Intraspecific Variation in Canid Social Systems

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The family Canidae is composed of approximately 37 species that are categorized into 10–13 genera (Clutton-Brock et al. 1976; Macdonald 1984). Canids typically are lithe muscular runners possessing the ability to travel at speeds of up to 30 km/h for extended periods. They are diverse in body weight (1.5–31.1 kg), diet, and habitat (Gittleman 1984; Macdonald 1984). They usually breed once a year and initially raise their litters in ground dens. Compared with most mammals, they have a large litter size and a long period of infant dependency (Kleiman and Eisenberg 1973). The pervasive mating system among canids is obligatory monogamy, a trait that is rare in mammals (Kleiman 1977). Canids are also unusual in that family members share food and provide care for sick adults and dependent young. The larger canid species regurgitate food to family members, which allows greater efficiency in and opportunity for sharing food.

Interspecific Variation among Canidae

Among the canids there are general behavioral trends that correlate with body size (Macdonald and Moehlman 1983; Moehlman 1986). The smaller canids (<6.0 kg) like red foxes (Vulpes vulpes) and bat-eared foxes (Otocyon megalotis) are usually monogamous but are on occasion polygynous, and they tend to have a sex ratio biased toward females, female helpers, and male dispersal. Medium-sized canids (6.0–13.0 kg) like jackals (silverbacked jackal, Canis mesomelas, and golden jackal, C. aureus) and coyotes (C. latrans) appear to be strictly monogamous; their adult sex ratios are equal, and their male and female helping behavior and dispersal are equivalent. The largest canids (>13.0 kg) like the African hunting dog (Lycaon pictus) have a monogamous mating system with a tendency toward polyandry and an adult sex ratio skewed toward males, male helpers, and female emigration. Feeding ecology also shows a body size trend: smaller canids tend to be solitary hunters, and
medium-sized canids sometimes hunt cooperatively. Among most large canids cooperative hunting is an important if not critical method of obtaining food.

Allometric analyses indicate that there are strong correlations between mean female body weight and a number of important life history traits (Bekoff et al. 1981; Gittleman 1984, 1985; Moehlman 1986). In particular there are strong correlations when (1) natural log median birth weight is regressed against natural log mean female body weight \( r^2 = 0.97, \text{ slope } = 0.76 \pm 0.08 \) at \( t_{0.05} \), (2) natural log mean litter size is regressed against natural log mean female body weight \( r^2 = 0.72, \text{ slope } = 0.33 \pm 0.12 \), and (3) natural log litter weight is regressed against natural log mean female body weight \( r^2 = 0.89, \text{ slope } = 1.14 \pm 0.24 \) (Moehlman 1986). The correlations indicate that as canid females increase in body weight, they tend to have relatively smaller and potentially more altricial young. Unlike most mammals (Eisenberg 1981) and carnivores (Gittleman 1984), canids have a positive correlation between litter size and female body weight. Thus, larger females will not only be producing increasingly altricial young, but more of them. Concurrently, their prepartum investment will remain high and may even increase with the larger females. As maternal weight increases, the trend is toward more prepartum investment in gestation of larger litters composed of proportionally smaller neonates. Correspondingly, more postpartum investment may be needed to rear these larger litters to the age of independence.

This allometric and essentially physiological scenario is consistent with the general interspecific behavioral pattern observed in Canidae. Smaller females will produce fewer, more developed neonates that will potentially require less postpartum investment. Parental investment and sexual selection theory predicts that as males contribute less, there will be reduced competition by females for males, there will be a tendency toward polygyny, the adult sex ratio will skew toward females, and males will disperse (Trivers 1972). This suite of behaviors has been observed in small canids like kit foxes (Vulpes macrotis), arctic foxes (Alopex lagopus), bat-eared foxes, and red foxes (Storm and Ables 1966; Ables 1975; Storm et al. 1976; Brady 1978, 1979; Nel 1978; Egoscue 1979; Lamprecht 1979; Macdonald 1979b, 1980, 1981; Hersteinsson 1984; Nel et al. 1984; Moehlman 1986).

By contrast, large canid females produce larger litters of relatively less developed neonates. They appear to be making a larger prepartum investment that will potentially require substantial male investment in the rearing of these offspring. Females cannot afford to share this investment with other females (e.g., polygyny is unlikely), and competition for males could be intense. In the cases of both African hunting dogs and gray wolves (Canis lupus), males tend to provide more food than do females to pups (Malcolm 1980; Fentress and Ryon 1982), there is fierce competition between females for males, and there are limited observations of polyandrous matings (van Lawick 1973; Davidar 1975; Reich 1981; Harrington and Mech 1982; Harrington et al. 1982, 1983; M. Rabb, pers. comm.). African hunting dogs do exhibit a significant pup and