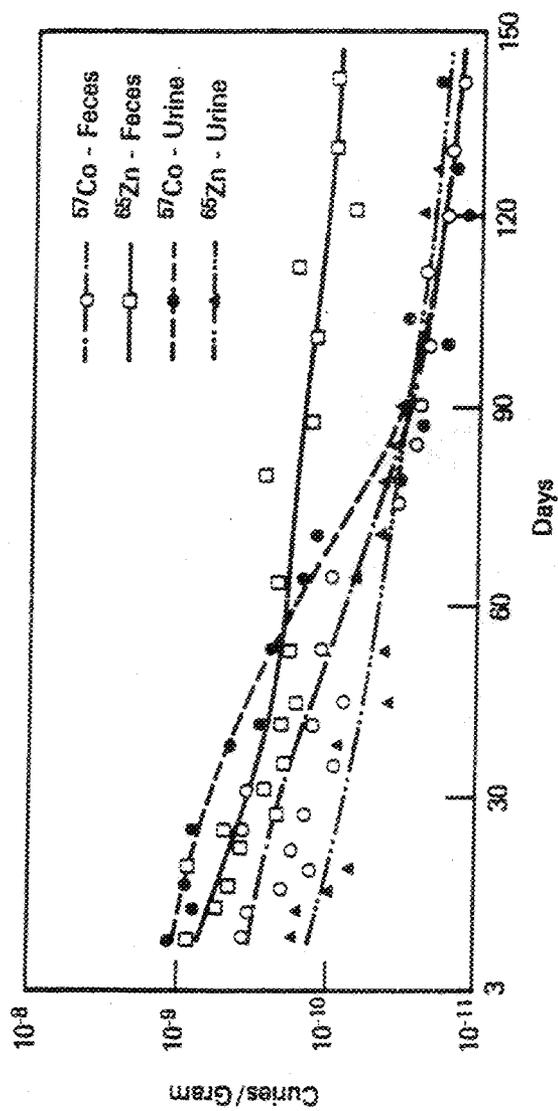
Table 1. Physical and biological properties of 6 radioisotopes in polylactic acid implants in penned coyotes.

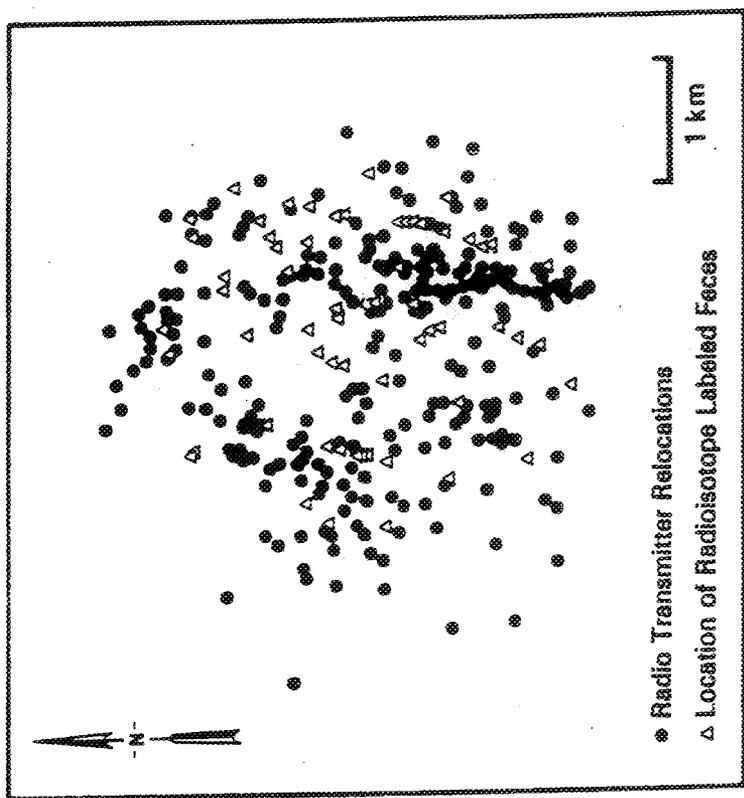
Isotope	Physical half-life (days)	Major gamma energy (mev)	Biological half-life (days)	Minimum detectability period (months)	Subjective rating as feces/urine tag
Manganese-54	300	0.835	17	15	very good/poor
Cobalt-57	270	0.12	10	6	fair/excellent
Zinc-65	245	1.12	933	20	excellent/poor
Cadmium-109	475	0.09	200	10	good/fair
Antimony-125	876	0.30, 0.43	38	10	fair/fair
Cesium-134	840	0.605, 0.80	70	12	good/fair

FIGURE LEGENDS

Figure 1. Activity present in feces and urine samples of penned coyotes marked with slow-release radioisotope implants.

Figure 2. Home range pattern of a 4-year-old territorial male coyote based on locations of radio-telemetry fixes and radioisotope-labeled feces.





CHAPTER II

SOCIAL AND SPATIAL DYNAMICS OF AN UNEXPLOITED COYOTE POPULATION
IN THE SHRUBSTEPPE OF WASHINGTON

SOCIAL AND SPATIAL DYNAMICS OF AN UNEXPLOITED COYOTE
POPULATION IN THE SHRUBSTEPPE OF WASHINGTON

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Abstract: We describe the social and spatial organization of an unexploited, stable, and old-aged coyote (Canis latrans) population in south-central Washington. We were able to categorize 79 of 87 radio-collared adult coyotes by social class based on physical characteristics, space use, site fidelity, movements patterns, and social interactions with other coyotes. Adult coyotes exhibited a high degree of spatial structuring according to well-defined social classes and subclasses. Territorial social groups comprised 67% of the spring prewhelping population and contained an older-aged alpha pair and an average of 1.4 young adult associates. Loners (non-territorial) comprised 33% of the spring population and were divided into 2 major social classes: solitary residents (with younger and older subclasses) and nomadic transients (nomads). The average range size of social group members, solitary residents, and nomads was 14.5, 54, and 220 km², respectively. Territory size and site fidelity varied seasonally; the expanded fall and winter ranges included the central spring range. Territories were contiguous, non-overlapping, and uniform in size. Loners were located on the periphery of and in narrow corridors between territorial ranges. Loner "trespassing" in the core areas of territories was minimal but significantly increased in winter

from that during whelping and pup-rearing. Social class membership was constant in spring and summer but a complicated reassortment occurred during winter starting with the fall dispersal of pups and associates. The integrity of a territory persisted beyond the occupancy time of owners which may reside there for up to 10 years in the absence of human exploitation. A healthy class of 2 to 4 year-old mature loners form a reservoir of potential territorial replacements, followed by a young group of 1 and 2 year-old nomads. Additional intraspecific "pressure" may result from old-aged solitary residents that were former territorial owners. We provide a general, spatially-based model of social class dynamics for an unexploited population that may explain the discrepancies in previous studies of exploited populations.

The coyote (Canis latrans) now inhabits all states except Hawaii and has extended its range to the Panama canal and the northern extent of the boreal forest in Canada and Alaska. Its success has been partially attributed to its flexible social behavior. However, descriptions of coyote social and spatial organization differ substantially (Berg and Chesness 1978, Camenzind 1978, Danner and Smith 1980, Bowen 1981, Messier and Barrette 1981, Andelt 1985, Beckoff and Wells 1986). These differences may be due, in part, to human exploitation, and to a lesser extent, unnatural and disturbed conditions.

Our objectives were to describe, both qualitatively and quantitatively, the social and spatial characteristics of a natural, unexploited coyote population. This study provides a general model with which the results of previous studies of disturbed populations can be compared.

STUDY AREA

The study was conducted from 1984 to 1988 on the western portion of the Arid Lands Ecology (ALE) Reserve in southcentral Washington State. The ALE Reserve is a 330 km² section of the Hanford National Environmental Research Park that lies in the rainshadow of the Cascade Mountains. Summers are hot and dry (x July max.=33.3° C) and winters are cool (x Jan. min.=-10.2° C) (Rickard 1972). Annual precipitation, falling mostly from November to February, ranges from an average of 17 cm on the plain to 23 cm in the Rattlesnake Hills region (Hinds and Thorp 1974). This physiographic gradient is characterized by a flat plain on the northern boundary, the extensive Rattlesnake Hills on the southern boundary, and a large central undulating zone (McCorquodale 1986). Elevation ranges from 200 to 1,090 m.

The ALE reserve is entirely within the Artemesia tridentata/Agropyron spicatum (big sagebrush/bluebunch wheatgrass) zone (Daubenmire 1970). Big sagebrush dominates the overstory at all elevations. However, periodic fires have resulted in a patchy distribution and 70% removal of big sagebrush on the study area. Understories are dominated by bluebunch wheatgrass at mid- and upper elevations and Sandberg bluegrass (Poa sandbergii) and cheatgrass brome (Bromus tectorum) at lower elevations and disturbed sites, respectively. A diverse variety of forbs exists on the study area. Riparian vegetation is limited to 6 isolated locations.

A coyote food habits study was conducted on the same study area and indicated a diverse diet (Stoel 1977). Great Basin pocket mice (Perognathus parvus) are exceptionally numerous in this region of shrubsteppe (Hedlund et al. 1977) and the coyotes' diet reflected this abundance. In addition to pocket mice, leporids (Sylvilagus nuttallii and Lepus californicus), voles (Microtus montanus and Lagurus curtatus),

pocket gophers (Thomomys talpoides), darkling beetles and grasshoppers (Coleoptera and Orthoptera), ground squirrels (Spermophilus townsendii), birds, and reptiles were represented in the coyotes' diet. Another study conducted on an adjacent portion of the Hanford NERP found coyotes a major predator on mule deer fawns (Odocoileus hemionus), accounting for 10 of 14 deaths (Steigers and Flinders 1980).

Absence of grazing and other land-use practices the last 45 years were of particular significance to this study. The Hanford Reservation, which now includes the ALE Reserve, was created in 1943 and became restricted from all private and public use. Prior to that time, portions of what is now the ALE Reserve received light to moderate levels of sheep grazing mostly during winter. In 1967, the ALE Reserve was created to further preserve a near pristine shrubsteppe community (Vaughan and Rickard 1977) and it now serves as a research area for ecological studies. Exploitation of coyotes via predator control efforts last occurred in 1952.

METHODS

Field Investigations

Eighty adult coyotes were captured with #3 offset jaw, leg-hold traps, most of which were padded and equipped with tranquilizer tabs (Balser 1965). Twenty-seven adults (20 recaptures) were captured with a netgun from a helicopter. Fifty-eight pups were trapped, hand captured in excavated dens, or hand-netted near dens. All adults and pups older than 10 weeks were fitted with a radio-telemetry collar. Pups captured near dens when 10-14 weeks old were fitted with a special expandable radio-collar (Crabtree et al., unpublished). This provided estimates of dispersal, and social class transition up to 2.5 yrs of age. The sex, weight, estimated age, estimated condition index, presence of scars and unique marks, and description of genitalia and

mammae were recorded. A first premolar was removed for age determination by examination of cementum annuli from prepared tooth sections (Matson's, Milltown, MT). Each collared coyote was marked with numbered ear tags and 2 x 6 cm colored ear flags.

The condition index was integer-valued from 1.0 to 10.0 subjectively based on subcutaneous fat thickness measured at the hip (Whittemore 1984), palpated subcutaneous fat at the ribs and spine, weight relative to body length, and general physical appearance. We monitored radio-marked coyotes from fixed-station shelters located atop 240 and 390 m escarpments on the eastern and southern boundaries of the study area, respectively. These locations provided complete coverage of a large 150 km² tracking area. We simultaneously triangulated coyotes with arrays of 2 4-element yagi antennas coupled to a 180 degree phase-shifter (null system). Six to 12 relocations were taken at hourly intervals on coyotes every second or third night during 3 tracking periods annually. Fixes were obtained on 10-30 individuals during active periods only.

Correct antenna orientation was checked with beacon transmitters at least once an hour. The degree error of our tracking system was estimated during various seasons from multiple readings at multiple locations unknown to the observers. The low degree error (0.5°) was attributable to the design of the tracking system and line-of-sight coverage of the study area.

We made numerous, non-systematic behavioral observations seasonally. These consisted of visual sightings from the ground and fixed-wing aircraft, den observations, and vocalization monitoring. The ALE population was particularly easy to observe because of the flat terrain, isolated vantage points, and removal of sagebrush from periodic fires in the past.

Definitions and Decision Criteria

Relocation data provided an estimate of an animal's resident equivalent (RE), a measure of site fidelity. RE is defined as the proportion of time an individual spends on a defined sampling area during a defined sampling period. The study population consisted of resident coyotes that spent all or some of their time on or near the Hanford Reservation plus loners that spent >10% of their time there. The tracking area was considered the portion of the study area in which animals could be relocated from the 2 main tracking shelters and was used as the reference area for measuring home range fidelity. We defined a core area, central to and within the tracking area, that included the partial or entire portion of 12 contiguous territorial breeding groups that were intensively examined. The percent composition of the population according to social class was estimated from the sum total of REs from all animals in each social class on the core area.

Beginning in fall 1984, we trapped during 8 consecutive spring and fall periods in an attempt to capture all coyotes in and around the core area. Pups or juveniles are considered young adults after March 1 (0.9 years old). Based on major biological activities we tracked coyotes during 3 designated periods: whelping, March to mid-June; pup-rearing, July through October; and winter (breeding), late November through February.

Assignment of adult coyotes into 5 initial social classes was based on physical characteristics, space use, site fidelity, movements patterns, and associations with other coyotes. Vocal response to playbacks and visual observations also aided in determination of possible social class. Adult coyotes were first classified as either social group members (territorial) or loners (non-territorial). These 2 were the only categories consistent with those reported in the

literature. Social or territorial breeding groups consisted of the alpha male and female (breeding adults) and associates. Loners consisted of solitary residents and nomadic transients (nomads). The term transient, used to describe non-territorial status in previous studies, was inappropriate because a significant portion of the non-territorial category exhibited little or no transitory movement (i.e., solitary residents). Coyote pups were classified as associates if they had not dispersed from their natal territory by 31 November when they were nearly 8 months old.

Breeding or territorial adults were recognized by 2 or more criteria similar to that of Andelt (1985): 1) 2 adults of opposite sex traveling closest together during the breeding and nursing period; 2) female with distended abdomen and/or dark, elongated mammae; and 3) female with a high frequency of locations near a natal den during parturition and lactation. Only territorial females successfully whelped (Crabtree et al. 1989). Adult coyotes were termed associates if they interacted with breeding adults and their pups and occupied the same home range. The distinction within the non-territorial category of coyotes was made primarily on relocation data.

Analytical Methods

We sought to determine an animal's space-use, commonly referred to as a utilization distribution (Ford and Krumme 1979). We technically define a utilization distribution as a probability density function whose underlying volume is equal to 1.0. The height of a "z" point on the variable surface of the utilization distribution is the probability of locating the animal at the corresponding x-y area. We used a modification of the grid cell method described by Rongstad and Tester (1969) that assumes no underlying distribution. The grid cell probability or z value, was equal to the number of

relocations in that cell divided by the total number of relocations. Grid cell values were smoothed based on a nearest-neighbor method which weighted the nearest 16 cells by the inverse of their distances. We estimated the range area (km^2) by calculating the area inside the 0.001 probability contour of the smoothed utilization distribution. We will refer to this value henceforth, as UD.001. For comparative purposes we also calculated the 95% minimum convex polygon (Mohr 1947), and will refer to it as 95%MCP.

Spatial avoidance was assessed by calculating an overlap index. The index was the sum of the minimum of 2 probability values in each grid cell used in common by the 2 animals or 2 pooled social classes within a season. This statistic is the overlap volume of their respective utilization distributions. A grid cell with a width of 750 m (0.56 km^2) was used in all overlap calculations. This was based on an average of 5 relocations per grid cell of an average territorial range.

Annual territorial turnover rate and residency time was estimated using program SURVIV (White 1983). Loss of territorial ownership was treated as a mortality. Chisquare analyses were performed to test for differences in frequency of trespassing by individual and by season. ANOVA was used to test differences in range size, range shifts, and differences in overlap indices among individuals and social classes. We used student t-tests for paired comparisons when data were normally distributed, ranked sum tests when data were non-normal but unimodal, and median tests when distributions were contaminated. Unless otherwise noted the terms significant and highly significant refer to P-values <0.05 and <0.001 , respectively.

RESULTS

Social Class Characteristics

There was a 67:33 percent ratio of social group members to loners in the spring, pre-whelping population. This ratio increased to 74:26 in the fall population (80:20 including 6 month-old pups). The social class composition of the spring and fall populations were, respectively: 40 and 44% for breeding adults, 27 and 30% for associates, 18 and 20% for solitary residents, and 15 and 6% for nomads. Group size during the whelping period averaged 3.4 adults per territory.

The age, weight, and condition of adult coyotes are summarized in Table 2 by social class. The average age of breeding males was slightly higher than that of breeding females. The age differential of breeding pairs in 8 social groups were: 4 of equal age, 3 with the male 1 yr older, and in 1 old pair the male was 1 yr younger. The mean age of associates was significantly lower than for breeding adults. We expected this because previous studies have reported associates to be offspring that have foregone dispersal and remained in the natal area for extended periods (Andelt 1985, Bowen 1978, Camenzind 1978, Windberg and Knowlton 1988). Associates as parental offspring were positively known for 3 of 10 cases and suspected for the remaining 7.

The only significant weight difference besides sexual dimorphism occurred with territorial males, who weighed significantly more than male nomads. The ratio of male:female body weight was 1.12, for breeding adults and for the overall population.

The condition index for breeding females was the lowest among all social classes and was significantly lower than that for breeding males and loner females. Breeding males had the highest (but non-significant) condition index among all social classes. The condition indices of the 2 loner categories were

similar ($P=0.89$); however, solitary residents weighed more ($P=0.11$) and were older than nomads ($P=0.002$). Nomads, as compared to breeding adults, were significantly younger ($P<0.001$) and weighed less ($P=0.10$), whereas condition indices were similar. The physical characteristics of solitary residents were similar ($P>0.46$) to those of breeding adults, but ages ranged widely for solitary residents (1.5 to 13.5 yr).

Range Size and Seasonal Shifts

The estimated annual range size for coyotes according to social class is summarized in Table 2. Mean differences in annual range size between the 3 social classes were highly significant ($F>90.4$, $P<0.0001$ for both methods). Many marked nomads were excluded from the analysis because they spent a majority of time outside the tracking area (i.e., $RE<0.4$). Therefore, annual range sizes for nomads are minimum estimates and are probably much larger.

The average annual RE values varied significantly with social class ($P=0.001$). Low RE values not only indicate low fidelity and a larger range size, but may also provide a means of correction. If the area used by an animal on the tracking area is proportional in size to its RE, then the range size divided by the RE may be more representative of the true range size. This corrected range size (km^2), for coyotes included in Table 2 (UD.001), averaged 14.5 for social group members, 54 for solitary residents, and 220 for nomads.

The distribution of annual range sizes (UD.001), illustrated in Figure 1, indicates overlap among social classes. Variation in range size of territorial members was low compared to that of loners. The distribution of range sizes for solitary residents was bimodal. The first mode includes ranges similar in size to that of territorial members, while the second includes much larger range sizes.

Taking into the account the RE correction discussed above, the difference in average range size between solitary residents and nomads is greater with virtually no overlap.

Territory size (UD.001) varied seasonally ($P=0.0001$). Size of territorial ranges (km^2) averaged 11.1 ($SD=2.1$) during the whelping period, 14.5 ($SD=3.9$) during the pup-rearing period, and 16.9 ($SD=5.4$) during the winter period. Territory size during the whelping period was significantly smaller than that during pup-rearing and winter ($P<0.002$), whereas size in winter was somewhat larger than during pup-rearing ($P=0.13$). Range estimates of 95%MCP during winter were larger (18.4 km^2) than those of UD.001. The 95%MCP ranges were more sensitive to the substantial increase in outliers (forays outside the normal home range) that frequently occurred during the winter period. The average RE for social group members was 1.0 during whelping, 0.97 during pup-rearing, and dropped to 0.82 during winter. The expanded fall and winter ranges included the central spring range.

Although seasonal range sizes for loners were not calculated because of small sample sizes and low RE, it appears that seasonal territorial expansion also occurred for solitary residents as well as nomads. Winter and spring decreases in RE for nomads indicates that they were still traveling over large areas in the whelping period when territories had already contracted.

Spatial Dynamics and Tolerance

Territories on the ALE Reserve were contiguous, non-overlapping, and similar in size. The spatial distribution of territories is represented in Figure 2 for 12 adjacent spring territories.

Although territorial groups appeared to cover the total land area, they exclusively "held" only interior portions of their territories (Figure 3). Although trespassing by loners

was common, the core of the territory was clearly avoided ($X^2 > 100$, $P < 0.0001$). We defined the territorial core as that enclosed by the 0.004 probability contour because of the drastic increase in loner relocations immediately peripheral (< 0.004). The size of the core area averaged 40% (SD=3.6) of total territory size and included approximately 70% of territorial relocations.

Trespassing by loners in territorial core areas differed seasonally ($X^2 = 58.18$, $P < 0.0001$) (Figure 3). Although the lowest amount of trespassing by loners occurred during the whelping period it was not significantly lower than during the following pup-rearing period ($P = 0.13$). Trespassing during both whelping and pup-rearing was significantly lower than during the winter period ($P < 0.0001$).

Spatial tolerance among coyote social classes was assessed by estimating volume overlap of their seasonal utilization distributions. This resulted in a relative "tolerance gradient" ranging from an extreme low between adjacent territorial groups to a high between mated pairs. Territorial members were less tolerant of members of adjacent territorial groups than of loners. Overlap indices between adjacent territories were virtually identical during the 3 periods in 1986 and 1987 ($P = 0.82$) and averaged 4.3%, 4.8%, and 4.1% for the whelping, pup-rearing, and winter periods, respectively. The average overlap indices between territorials and nomads were the same as those between territorials and solitary residents (14.1% and 14.7%, respectively) and were pooled for subsequent analysis. Overlap indices between territorials and loners were remarkably similar between 1986 and 1987 and were 13.5 and 13.5%, respectively, for the whelping period, 15.8 and 15.9% for the pup-rearing period, and 19.9 and 19.4% for the winter period.

The alpha male, alpha female, and associates of a social group had highly overlapping ranges which were not significantly different in size and were pooled. Average overlap indices between territorial members of the same group, within the same season, averaged 68% (SD=0.06). Overlap indices between the 2 loner social classes were intermediate to above values (38.5, 35.8%, and 29.4% for the whelping, pup-rearing, and winter periods, respectively). Overlap values within the solitary residents and within nomads could not be calculated. However on a qualitative basis, solitary residents were more regularly spaced than the widely overlapping nomads.

Social Dynamics

The social dynamics of coyotes on the ALE Reserve occurred on 2 levels: individual transition between social classes and numerical change within a social class of individuals. Individual transitions between social classes occurred during the fall and winter. They began in fall when dispersing pups and associates became nomads, and ended in late winter with the establishment of new territorial members--both new breeding pairs and new associates. During the whelping and pup-rearing periods there was no change in social status of adults. Numerical change within social classes occurred throughout the year but could only be assessed from the end of the fall/winter transition period to fall dispersal.

Fifty-nine percent of pups dispersed from natal areas during September through November (Crabtree 1989). Of 7 pups that remained, 5 became associates, one resided on the periphery of its natal territory, and one was undetermined because of radio failure in December. It was recovered next to its natal territory the following summer. Age structure and actual dispersal data indicate that half the associates

disperse each year (Crabtree 1989).

The estimated annual turnover rate of territorial occupants was 0.17 (SE=0.06) which represents an average occupancy time of 6 years. Ages of breeding adults that lost their territories were 4.5, 5.8, 6.8, 8.0, 9.8, 10.8, and 11.0 and corroborates the estimated 6 year tenure period. Coyotes appear to be 2 or 3 years-old when they first occupy a territory. Ages of first-time territorial occupants were 3, 3, and 3 for males and 2, 3, 3, and 4 for females. Two other 3 year-old females were suspected to have bred when 2 years-old because of the presence of associates. Crabtree (1989) indicates that females are either age 2 or 3 when they first attain alpha breeding status. Two new territorial occupants were previously nomads.

The annual change in numbers of individuals in each social class is presented as a deterministic model in Figure 4. Annual population fluctuation is calculated from the sum total RE of all social classes.

DISCUSSION

Socio-spatial structure

The social structure of the coyote consisted of various classes and subclasses. Loners or non-territorials were classified as either solitary residents or nomads based primarily on range size, space use, and physical characteristics. Territorial social groups consisted of alpha pairs and associates and were classified by behavioral observations, physical characteristics, and movement patterns. Beckoff and Wells (1980) made the distinction between territorial coyote packs and non-territorial mated pairs. We observed no differences between groups with 3 or more adults and groups that consisted of just the mated pair. Several groups of only 2 adults had associates present the year before or after. The contention by Beckoff and Wells (1980) of

non-territorial mated pairs was apparently based on a sample of 1. The major distinguishing characteristic of a loner was its spatial avoidance of territorial core areas. Other studies have reported that loners were restricted to the peripheral and interstitial zone of territories (Bowen 1982, Windberg and Knowlton 1988). Discrimination among social group members was distinct as was the difference between solitary residents and nomads. However, many similarities existed between spatial and physical characteristics of social group members and those of solitary residents. In fact, adult coyotes in general occupied positions across the entire spectrum of possible range size and site fidelity.

Alpha adults were older-aged, occupied the smallest range, and successfully reproduced. Exclusive breeding by alpha females has been previously reported (Knowlton et al. 1986, Crabtree 1989). They had the highest seasonal site fidelity and apparently reside in their ranges for up to 10 years. The successful acquisition of a territory may have been related to the larger size and older age of alpha males compared to male nomads. Among the sub-population of presumed full-grown and competing males, older-aged males appeared the most successful at initially acquiring a territory and a mate.

The low to moderate condition index of alpha adults, especially females, was partially due to the energetic costs of reproduction. These and the costs of territorial maintenance and defense are offset by the exclusive rights to food resources and concomitant nutritional advantages. A high level of intraspecific strife in the saturated ALE population (Crabtree 1989) may have placed increased energetic demands on territorial members.

We feel the group size estimates were reliable because various methods provided the same estimate; however, on several occasions we recorded the presence of an additional

adult interacting in the group. Therefore, some estimates of group size may be minimums and some adults may be loosely affiliated with a group. Based on relocations, 2 adults classified as loners may have held group affiliation.

The typical number of associates per group was 1 or 2 (range 0 to 4), similar to that reported for lightly exploited populations (Messier and Barrette 1981, Andelt 1985, Gese 1987, Windberg and Knowlton 1988). Bowen (1985), Beckoff and Wells (1980), and Gese (1988) report that larger group size was related to the availability of larger ungulate prey or defense of carcasses. The large ephemeral aggregations of coyotes in winter and early spring observed by Camenzind (1978) were due to the presence of carcasses or possibly the delayed dispersal of full-grown pups (Messier and Barrette (1981). Because the mean number of associates per group in the spring does not appear to be different between populations that rely heavily on large ungulate food and those that do not, we support the hypothesis proposed by Messier and Barrette (1981). Their more parsimonious explanation contends that formation of territorial groups is related to pup survival and increased foraging efficiency of parents that must feed pups.

Solitary residents were the most heterogeneous social class and appeared to consist of several subclasses. Younger solitary residents, ages 1 to 3, showed weaker fidelity to an area, and ranged over a larger area than most older solitary residents. They spent substantial amounts of time on the periphery of 1 or 2 territories. One yearling was located outside its original natal territory, while others appeared to have some unknown affiliation with a territorial group. The characteristics of this subclass match that of a "roamer" described by Beckoff and Wells (1986) and individuals described by Messier and Barrette (1981). One 4 year-old male

entered an adjacent territory and became an associate after 2 years as a solitary resident, while another took over territorial ownership.

The second subclass of solitary residents consisted of older adults, age 3.5 to 13.5, with a high degree of site fidelity. Evidence suggests that many individuals in this subclass were former territorial owners. Noticeable head and facial scars were common on breeding males as well as a majority of older-aged (age 5 and older) males classified as solitary residents. In addition, several older-aged females had dark, extended, and scarred mammae, indicative of previous lactation and alpha female status. In 5 known cases where breeding adults lost ownership of their territory, 4 became solitary residents in the vicinity of their former range while one became nomadic.

Middle-aged solitary residents may serve other functions. In 1986, 3 solitary residents, one 5 year-old female and two 6 year-old males, occupied small ranges in "wide" corridors between territories and exhibited some territorial tendencies (e.g., vocalizations). In 1987, one of the males had paired with a 3 year-old female and produced a litter of 8. In winter 1988, the other male had apparently paired with a female and was observed with a pup the following summer. Evidence suggests that both these males were the original territorial owners and had picked up new mates after a 1 and 2 year waiting period, respectively. In the fall of 1987, the female had shifted her residency to an adjoining territory that had been abandoned that spring. Her reproductive status was unknown.

Nomads were generally young (80% were age 1 to 3), had little seasonal fidelity to an area, and ranged over very large areas. However, when sample sizes were adequate and $RE > 0.4$, most nomads had recurring patterns of movement on an

annual basis. Young nomads may be monitoring as many territories as possible for vacancies while still covering familiar foraging areas to take advantage of ephemeral prey abundances. The fact that young nomads were apparently traveling over extended ranges in early spring, when ranges of territorials and older loners had already contracted, may be indicative of this type of strategy.

Socio-spatial dynamics

The spatial intolerance between adjacent territorial groups probably reflects social intolerance as well. We observed several agonistic interactions, which evidently occur infrequently (Andelt 1985, Beckoff and Wells 1986). The stable seasonal overlap values may be further evidence of social intolerance. Even while territorial ranges increased in size from spring through winter, the low overlap values were unchanged.

Seasonal fluctuation in range size occurred among all social classes. We suspect this is due in part to spatial and temporal changes in prey abundance but no data are available to confirm it. It does appear that some concentrated resources are difficult to defend. Many of the loner relocations in the interior core of territories can be accounted for by forays to isolated water sources during the summer and to ungulate carcasses during winter.

The most well-defined social and spatial structure occurred during the whelping period and may indicate increased territoriality for the provision, protection, and survival of pups. Pup survival is contingent upon the nutritional condition of the alpha female and was found to be a major regulating factor of the ALE coyote population (Crabtree 1989). During the whelping period, when territories were contracted, loner trespassing was minimal, group cohesiveness was maximized (Andelt 1985), and frequency of vocalizations

associated with territorial maintenance peaked (K. Fulmer, unpubl. manuscript).

Contrary to the static adult social structure during the whelping and pup-rearing periods, a complicated reassortment of social transitions occurs from September through February. Dispersing associates and pups become loners and join the surplus of potential territorial replacements. We found a high density of young loner relocations in several vacated territories during the study. This and the fact that territorial turnover occurs at this time, suggests that territorial challenges may occur during the winter period. However, once a pair establishes a new territory, the territorial turnover and natural mortality rates (Crabtree 1989) predict that, in the absence of human exploitation, the pair may reside there for many years.

CONCLUSIONS

Coyotes exhibited a high degree of spatial structuring according to well-defined social classes and subclasses. The focus of social and spatial dynamics, as well as population dynamics (Crabtree 1989), was the territory. The integrity of a territory persisted beyond the occupancy time of owners which may reside there for up to 10 years in the absence of exploitation. A healthy class of 2 to 4 year-old mature loners forms a reservoir of potential territorial replacements, followed by a young group of 1 and 2 year-old nomads. Additional intraspecific "pressure" results from older-aged solitary residents that were former territorial owners.

Previous coyote studies of populations subjected to various levels of exploitation have ascribed to differing social class characteristics and even different social class divisions. For example, an underrepresentation or even absence of the older-aged, solitary resident social class is

probable in an exploited population. We agree with Windberg and Knowlton (1988) that discrepancies among previous coyote studies are also the result of a variety of ecological and methodological factors. One such factor may be artificial or disturbed conditions like those observed by Beckoff and Wells (1980) and Danner and Smith (1980) which describe social conditions under the influence of large quantities of carrion. However, the results from this unexploited population and similar results from recent studies of lightly exploited populations (Messier and Barrette 1981, Andelt 1985, Gese 1987, Windberg and Knowlton 1988) suggest that human exploitation, which differentially affects coyote social classes (Harris 1983, Windberg and Knowlton 1988, Crabtree 1989), accounts for most of the observed discrepancies in social classification and behavior. Until more research is conducted on natural, unexploited populations of coyotes, inference regarding the evolutionary significance of coyote social behavior is suspect.

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Table 1. Age (yr), weight (kg), and condition of adult coyotes categorized by social class on the Arid Lands Ecology Reserve near Hanford, Washington, 1984-1988.

Category				Condition
Social class	n	Age	Weight	index
Territorial groups				
Breeding males	11	4.82	11.78	6.55
Breeding females	15	4.50	10.49	4.53
Associate	7	1.21	9.98	5.36
Combined	33	3.91	10.81	5.38
Loners				
Solitary residents	21	4.74	11.17	5.81
Nomads	25	2.00	10.29	5.64
Combined	46	3.25	10.69	5.72
Population Total	79	3.53	10.74	5.58

Table 2. Average annual resident equivalents (RE) and mean annual range size (km²) of 2 methods for adult coyote social classes on the Arid Lands Ecology Reserve near Hanford, Washington, 1985-1987.

Social class	n	RE	UD.001 ^a	SD	95%MCP ^b	SD
Territorial	21	0.94	13.6	2.7	15.6	8.1
Solitary resident	25	0.74	40.5	22.7	56.2	29.0
Nomad	0.50	108.90	24.7	141.8	42.2	

^a0.001 probability contour of the utilization distribution (see Methods).

^b95% minimum convex polygon

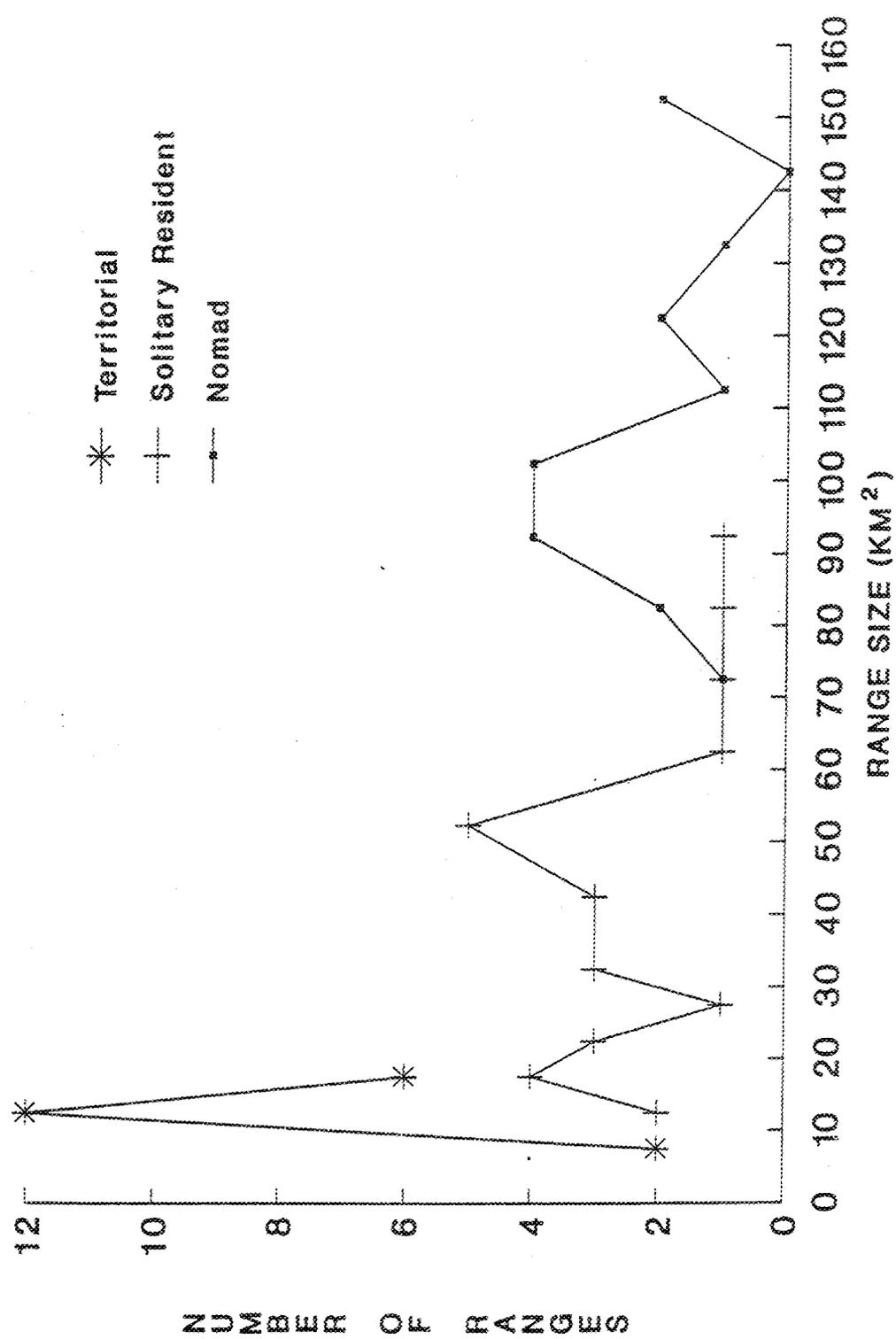
FIGURE LEGENDS

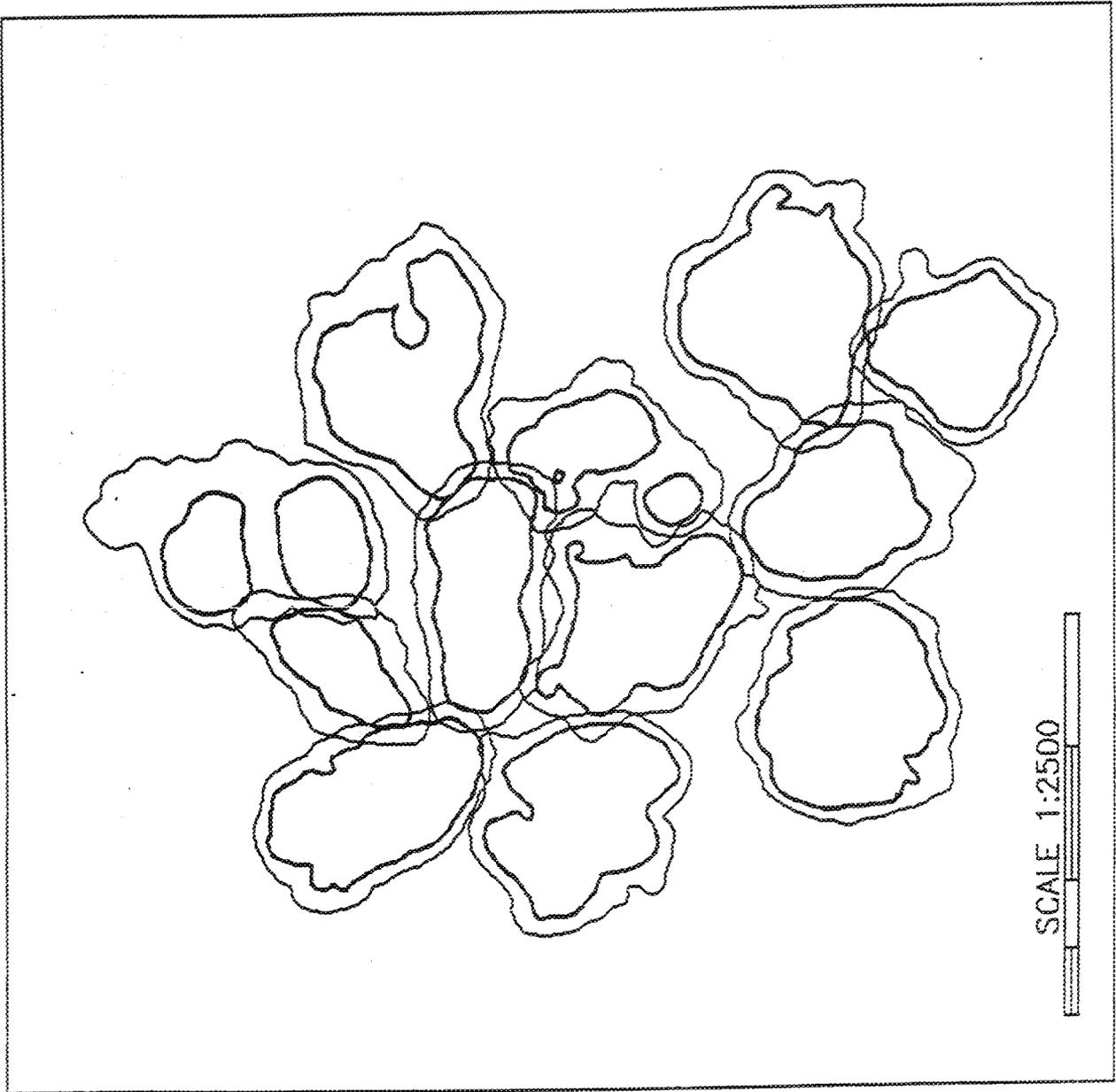
Figure 1. Distributions of range sizes (km^2) by social class for coyotes on the Arid Lands Ecology Reserve near Hanford, Washington, 1985-1987.

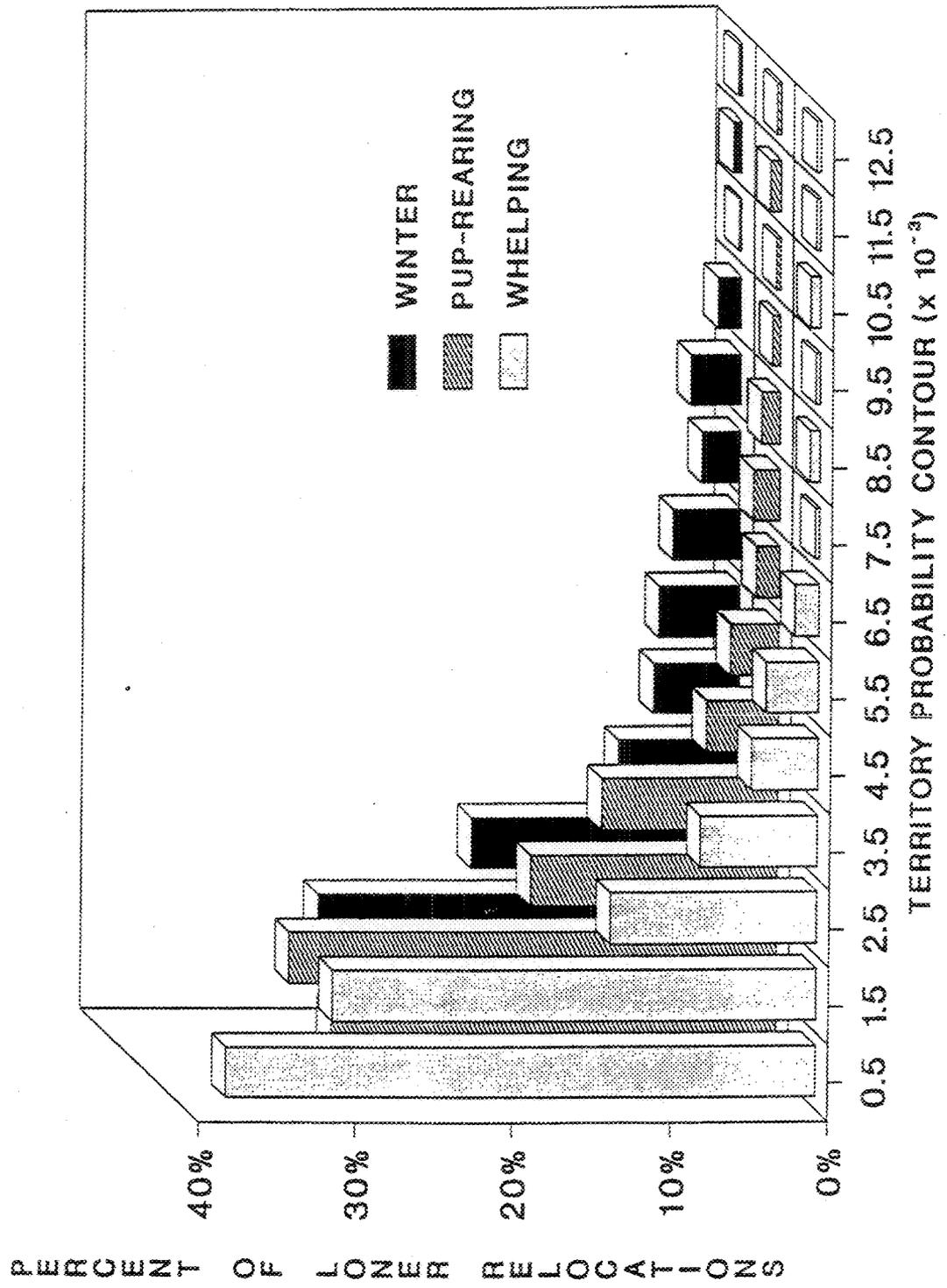
Figure 2. Spatial distribution of 12 spring territories on the Arid Lands Ecology Reserve near Hanford, Washington, 1986-87. The inner and outer probability contours represent 75% and 90% of the territory's utilization distribution, respectively.

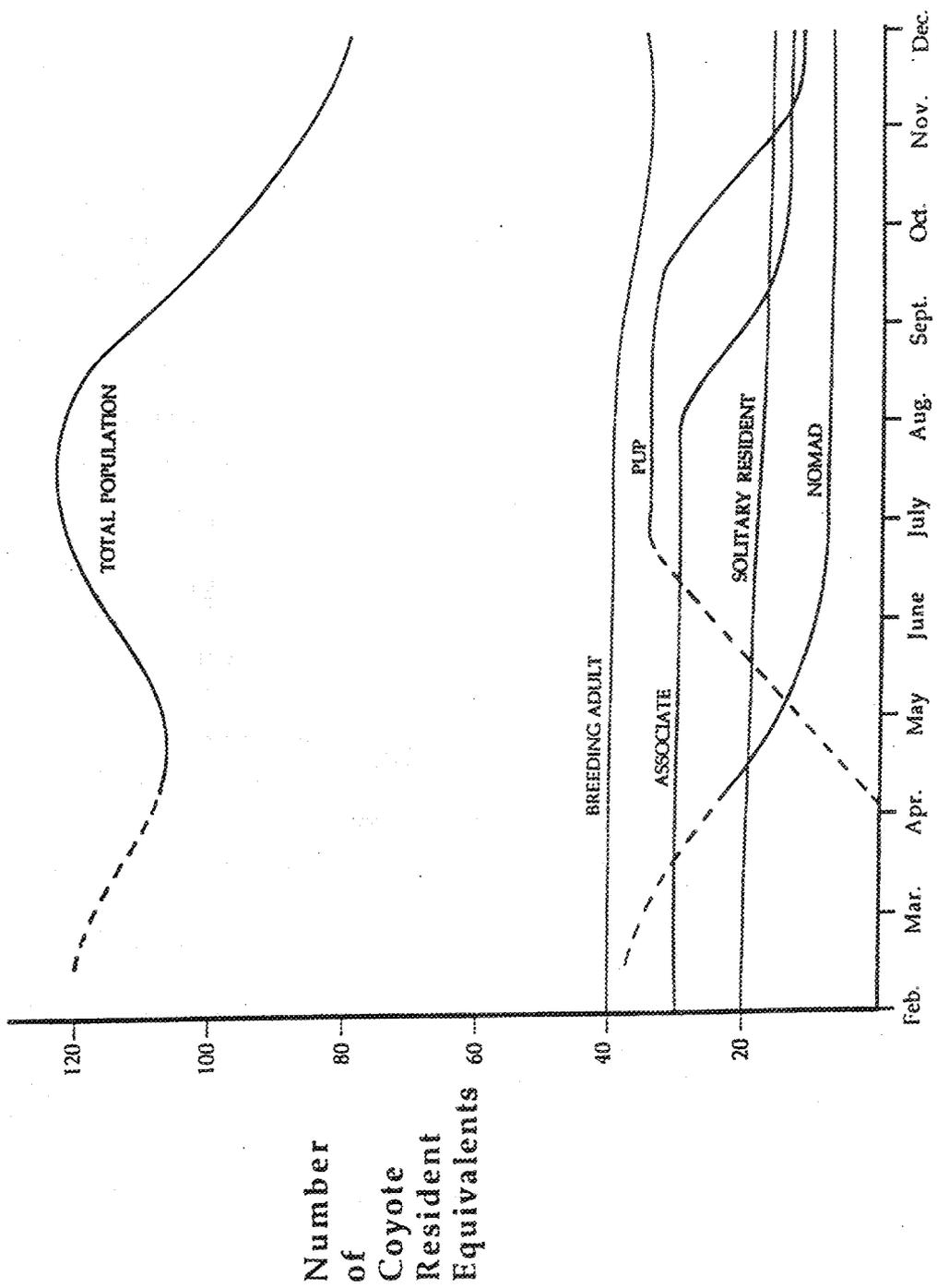
Figure 3. Seasonal frequency distributions of the number of relocations in various territorial contour probabilities for adult loner coyotes on the Arid Lands Ecology Reserve near Hanford, Washington, 1985-87.

Figure 4. Deterministic model of numerical changes among coyote social classes on the Arid Lands Ecology Reserve near Hanford, Washington, 1985-87.









Number of Coyote Resident Equivalents

Calendar Month

CHAPTER III**SOCIODEMOGRAPHIC CHARACTERISTICS
OF AN UNEXPLOITED COYOTE POPULATION
IN THE SHRUBSTEPPE OF WASHINGTON**

SOCIODEMOGRAPHIC CHARACTERISTICS OF AN UNEXPLOITED COYOTE
POPULATION IN THE SHRUBSTEPPE OF WASHINGTON

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Abstract: We estimated sociodemographic parameters of a natural, unexploited coyote (*Canis latrans*) population on the Arid Lands Ecology Reserve (ALE) near Hanford, Washington from 1984 to 1988. A large proportion of the population was sampled and resulted in the capture of 145 individuals. The adult population was comprised of older-aged breeding adults (40%), solitary residents (18%), breeding group associates (27%), and nomads (15%). The sex ratios of adults and pups at birth were equal. Successful breeding occurred at ages 2 through 6 for alpha females ranging in ages 2 through 11 years. Reproductive failure among territorial groups was 27% and mainly involved breeding adults age 6 years and older. Population productivity was 0.62 pups per female, whereas average litter size was 5.6. Pups weighed 27% below average and incurred a 58% mortality rate during the first 14 weeks following birth. The overall population survival rate was 0.90 with no observed natural mortality. Adult survival rates did not significantly differ with respect to year ($P=0.86$), sex ($P=0.61$), or age ($P=0.14$). However, survival was strongly a function of social class ($P<0.001$). Emigration from the population was low (16%) and consisted primarily of pups and associates. Immigration was low (6%) and limited mainly to younger nomads. Density averaged 0.41 and 0.38 coyotes per km² for an absolute density estimate and complete enumeration, respectively. The ALE coyote population was stable and

appeared to have a high degree of intraspecific strife. We propose a theory of population regulation similar to that described for wolves (Canis lupus) and discuss the possible compensatory responses to exploitation.

Although numerous studies on the demographics of coyote populations have been conducted in the last 15 years, all populations were subject to moderate to heavy levels of exploitation. The demographics of unexploited coyote populations are, for the most part, unknown. Frank (1979) stated that if a coyote population is subjected to substantial exploitation, neither its social organization nor population dynamics will be remotely representative of the natural, and therefore evolutionary significant, situation.

Hornocker (1972) expressed the need for an objective study of unexploited coyote populations to identify self-regulating mechanisms and their implications regarding control. Davison (1980) compared population parameters of a heavily exploited area and a presumed unexploited area, which incurred a 25% annual hunting mortality. Other recent studies on social aspects of coyotes were conducted on populations with light to moderate levels of exploitation (Bowen 1978, Beckoff and Wells 1986, Andelt 1985, Windberg and Knowlton 1988).

The objectives of this study were to examine and estimate the composition, natality, mortality, immigration, emigration, density and stability of a natural, unexploited coyote population and to relate these to population control.

STUDY AREA

The study was conducted from 1984 to 1987 on the western portion of the Arid Lands Ecology (ALE) Reserve in southcentral Washington State. The ALE Reserve is a 330 km² section of the Hanford National Environmental Research Park

that lies in the rainshadow of the Cascade Mountains. Summers are hot and dry (x July max.=33.3° C) and winters are cool (x Jan. min.=-10.2° C) (Rickard 1972). Annual precipitation, falling mostly from November to February, ranges from an average of 17 cm on the plain to 23 cm in the Rattlesnake Hills region (Hinds and Thorp 1974). This physiographic gradient is characterized by a flat plain on the northern boundary, the extensive Rattlesnake Hills on the southern boundary, and a large central undulating zone (McCorquodale 1986). Elevation ranges from 200 to 1,090 m.

The ALE reserve is entirely within the Artemesia tridentata/Agropyron spicatum (big sagebrush/bluebunch wheatgrass) zone (Daubenmire 1970). Big sagebrush dominates the overstory at all elevations. However, periodic fires have resulted in a patchy distribution and 70% removal of big sagebrush on the study area. Understories are dominated by bluebunch wheatgrass at mid- and upper elevations and Sandberg bluegrass (Poa sandbergii) and cheatgrass brome (Bromus tectorum) at lower elevations and disturbed sites, respectively. A diverse variety of forbs exists on the study area. Riparian vegetation is limited to 6 isolated locations.

A coyote food habits study was conducted on the same study area and indicated a diverse diet (Stoel 1977). Great basin pocket mice (Perognathus parvus) are exceptionally numerous in this region of shrubsteppe (Hedlund et al. 1977) and the coyotes' diet reflected this abundance. In addition to pocket mice, leporids (Sylvilagus nuttallii and Lepus californicus), voles (Microtus montanus and Lagurus curtatus), pocket gophers (Thomomys talpoides), darkling beetles and grasshoppers (Coleoptera and Orthoptera), ground squirrels (Spermophilus townsendii), birds, and reptiles were important dietary components. Another study conducted on an adjacent portion of the Hanford NERP found coyotes a major predator on

mule deer fawns (Odocoileus hemionus), accounting for 10 of 14 deaths (Steigers and Flinders 1980).

Absence of grazing and other land-use practices the last 45 years were of particular significance to this study. The Hanford Reservation, which now includes the ALE Reserve, was created in 1943 and became restricted from all private and public use. Prior to that time, portions of what is now the ALE Reserve received light to moderate levels of sheep grazing mostly during winter. In 1967, the ALE Reserve was created to further preserve a near pristine shrubsteppe community (Vaughan and Rickard 1977) and it now serves as a research area for ecological studies. Exploitation of coyotes via predator control efforts last occurred in 1952.

METHODS

Field Investigations

Adult coyotes were captured with #3 offset jaw, leg-hold traps, most of which were padded and equipped with tranquillizer tabs (Balsler 1965). Twenty-seven adults (20 recaptures) were captured with a netgun from a helicopter. Pups were trapped, hand captured in excavated dens, or hand-netted near dens. All adults and pups older than 10 weeks were fitted with a radio-collar. The antenna was routed between the 2 layers of collar material to the nape of the neck where it exited dorsally and was encased in a 15 cm section of heavy, 0.64 cm air hose. This protected the antenna from abrasion and potentially enhanced the effective signal strength by increasing the vertical free-space by 10-15 cm. Pups captured near dens when 10-14 weeks old were fitted with a special expandable radio-collar (Crabtree et al., unpublished) to provide estimates of survival, dispersal, and social interactions up to 2.5 years of age.

The sex, weight, estimated age, estimated condition index (Crabtree 1989), presence of scars and unique marks, and

description of genitalia and mammae were recorded. A first premolar was removed for age determination by examination of cementum annuli from prepared tooth sections (Matson's, Milltown, MT). Each collared coyote was marked with numbered ear tags and 2 x 6 cm colored ear flags. Blood samples were taken from the brachial artery for serological analysis.

We monitored radio-marked coyotes from fixed-station shelters located atop 240 and 390 m escarpments on the eastern and southern boundaries of the study area, respectively. These locations provided complete coverage of the 150 km² tracking area. We simultaneously triangulated coyotes with arrays of 2 4-element yagi antennas coupled to a 180 degree phase-shifter (null system). Six to 12 relocations were taken at hourly intervals on coyotes every second or third night during 3 tracking periods annually. Fixes were obtained on 10-30 individuals only during active periods.

Correct antenna orientation was checked with beacon transmitters at least once an hour. The degree error of our tracking system was estimated periodically at multiple locations unknown to the observers. The low degree error (0.5°) was attributable to the design of the tracking system and line-of-sight coverage of the study area. Relocations were plotted on a grid system with 0.25 km² cells to assess home range size and movement patterns which aided in the determination of social class.

Definitions and Decision Criteria

Relocation data also provided an estimate of an animal's resident equivalent (RE), used in density estimation and social classification. We define RE as the proportion of time an individual spent on a defined sampling area during a defined sampling period. The study population consisted of resident coyotes and radio-collared coyotes that were present at least 10% of the time during a tracking period. The

tracking area was considered the portion of the study area in which coyotes could be relocated from the 2 main tracking shelters. We defined a core area, central to and within the tracking area, that included 12 contiguous territorial breeding groups. The social composition of the population was estimated from the sum total of REs from all animals in each social class on the core area.

Beginning in fall 1984, we trapped during 8 consecutive spring and fall trapping periods in an attempt to capture all coyotes in and around the core area. Age classes were comprised of the age at capture in fall and spring: 0.5 and 0.9 year-olds for the first year age class; 1.5 and 1.9 year-olds for the second year age class; and so on. Litter size at birth was estimated from den excavations the first few weeks after birth and placental scar counts from females that had successfully whelped. Pups or juveniles are considered young adults after March 1 (0.9 years old). Coyotes age 2.5 year and older were classified as mature adults. Based on major biological activities we designated 3 periods: whelping, March to mid-June; pup-rearing, July through October; and winter (breeding), late November through February.

Adult coyotes were assigned to social classes based on their space use, home range fidelity, movements patterns, and associations with other coyotes during the pup rearing period (Crabtree 1989). Vocal response to playbacks and visual observations also aided in determination of social class. Adult coyotes were classified as either **social group members** or **loners**. Social or territorial breeding groups consisted of the **alpha male and female** (breeding adults) and **associates**. Loners consisted of **solitary residents** and **nomads**. The term transient is used with caution because a significant portion of the loner social class exhibited little or no transitory movements. Coyote pups were classified as associates if they

had not dispersed from their natal territory by 31 November when they were nearly 8 months old.

Breeding adults were recognized by 2 or more criteria similar to that of Andelt (1985): 1) adults of opposite sex traveling closest together during the breeding and nursing period; 2) female with distended abdomen and/or dark, scarred, and elongated mammae; and 3) female with a high frequency of locations near a natal den during parturition and lactation. Adult coyotes were termed associates if they interacted with breeding adults and their pups and occupied the same home range. The distinction between nomads and solitary residents was made solely on relocation data and occasional direct observation. Solitary residents exhibited a higher degree of home range fidelity than did nomads and had a home range size closer to that of group members (Crabtree 1989). Nomads had little or no recurring movement pattern and ranged widely ($>60 \text{ km}^2$).

Reproductive failure was defined as the absence of pups in a territorial breeding group during the whelping and lactation period. This was recognized by absence of the typical, confined movements of successfully breeding females near natal den areas during whelping and lactation. Determinations were later verified by monitoring group vocalizations in July and August. Pup recruitment was calculated as the number of pups surviving to 14 weeks of age per female in the population. Low fecundity resulted in a small, but representative, sample of pups used to estimate natality and pup survival.

Analytical Methods

We estimated population abundance by a modified version of statistical techniques described by Dennis et al. (1989, unpubl. manuscript). Estimates of RE for marked animals enabled estimation of density under an open population

condition rather than assuming population closure as in Dennis et al. 1989 (unpubl. manuscript). The marked sample consisted of isotope-tagged feces from 42 adult coyotes implanted subcutaneously with slow-release radioisotope discs (Crabtree et al. 1989). The estimator is analogous to the Lincoln index $N = M(n/m)$, with M , the number of marked animals in the population, replaced with the sum of RE for the M marked animals and n and m are the total number of scats and the number of marked scats collected, respectively. Density was estimated as the total number of REs from all N animals that utilized the sampling area, divided by the sampling area.

We censused all roads and major trails in the core area, and then systematically selected the transects before trapping and marking adults. After initial clearing, we collected scats on 70 1.6 km transects in late June and October 1985 and 1986. Assumptions, field techniques, variance estimators, and model testing are provided in Dennis et al. (1989, unpubl. manuscript). Concurrent with scat sampling we recorded the number of scats/km as an index to coyote density. We counted the number of scats on a representative 38.4 km collection route during early July in 1985-1987. To assess our estimates of density we attempted a complete enumeration of coyotes on the core area by an intensive trapping effort, visual identification of unmarked animals, and monitoring of group vocalizations.

Estimation and statistical testing of adult survival was accomplished with program SURVIV (White 1983). We used student t-tests for paired comparisons when data were normally distributed, ranked sum tests when data were non-normal but asymptotic, and median tests when distributions were contaminated. Unless otherwise noted the terms significant and highly significant refer to P-values <0.05 and <0.01 , respectively.

RESULTS

Captures and Composition

All 87 adults and 23 of 58 pups captured were fitted with radio-transmitter collars that averaged 3.5% of body weight. The ratio of captured males:females was 46:54 for adults and 45:55 for pups, respectively; neither of which was significantly different from an equal sex ratio ($P > 0.40$). The sex ratio at birth (47.4% males, $n=38$) was also balanced ($P=0.88$). The age structure of the ALE population from spring and fall capture periods ($n=92$) is presented in Figure 1. The ALE coyote age structure was substantially older than the age structure of a typically exploited population.

There was a 67:33 percent ratio of territorial group members to loners in the spring, pre-whelping population. This ratio increased to 74:26 for adults in the fall, pre-dispersal, population (80:20 including 6 month-old pups). The composition of the spring and fall populations were: 40 and 44% for breeding adults, 27 and 30% for associates, 18 and 20% for solitary residents, and 15 and 6%, respectively.

Natality

Based on a sample of 81 female breeding-seasons (from $n=45$ radio-tracked individuals), successful whelping occurred only for alpha females, aged 2 through 6 years (Figure 2). None of the yearlings and only 29% of 2 year-olds produced pups. These data suggest that breeding females secure territories and produce their first litter when they are either age 2 or 3. Assuming an equal sex ratio, we estimated 40% of the females in the spring population successfully reproduced.

The reproductive failure rate among 33 territorial female breeding-seasons ($n=14$ alpha females) was 0.27 ($SE=0.078$). Territorial groups with 1 or both breeding adults age 6 and older did not produce litters and accounted for 6 of 9

failures (Figure 2). Based on intensive radio-tracking and direct observation, reproductive failure resulted from failure to whelp or loss of entire litters shortly after parturition. Four older-aged (age 6-12) coyote social groups maintained territories for up to 3 consecutive years without producing any pups.

The estimate of litter size at birth (excluding the 9 cases of reproductive failure) was 5.55 (n=9). The estimate of litter size at 14 weeks of age was 2.33 (n=12). This can be considered an estimate of pup recruitment because little natural mortality was observed between 14 weeks of age and fall dispersal from the population. These data result in a population productivity estimate of 0.62 pups/female. The percentage of pups in the fall population based on captures during 4 consecutive fall seasons (August-November) was 17.8% (8 of 45). Although the use of fall capture data as an index to productivity is probably biased (Caughley 1966), it was consistent with our estimate from litter size data (23.6%).

Mortality

Three cases of mortality among radio-collared adults occurred during 1984-1987 on the Hanford Reservation. Two were due to vehicle collisions the other was human related. An additional 12 loner adults that spent the majority of the time off the study area died as a result of trapping (n=9), shooting (n=2), or vehicle collision (n=1).

The overall estimate of annual survival for adult coyotes during the study was 0.90 (SE=0.033). The effect of social class on survival estimates was highly significant (P=0.0008), whereas the expected effect of age was non-significant (P=0.14). Survival estimates for adult coyotes varied little (P=0.90) from 1985 to 1987 (0.92, 0.93, and 0.88, respectively). Adult male and female survival estimates were also similar (P=0.61); consequently, we pooled the data by sex

and age classes and combined years.

Estimates of adult survival by social class are presented in Table 2. Social group members in a territory had a significantly higher ($P=0.0007$) survival rate than loners. The survival rate for associates was somewhat lower ($P=0.07$) than that for breeding adults; whereas survival of solitary residents was not significantly different from that for nomads ($P=0.15$).

The estimate of pup survival during the nursing period was 0.42 ($SE=0.16$), excluding cases of reproductive failure described above. Serological analysis of a pup that later died (3 died in a litter of 6) revealed a high level of canine parvovirus antibody. Its weight was 33% lower than predicted from captive pup growth curves (Jamieson and Beckoff 1975, Barnum et al. 1979). Pup weights ($n=18$) at known ages ranging from 0 to 38 days old averaged 27% below expected.

Only 2 cases of mortality occurred (survival rate=0.91, $SE=0.072$) from 14 weeks-old to dispersal. The estimate of pup survival during the dispersal period was 0.58 ($SE=0.14$). All 5 cases of mortality were due to trapping of pups that had dispersed from the population. No mortality occurred for pups that did not disperse. The overall survival rate of pups from whelping to young adult status was 0.22.

Immigration and Emigration

Emigration can be estimated from the proportion of marked animals dispersing. Immigration was assessed from information on new individuals captured during 8 consecutive spring and fall trapping periods. Most immigrants were young adult nomads. The annual immigration rate for the population was estimated at 6%.

Immigration by pups in the fall was negligible. All 8 pups captured in the fall were members of adjacent territories with only 2 of these trapped during October and November, the

major dispersal period for pups. The following spring periods, 12 of 23 (52%) total captures were older pups (0.9 years). Of these 12, 2 were affiliated with adjacent territories, 5 left the area shortly after capture, and 5 had an average RE of 0.25 in spring that fell to 0.12 by fall. Of only 3 yearlings (age 1.5) captured during 4 fall trapping periods (n=45 captures), 2 were wide-ranging nomads with a $RE < 0.05$).

An apparent influx of young adult nomads (age 1 to 3) began after fall trapping (December) and continued to the spring trapping period. The timing of the winter/spring immigration by young adult nomads corresponds with pair bonding, territorial establishment, and breeding in coyotes. Of 23 loners, (\bar{x} age=1.95 years) captured during the spring trapping periods, 17 (74%) were young nomads; whereas, of 19 loners (\bar{x} age=4.21 years) captured during fall trapping, only 6 (32%) were young nomads. The ratio of nomads:solitary residents captured was significantly greater in the spring than in fall.

Not only were there fewer young nomads in the fall population but they also spent less time there. The average RE for young adult nomads was 0.30 in the spring and 0.15 by fall. The spring/summer emigration trend of newly immigrated nomads also held for young loners (age 1 to 3) in general. This emigration immediately preceded pup recruitment. Conversely, the older-aged solitary residents (ages 3 to 13), of which 80% were captured during the fall, had a degree of home range fidelity approaching that of social group individuals. They likely resided in the population before their initial capture.

Population emigration was comprised of pups and associates dispersing in the fall and nomads (discussed above). Ten (59%) of 16 marked pups dispersed from the

population during the fall with the remainder staying as associates or solitary residents. Emigration by 3 of 6 associates and their age structure ($n=12$) both indicate that approximately 50% emigrate each year. The age structure of associates was 50% 1 year old, 25% 2 years old, 17% 3 years old, 8% 4 years old, and 0% for the 5+ year age class. Emigration of breeding adults and solitary residents was not observed. The annual emigration rate for the adult population was estimated at 15%.

Density

Estimates of coyote density did not significantly differ among 4 sampling periods ($P=0.69$) in 1985 and 1986 (Figure 3). The scat index, an uncalibrated measure of population trend, also indicated no significant differences from 1985 to 1987 ($P=0.29$). The low production and survival of pups, emigration of nomads, and absence of immigrant pups led to decreased density estimates in the fall (Figure 3). The spring:fall ratio of coyote density estimates and scat indices indicated only a 20-30% within-year population fluctuation.

The spring, pre-whelping estimate of coyote density was 0.402 ($SE=0.014$) coyotes per km^2 . A complete enumeration of coyotes on the study area, based on an intensive capture effort, vocalizations, and visual observation, allowed us to evaluate the density estimate. We either captured or visually identified all breeding adults on the study area. Of 8 central groups we captured 81% of the breeding adults and captured at least 1 adult in 17 of 23 groups on the ALE Reserve. The number of associates per territory ($x=1.4$) was determined from group vocalizations and direct observation. We assumed that we captured nearly all loners that used the study area because of their vulnerability to trapping. Complete enumeration resulted in a pre-whelping density of 0.376 coyotes per km^2 , only slightly lower than the density

estimate above. Several loner coyotes not captured that partially utilized the study area may account for the difference.

DISCUSSION

Captures and Composition

Trapping was not biased with respect to sex. The sex ratio of trapped adults was the same as the sex ratio at birth and adult survival did not differ between sexes. However, both population age structure, and especially social composition based on trapping data appear to be biased. The social composition based on trapping was markedly different from estimates independent of trapping (40:27:18:15 vs 33:13:24:30, respectively). However, the general age structure of the ALE population reflected the low estimates of mortality and recruitment. Over 50% of the population was age 3 or older, in contrast to exploited populations where the majority of the population is often in the first age class. Because age is an important component of social status, and interpretations of age ratios can be biased (Caughley 1974), inference based on capture is suspect.

Sociodemographic Limitation

The ALE Reserve contained a naturally regulated coyote population, with a small subset of loners exposed to light levels of human exploitation. Previous studies reflect the exploitative conditions which are prevalent throughout the coyotes range. It is not surprising then, that many of the demographic parameters estimated in our study exceed the range of values reported for coyote populations, although there was similarity in parameter estimates between our study and recent studies of exploited populations.

Natality and perinatal mortality

The productivity of the ALE population was exceptionally low because: (1) 40% of the females (only alpha females) were

productive, (2) age at first breeding was 2 or 3 years, (3) 27% of alpha females experienced reproductive failure, (4) reproductive success decreased for older-aged breeding females, (5) average litter size at birth was estimated at 5.6, and (6) perinatal pup mortality was high.

Female establishment of a territory was required for successful breeding. Knowlton et al. (1986) demonstrated that most females, regardless of social status, enter estrus, but only territorial females successfully whelp. He found substantial numbers of transient females with implantation sites but none successfully whelped. Of 6 female carcasses examined in our study: 4 were loners or associates that had not whelped, one 7 year-old solitary resident had previously whelped as an alpha female, and one 6 year-old solitary resident, previously affiliated with a territorial male, had 5 resorbing embryos.

The percentage of females breeding was similar to that in other studies. Based on percent of the population in breeding groups, group size during pup rearing, and an equal sex ratio, the percent of alpha females in studies subjected to light and moderate levels of exploitation was 42, 50, 45, 60, 44, and 40% (Camenzind 1978, Bowen 1978, Messier and Barrette 1982, Andelt 1985, Windberg and Knowlton 1988, and this study, respectively). Gier (1968) and Knowlton (1972) inferred that 50% females breeding was average.

Age of breeding female was also an important determinant of population productivity. Only females age 2-6 successfully reproduced; however, ages of territorial females ranged from 2 to 11 years. The 27% reproductive failure among alpha females represents an effective form of population limitation. The non-reproductive occupants defended the territory from younger, presumably productive, replacements. The existence of unsuccessful, older-aged breeding females has not been

previously documented in the wild, but a decrease in litter size after age 6 years was demonstrated in captive coyotes (J. Green, personal commun.).

Although our sample size was small, litter size at birth in our population was only slightly smaller than the average coyote litter of 6 (Beckoff 1977). Estimates of litter size at birth have ranged from 5.0 to 6.5 in recent studies with populations subjected to various levels of exploitation (Nellis and Keith 1976, Bowen 1978, Messier and Barrette 1982, Andelt 1985, Beckoff and Wells 1986, this study). Gier (1968:46) reported average litter sizes of 5.6 to 6.2 for various populations.

Knowlton and Stoddart (1983) state that little attention has been directed toward pup mortality the first few months of life. They state that entire captive litters were lost shortly after birth, primarily among females that were nutritionally or socially stressed. Available estimates of early pup mortality were variable (Gier 1968, 50%; Nellis and Keith 1976, 9%; Andelt 1982, 36 to 64%; this study, 54 to 67%).

We submit that substantial levels of social and nutritional stress will affect productivity, primarily through early post-partum pup mortality rather than decreased litter size at birth. Energetic demands the first 14 weeks of life (i.e., lactation) are much greater than during, and prior to, gestation (Millar 1977). Territoriality should insure the minimum nutritional requirements for ovulation and implantation but not necessarily a healthy litter of pups.

Adult mortality and dispersal

The annual estimates of natural and human-related mortality were 0.0 and 10% during the 4 year study. In the ALE population, once pups survive to 14 weeks of age the probability of survival is near 1.0 until old age. Excluding

highway deaths, we suspect the estimates of adult mortality at ALE would have been 0.0, except for death at old age.

At least 90% of adult mortality in coyote population studies (including ours) was directly or indirectly human-related (Knowlton et al. 1986). We reject the hypothesis by Knowlton (1972) that natural mortality may exceed 40% in the absence of human exploitation and suggest 10% as more realistic. Populations with mortality from control practices below 40%, had low to non-existent natural mortality (Bowen 1978, Davison 1980, Andelt 1985, Windberg et al. 1985, this study). Exceptions may be due to winter starvation in populations near the limits of their range (Murie 1940) and disease in disturbed areas.

Adult survival was clearly a function of social class rather than sex or age. Although age is a component of social class, mortality acted more directly on the social structure, rather than age structure, of the population. Home range fidelity was inversely related with human-induced mortality. Although we suspect that the degree of fidelity is similarly related to natural mortality, we observed no natural mortality to confirm this.

Nomads are considered more vulnerable to trapping (Hibler 1977, Roy and Dorrance 1982, Harris 1983, Pyrah 1984). Although they comprise a substantial portion of the captured animals (35%), they constituted a much smaller proportion of the population (15%). Territorial adults comprised a larger proportion (67%) of the population (67%) than that from trap captures (42%), perhaps because territorial coyotes have an aversion to novel stimuli (Harris 1983).

We agree with Knowlton and Stoddart (1986) that immigration may be the primary means by which coyote populations initially compensate for exploitation loss. The winter/spring immigration period corresponded to social

bonding between groups and breeding pairs (Andelt 1985). Immigrants provide a reservoir of breeding replacements if territorial vacancies occur. The emigration period that immediately followed was probably the result of few vacant territories and habitat-saturated conditions on the ALE Reserve.

Stability and Regulation

Annual survival estimates, age structure, rates of reproductive failure, and similarity among density estimates indicate that the ALE population was stable. The contiguous distribution and stability of territories, concentration of loners in vacancies and corridors between territories (Crabtree 1989), magnitude of pup and nomad dispersal, and low productivity suggest that this population is saturated. Annual gain to the population consisted of a 19% increase from pup recruitment (after mortality and fall dispersal) and a calculated 6% immigration by nomads. Annual losses balanced gains and consisted of 10% adult mortality and an estimated 15% emigration by non-breeding adults, most of which were associates.

The social structure and population ecology of coyotes and wolves (Canis lupus) are often compared (Camenzind 1978, Bowen 1978, Beckoff and Wells 1986). Our study revealed additional sociodemographic factors of coyotes that closely parallel those of wolves (see Mech 1970, 1977, Packer and Mech 1980) were revealed or further emphasized in our study. These factors include: a high degree of spatial structuring according to various social classes (Crabtree 1989), delayed age at first breeding, exclusive breeding by dominants, and the significance of adult dispersal and pup mortality.

The above factors, with the addition of low pup weights, low condition indices of alpha females (Crabtree 1989), low productivity, wounds on males (Crabtree 1989), eviction of

previous territorial owners, and observed territorial interactions indicate strong intraspecific strife. Based on this evidence and observed similarities between coyotes and wolves, the social/nutritional hypothesis of wolf regulation described by Packer and Mech (1980) appears applicable to this case with some initial amendments. Social and nutritional stress on territorial females, rather than summer food availability, more directly influenced early pup mortality. We also hypothesize a shorter lag time of population response to exploitation by coyotes than for wolves. Additional comparisons and differences should provide stimulus for future research.

Among the demographic parameters examined in this study, we contend the 2 factors with the greatest influence on population response are pup survival and adult immigration. Immigration and territorial replacement by surplus animals may be an immediate and totally compensatory response to exploitation while increases in pup survival are slower and strongly influenced by prey resources. The influence of juvenile survival on population increase has also been singled out in ungulates (Caughley 1970, Clutton-Brock 1983).

We also predict that the number of females per unit area is relatively fixed as is the proportion of females breeding except at the highest levels of exploitation. Finally, we propose that litter size is relatively insensitive to the level of exploitation; early pup survival is the major reproductive response to exploitation. Finally, there may be a threshold level of heavy exploitation, above which the major social mechanisms of regulation (e.g., land-tenure territoriality) break down.

CONCLUSIONS

Social behavior appears to be the driving force underpinning the population demography of coyotes at the ALE

Reserve and other lightly exploited populations. In exploited populations, human-related mortality overrides socio-population dynamics, but probably disrupts social organization to a point that negates the socially-induced population mechanisms observed in this study. We must understand population dynamics in the absence of human influence before we can understand human effects. Until more research is conducted on natural, unexploited populations of coyotes, inefficient management will continue.

Social behavior, namely territoriality and prey availability, have been identified as regulating mechanisms in previous coyote studies (Knowlton 1983, Gier 1968, Wagner 1972, Todd et al. 1981). We suggest that the ultimate interaction of coyote populations with available food resources is strongly mediated and buffered by social mechanisms. Despite numerous studies, the mechanisms of this process are not fully understood and are severely clouded by human exploitation.

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Table 1. Estimates of annual survival categorized by social class for radio-collared adult coyotes captured on the Arid Lands Ecology Reserve, Hanford, Washington. Data were combined from 1985 through 1987.

Category			
Social class	n	Survival rate	SE
Territorial groups			
Breeding adults	26	1.00	0.110
Associates	10	0.90	0.095
Combined	36	0.98	0.021
Loners			
Solitary residents	19	0.86	0.066
Nomads	24	0.70	0.086
Combined	43	0.78	0.055
Population Total	79	0.90	0.033

Figure Legends

Figure 1. Age structure of the ALE coyote population, 1984-88, Hanford, Washington and a typical exploited coyote population.

Figure 2. Distribution of successful and unsuccessful female breeding-seasons according to age and territorial status (shaded) on the Arids Lands Ecology Reserve, Hanford, Washington from 1984-1988.

Figure 3. Absolute density estimates and scat indices of abundance for coyotes on the Arid Lands Ecology Reserve, Hanford, Washington.

Exploited Population
 ALE Population, N=90

