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Population and Social Biology of Free-Ranging Dogs, Canis familiaris

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ABSTRACT

Population size and density, age structure, survivorship patterns, sex ratios, social organization of urban, rural, and feral dog (Canis familiaris) populations were examined in Cd. Juarez, Mexico (urban site) and on the Navajo reservation (rural and wild sites) between June 1983 and December 1984. Urban and rural dogs were less social than expected whereas dogs characteristically lived in packs. Seasonal variation in the structure of feral dog packs influenced by reproduction, both directly (pups born into the pack) and indirectly (pregnant females may temporarily emigrate form the pack to give birth).

Social organization refers to the spatial relationships, group composition, and patterns of social interaction among individuals, and the overall manner in which these variables interact to characterize a population (Bekoff and Wells, 1986). Among carnivores, intraspecific variation in social organization often is a response to the quantity and distribution of local food reseources (Bekoff et al., 1984), and the strategy for acquiring those resources (Caraco and Wolf, 1975; Nudds, 1978).

Few detailed data on the social organization of free-ranging domestic dogs (*Canis familiaris*), (those having unrestricted access to public property-Beck, 1973), have been reported (Beck, 1973; Daniels, 1983a, 1983b; Fox, 1978), and no comparative studies of populations in different habitats have been conducted previously. Likewise, factors that influence patterns of social behavior have remained largely unexamined despite the 10,000–14,000-year (Davis and Valla, 1978; Fox and Bekoff, 1975; Scott, 1967) association between dogs and humans. However, dogs provide an excellent model to study comparative aspects of canid ecology and behavioral plasticity (Daniels, 1987a); they are found in every terrestrial habitat in which humans reside and may be the most abundant extant land carnivore.

In this paper, we present data on survivorship patterns, population size and density, age structure, and sex ratios for urban, rural, and "wild" or feral dogs. In addition, we describe the social organization of three populations of free-ranging dogs and factors that influence it.

MATERIALS AND METHODS

Dogs were observed between June 1983 and December 1984 on the Navajo reservation in the southwestern United States and in Ciudad (Cd.) Juarez, Chihuahua, Mexico. Three habitat types were

selected: urban, rural, and wild. Urban sites were defined as areas with a human population density ≥386/km^2 (U.S. Bureau of the Census, 1982). Urban dogs were studied in Cd. Juarez (1,200 m elev.), on the United States-Mexico border directly across the Rio Grande from El Paso, Texas. Cd. Juarez is the largest Mexican border city, with a human population approaching 1 million and an area of 4,854 km^2. The city is located in the northernmost reaches of the Chihuahuan desert (Schmidt, 1979), with a mean annual precipitation of about 20 cm. Two study sites were selected in poorer sections of Cd. Juarez because of the high correlation between economically depressed areas and the occurrence of free-ranging dogs (Beck, 1973; Daniels,1983a) Site 1 was 0.91 km^2 and site 2, about 12 km ESE of site 1, was 0.67 km^2.

Study sites in rural and wild areas were located on the Navajo reservation, a 64,750-km^2 area located primarily in Arizona, and extending into New Mexico and Utah. Rural sites were less populated and more isolated geographically (surrounded by broad expanses of sparsely inhabited land) than urban areas. Wild sites were uninhabited or sparsely inhabited by humans. Mean human density was 1.7/km^2 although most people lived at higher densities in the approximately 110 communities that compose the reservation. Field work was conducted in and near the communities of Window Rock, Arizona and Navajo, New Mexico, on the Arizona-New Mexico border. Reservation communities typically have ≤2,000 residents distributed among several small housing areas. Virtually every reservation community was rural in that it provided habitat intermediate between the urban and wild areas. Rural dogs came in contact with people at a greater rate than feral animals, although not as frequently as dogs in urban areas, and had access to more isolated areas free of human residents. Thus, rural dogs had resources available within the community and the potential to roam beyond community boundaries and to encounter wildlife and feral dogs.

Efforts to locate feral dogs were centered on a dump on the outskirts of Navajo, New Mexico. Dumps provided locally abundant food resources that attracted feral dogs (Daniels, 1988).

The reservation habitat is dominated by a mix of pinon pine *(Pinus edulis)* and Rocky Mountain juniper *(Juniperus scopulorum)* trees (Brown, 1982). Major subdominant shrub species were big sagebrush *(Artemisia tridentata),* cliffrose *(Cowania neomexicana),* and snakeweed *(Gutierrezia sarothrae).* Mean annual precipitation is between 25 and 50 cm, and the sites were at 1,500-2,300 m elevation. The numerous sandstone canyons may be 2.0-3.5 km long, bordered by walls reaching 30 m or more high. Natural depressions in these walls provided cave-like shelters that served as dens for litters of pups.

To estimate dog populations, the same route through a study site was traveled by auto for 5 mornings, when dogs were most active (Daniels, 1983a); every free-ranging dog within about 70 m of the vehicle was photographed. Descriptions of each dog were recorded on cassette tapes to complement the photographs. Photos of dogs taken on successive days were compared and the number of "recaptures" noted (Beck, 1973). This is a modification of Schnabel's (1938) technique that had the advantage of avoiding incidents of trap-shy and trap-prone animals. Further marking of dogs was unnecessary because of their distinctive coat colors and patterns. Confidence limits were calculated for the population estimates (Overton, 1971).

Feral dogs were censused by enumeration of all individuals observed during the study. The number of feral dogs reported is the minimum number present (Davis and Winstead, 1980). However, live trapping was conducted (Daniels and Bekoff, 1989) to fit several feral dogs with radio collars (A VM Instrument Co., Dublin, CA). Telemetry permitted estimation of home-range use (Daniels and Bekoff, 1989) and aided in locating uncollared animals. Sex of dogs generally was determined easily by observation of the animal and its behavior, especially patterns of urination (Bekoff, 1979).

Visual observation was used to distinguish pups (birth-4 months), juveniles (4 months-1 year), adults (1-7 years), and old adults (>7 years). Interviews of area residents were conducted as necessary to determine a dog's age, if it was owned. Age classification of feral dogs also was based on visual estimates of tooth wear (Gier, 1968; Kirk, 1977) when possible, and the animal's general appearance.

All occurrences of single dogs, pairs, or groups of three or more animals were recorded during daily auto surveys through study sites. Frequency data were compared to expected values in a zero-truncated Poisson distribution to determine if grouping patterns were random (Beck, 1973; Cohen, 1960). Details of statistical methods may be found in Beck (1973) and Daniels (1987a).

RESULTS

A population of 376 ± 53 (95% confidence interval) free-ranging dogs was estimated in Cd. Juarez study site 1, whereas 556 ± 70 free-ranging dogs were estimated in study site 2. Study site 1 was larger (0.91 km^2) than site 2 (0.67 km^2), thus the estimated density of dogs was 534 dogs/km^2 at site 1 and 936 dogs/km^2 at site 2.

Dog populations were estimated to be 228 ± 29 in the St. Michael's housing area of Window Rock, Arizona and 431 ± 56 in Navajo, New Mexico. Because of the disjunct pattern of small, concentrated housing areas surrounded by large expanses of uninhabited land, population estimates could not be extrapolated reliably to areas larger than the sampling area itself. However, the Window Rock sampling area was approximately 0.52 km^2, whereas the Navajo site measured 1.94 km^2. Thus, Window Rock supported approximately twice the density of free-ranging dogs as Navajo.

Population estimates based on mark-recapture techniques were not calculated for feral dogs because of problems associated with repetitive live trapping (e.g., trap shyness, trap proneness) and the difficulty of otherwise locating dogs. Enumeration of individuals indicated a minimum population of 12 dogs (three juveniles, nine adults), excluding pups, in the immediate vicinity of Navajo dump.

The frequency distribution of groups composed of 1, 2, or ≥3 dogs, when compared to a zero-truncated Poisson distribution (Beck, 1973), was significantly different from expected for both urban site 1 (x^2 = 30.87, d.f. = 1, P < 0.001) and site 2 (x^2 = 29.59, d.f. = 1, P < 0.001). There were more singles, fewer pairs, and slightly more large groups than expected at both sites. Overall, there was a stronger tendency for dogs to avoid conspecifics than to group. A total of 1,987 dogs in 1,596 groups resulted in a mean group size of 1.24 dogs at site 1, and 2,781 dogs in 2,517 groups resulted in a mean group size of 1.10 dogs at site 2. The difference in mean size of groups was significant (Table 1) when compared using a test of means when variances were unequal (Sokal and Rohlf, 1981).

The frequency distribution of different-sized dog groups differed significantly from the expected zero-truncated Poisson for both Window Rock (x^2 = 75.26, d.f. = 3, P < 0.001) and Navajo (x^2 = 104.58, d.f. = 3, P < 0.001) populations, indicating that grouping patterns were not random. As with the urban population, dogs in the reservation communities were observed more frequently as singles, less often in pairs, and somewhat more frequently in large groups than expected.

Mean sizes of groups were 1.29 and 1.32 dogs for Navajo and Window Rock, respectively, and comparison of the means indicated that they were not significantly different (Table 1). Data from Window Rock thus were considered representative of rural dog populations on the reservation and were compared individually to each of the two urban sites. In both instances the mean size of groups was significantly larger for the rural population than for either urban site (Table 1), indicating a trend toward greater sociality on the reservation.

TABLE 1. Summary statistics of mean group sizes of domestic dogs for two rural and two urban sites. The test statistic, t, is based on a test of means when variances are unequal.

Site	Group size ($\overline{x}$)	Groups observed (n)	Variance	Sites compared	t
Window Rock	1.32	2,586	0.65	Window Rock-Cd. Juarez 1	–2.96*
Navajo	1.29	749	0.68	Navajo-Window Rock	–0.88
Cd. Juarez 1	1.24	1,596	0.78	Cd. Juarez 1-Cd. Juarez 2	5.19**
Cd. Juarez 2	1.10	2,517	0.61	Cd. Juarez 2-Window Rock	10.0**

* $P < 0.01$.

** $P < 0.001$.

A pack was defined as a group of animals that traveled, rested, foraged, and hunted together. Although canid packs usually are groups of related individuals (Bekoff et al., 1984; Mech, 1970), the criterion of relatedness was not applied to dog groups because these data could not be collected. Most feral dogs were members of either the Canyon or Corral pack, designated by homesite location.

The Canyon pack consisted of a core of four adults. Adult membership occasionally varied, however, as transients ($n = 4$) joined the pack temporarily, remaining with them for 1 day to 1 week. The Corral pack consisted of a core of one adult female and a juvenile female; their relationship could not be determined. A third pack, consisting of two juvenile males and an adult female, was observed infrequently.

Pack composition changed in both the Corral and Canyon packs with parturition in late autumn (November 1983; Corral pack) and early winter (January 1984; Canyon pack). Two pups in the Corral pack were discovered when they were approximately 4 weeks old but litter size may have been higher at birth; domestic dogs typically produce six to 12 pups per breeding period (Palmer and Fowler, 1975). Ten pups were born in the Canyon pack and all were discovered in a sandstone cave along a canyon wall when 2-3 weeks old. However, subsequent capture of a female from the Canyon pack shortly after the pups were discovered, and observations of the dominant female in the pack, indicated that both were lactating. It is likely that the 10 pups actually composed two litters and that both females gave birth at nearly the same time; there was no discernible difference in age of the pups and all were being reared communally. Pups from both litters remained together into early summer 1984, when observations of surviving young ceased.

In addition to communal denning, feral dogs also may employ a strategy of pack splitting. Pack splitting refers to the temporary emigration from the pack of one or more individuals that travel and feed on their own (Burkholder, 1959; Jordan etal., 1967; Mech, 1966). Behavior data collected from two solitary females, neither of which moved far from established packs, strongly suggest that these dogs previously were part of the Corral and Canyon packs, respectively.

Both females reared their young apart from the packs for approximately 2 months after parturition, although regular contact between the females and other pack members was observed. At the end of this period, none of the three pups of the first female could be found (initial litter size was not known) and interactions of the female with the Corral pack increased, including joint foraging trips to the dump. Pups of the second female actively left the den-site cave by 10 February 1984, approximately 5 weeks after birth, and briefly interacted with the pups of the Canyon pack by 24 February 1984. The litters again separated as the solitary female and its pups moved farther up the canyon, away from the Canyon pack, in early March 1984. Subsequent observations indicated that the female had rejoined the pack fully by late May 1984 and traveled with it through the summer. A single observation of the female on 24 October 1984 indicated that it was still with the Canyon pack.

The distributions of different-aged dogs at urban sites 1 and 2 were not significantly different (Kolmogorov-Smirnov two-sample test, $D = 0.6$, $P > 0.05$); pups and juveniles each represented 7-9% of the population, adults composed 73-75% of the population, and old adults approximately 1.5-2.5% of the population. Individuals of unknown age accounted for approximately 7.5% of the total population in each site.

Age distributions of dogs surveyed *(n = 45)* in Window Rock and Navajo did not differ significantly from that at either Cd. Juarez site 1 (Kolmogorov-Smirnov two-sample test, $D = 0.2$, $P > 0.05$) or site 2 ($D = 0.2$, $P > 0.05$). The proportion of pups in the feral population ranged from none in September-October to approximately 70% *(n = 30)* in December-February. Only one (8.3%) old dog, a member of the Canyon pack, was observed during this study.

The relative success of feral dogs in maintaining population levels by reproduction remains undetermined. Weaning begins when pups are about 5 weeks old (Scott and Fuller, 1965) and by the age of 4 months juveniles essentially are independent. Juveniles then may disperse to another part of the home range of the pack, and much mortality probably occurs during this period of early independence. Dogs commonly disappeared even though they had been relatively easy to observe earlier. The initiation of pup independence coincided with an increase in pack movement (Daniels and Bekoff, 1989), and pups simply may have dispersed from the pack as it expanded its home range.

A difficulty in estimating mortality was that carcasses of dogs seldom were found, particularly if the animals had initiated movement away from den sites and no longer were restricted to small areas. In addition, golden eagles, *Aquila chrysaetos (n = 2)*, coyotes *(n = 3)*, common crows, *Corvus hrachyrhynchos (n = 10)*, ravens, *Corvus corax (n = 2)*, and even other dogs *(n = 6*; Daniels, 1987b) were observed to feed on dog remains during the study. Thus, the likelihood of finding carcasses was reduced further.

Observations of 18 wild-born pups suggested that mortality was relatively high early in life. Three (17%) of the pups were known to have died and remains were recovered. Necropsy results indicated that one probably died of distemper, a common viral infection of young canids, but the cause of death could not be determined for two others. Both of these dogs had been dead for at least several days when the remains were recovered and further examination revealed little more. Only six (33%) pups were observed past 4 months of age, the age of independence. Of these, two sibling pairs remained together during the study and one pair was found in the company of an abandoned pup adopted (Daniels, 1987b) into the Canyon pack. The remaining pups were observed infrequently past 3 months of age and most, if not all, probably did not survive. Thus, the overall survival rate to 4 months of age was 34% for the litters of five females.

In Cd. Juarez, the sex ratio was estimated to be 1.6:1 in favor of males at site 1, and 2:1 in favor of males at site 2. On the reservation, males outnumbered females 4:1 in Window Rock and 3:1 in Navajo. In contrast, the sex ratio of the feral population living beyond the Navajo community borders favored females by about 3.5:1. The predominance of males in Navajo may have been maintained by removal of females from the community. However, there were few places to bring unwanted animals on the reservation and abandonment at dumps was a common practice. During this study, 54 dogs were known to have been abandoned. Abandoned dogs predominantly were pups (69%), and females outnumbered males two to one for those dogs for which sex could be determined.

DISCUSSION

Densities of free-ranging dogs in Cd. Juarez were 2-5 times greater than those reported in urban areas of the United States (ca. 232 dogs/km^2 in Baltimore, Maryland-Beck, 1973; ca. 154 dogs/km^2 in Newark,

New Jersey-Daniels, 1983a). The high overall density of dogs in Cd. Juarez may partly reflect beliefs of owners that many dogs help provide adequate protection of family and property in areas with high crime rates (J. G. Rodriguez Torres, pers. comm.). Differences in the population density of dogs between the two sites in Cd. Juarez may reflect variations in density of human populations or the local crime rate at each site, rather than differences in reproduction. The absence of an effective dog control program that encompasses removal of free-ranging dogs from the streets, leash laws that restrict abilities of dogs to wander, and spay and neuter programs to limit reproduction may contribute to the high density of dogs.

By comparison, dog densities in the relatively small patches of housing within the rural communities of Window Rock and Navajo were nearly as high as those in Cd. Juarez. Furthermore, urban and rural dogs in this study were predominantly solitary. Data from urban dog populations in Baltimore, Maryland (Beck, 1973) and Newark, New Jersey (Daniels, 1983a) indicate the same general pattern of avoidance of conspecifics. Thus, similar factors may influence social organization in all of these sites. The net effect of such urban-like "islands" on the reservation was that rural dogs behaved much like dogs in an urban population (Daniels, 1986).

The inverse relationship between mean group size and population density at the Cd. Juarez sites suggests that dog density may influence the observed social system. Site 2 contained approximately twice as many dogs per unit area as site 1, indicating that as density increased, the tendency for positive social interactions within the population decreased.

The effects of population density on social behavior are well documented (Alexander, 1974; Crook, 1965; Eisenberg et al., 1972; Wilson, 1975; Wynne-Edwards, 1962), although population density alone is not the most significant proximate influence on social organization. Rather, the distribution of local shelter and food resources, and the magnitude and direction of change in those resources as population density changes, more precisely define social organization. Urban and rural dogs, for example, exhibited territorial behavior restricted to the homesite. Food also was provided at these sites by the owner, thus, homesites represented relatively small (approximately 600 m^2), easily defended areas of local resource abundance.

In addition, dogs probably were not as social as expected because little advantage was conferred on group-living animals. Scarce resources beyond those provided by human residents at both the urban and rural sites would be exploited more efficiently by individuals than by larger groups (Beck, 1973). Further, individual differences in behavior among dogs largely accounted for the presence of those few groups that formed in urban areas (Daniels, 1983a). Dogs that did not share the homesite with a conspecific, typically because the owner cared for and fed only one dog, spent little time engaged in social activities with conspecifics. Dogs that shared the homesite with one or more conspecifics were social most of the time, although predominantly with only a few individuals. Observed patterns of social organization at urban and rural sites, therefore, were based largely on dog-ownership practices.

Feral dogs were the most social of the three populations examined. Of the 12 juvenile and adult feral dogs known living near Navajo dump, nine (75%) lived in packs year-round and two (17%) others apparently were seasonal pack members.

Mechanisms of pack formation in feral dogs remain unclear. Two packs observed in this study were formed before initiation of field work, so factors influencing selection of pack members are not known. However, the nucleus of a new pack may consist of siblings that disperse together (Bekoff, 1977). For instance, the two male offspring of the Corral pack female formed a new pack with an older female near the natal den site of the males. Because nursing females often leave their pups for long periods between feedings, stronger social relationships develop among littermates than between offspring and parent

(Scott and Fuller, 1965). Familiarity resulting from regular interactions between conspecifics that live in close proximity (Daniels, 1983a, 1983b, 1987a) may be a prerequisite to group formation because of the development of strong social bonds (Bekoff, 1977, 1981).

Pack composition (adult members) essentially was stable during the study. However, variations in pack size associated with the presence of dependent pups suggest that packs also may be maintained by assimilation of nondispersing young into the pack (Bekoff et al., 1984). Observations of the Canyon pack in late spring-early summer indicated that several pups >4 months of age were traveling with the pack. Further data are needed on the frequency of dispersal by juveniles and the role this has in determining pack size and stability.

There may be several advantages of pack living for feral dogs, including enhanced vigilance resulting in greater protection from potential predators (e.g., humans) and increased ability to gain access to higher-quality food resources (Daniels and Bekoff, 1989). However, pack living may at times be disadvantageous. Breeding by a second female in the pack might induce it to leave and establish a new homesite temporarily. In wolves *(Canis lupus),* for example, breeding generally is restricted to a single dominant female (Harrington et al., 1982; Mech, 1970), and pack splitting may reduce the burden of alloparental care on the pack. Pack splitting also may protect a subordinate female's pups from the threat of infanticide by the dominant female (Corbett, 1988; Macdonald, 1980; Van Lawick and Van Lawick-Goodall, 1971). Overt aggression by the dominant female might increase as parturition approaches, (e.g., in wolves-Fox, 1971), which could facilitate pack splitting. In this study, both females resumed living with their respective packs after pup rearing was complete (either because the young died or became independent), suggesting that the benefits of pack splitting were temporary. Presently, it is not understood why a second subordinate female in the Canyon pack reared its pups with those of the dominant female, whereas one female left to rear its pups alone.

The timing of reproduction is an important aspect of the biology of free-ranging dogs with respect to the number of breeding periods and the time of year breeding occurs. Dogs average breeding twice yearly but nondomestic canids have a single annual breeding cycle (Kleiman, 1968). Although only one litter was observed from each of four females in this study, a second litter by a female in the Corral pack indicates that feral dogs maintain two cycles per year. Although domestic dogs generally are thought not to exhibit seasonal patterns of breeding (Engle, 1946) because of artificial selection for faster reproductive rates, the relative synchrony of breeding among females suggests that breeding may be seasonal. Gipson (1972) also noticed an increase in breeding in spring and fall for dogs in Arkansas, though breeding occurred throughout the year. No pattern of seasonal breeding was noted for urban and rural populations, but further data are necessary to determine the degree of synchrony of breeding at specific times of the year.

Feral dogs differed in reproductive timing from coyotes *(Canis latrans),* their sympatric nondomestic congeners, which typically breed in January and February and give birth in March or April, about 63 days after fertilization (Kennelly, 1978). Feral dogs gave birth 2 months earlier, in midwinter, possibly contributing to early mortality of their pups.

In general, mortality early in life appears to be high in all three habitats. Although the proportion of adults in the Cd. Juarez population was high, the population appeared to be relatively young. Free-ranging dog populations in Baltimore, Maryland and St. Louis, Missouri also were young, with an average adult age of about 2.5 years (Beck, 1974) and a mortality rate estimated at 50% in the 1st year of life for the Baltimore population (Beck, 1973). This indicates a relatively high turnover rate, therefore, high mortality.

The likelihood of surviving to old age was low at both Cd. Juarez sites; only about 2% of the urban population was composed of old dogs. By comparison, populations of confined pets often have a higher mean age (Beck, 1973) reflecting lower early mortality. Thus, a free-ranging existence, despite a dog's ownership status, may reduce survival markedly.

Furthermore, the demands of gestation and lactation require that a breeding female increase its energy intake from 1.5 to 3 times the average nonbreeding rate (Gessaman, 1973; National Research Council, 1974), which may be difficult under conditions of scarce resources. A high density of dogs also increases the probability of disease transmission. Frequently lethal illnesses such as distemper and canine hepatitis (Carbyn, 1982; Choquette and Kuyt, 1974; Mongeau, 1961; Trainer and Knowlton, 1968) generally are contagious to conspecifics. Rabies, an important canid disease in Cd. Juarez (Rodriguez Torres, 1982), also may have a severe impact on pup survival (Chapman, 1978; Rausch, 1958). The relative importance of each of these factors and the roles they play in shaping social organization vary from one site to another and merit further investigation.

The sex ratio of the feral population differed markedly from those of the urban and rural populations. Sex ratios of dog populations in urban areas tend to be skewed for males. Beck (1973) found a ratio of 1.8:1 in favor of males in Baltimore, Maryland, and Daniels (1983a) reported a ratio of 3:1 in favor of males in each of three Newark, New Jersey study sites. Because most urban dogs are owned, the sex ratio probably results from selection of males as pets (Beck, 1973). Also, females may be removed selectively from the population during breeding periods to avoid unwanted matings and pups. Although the sex ratio may reflect higher mortality of females than males, this is unlikely in the absence of preferential treatment of males. A similar case may be made for the rural population observed in this study. Although male-biased sex ratios have been reported in several nondomestic canid species (Crespo, 1975; Egoscue, 1975; Mech, 1975; Storm et al., 1976; Trapp and Hallberg, 1975), the same factors (e.g., declining population in a saturated habitat, hunting pressure) are not at work on these dog populations.

The female-skewed sex ratio of feral dogs does not result from a bias in the production of female pups at birth, based on litters observed in this study. Likewise, there is no evidence of differential survival between sexes within a litter. Thus, an important source of feral dogs may be the abandonment of females in the vicinity of established packs. Although the probability of survival is low for abandoned animals (Daniels, 1987a), the continued addition of abandoned females to the area as a potential source of pack members may be critical to maintaining feral populations.

ACKNOWLEDGMENTS

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