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# Reproductive Behavior of the Red Fox (*Vulpes vulpes*): A Longitudinal Study of an Island Population

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# REPRODUCTIVE BEHAVIOR OF THE RED FOX (*VULPES VULPES*): A LONGITUDINAL STUDY OF AN ISLAND POPULATION

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## ABSTRACT

Canids have been classified as "obligate monogamists" because the male's help may be essential for capturing and delivering prey to a lactating female and her young. For this reason, it has been suggested that a male's help may be "depreciable" or nonshareable. However, due to their secretive behavior, past information about canids has been gathered primarily from radio telemetry and trapping data, or captive animal studies. I was able to overcome the limitations of previous fox studies by working on an island study site that lacked visual obstructions; thus it was possible to directly observe an entire population of approximately 30 adult foxes which were diurnally active, individually marked with ear tags, and had no fear of human observers.

Fifteen reproductive groups of red foxes were observed on Round Island, Alaska from May through September, 1980-1984. Bigamy occurred among these foxes, correlated with abundant food resources. The predictions of the polygyny threshold model were supported, i.e., bigamous females had equal or better reproductive success than monogamous females. However, beginning in 1982, widespread nesting failure of seabirds occurred (the primary prey item of foxes), corresponding with the occurrence of El Niño in the Bering Sea. This change in food resources apparently caused a shift from facultative polygyny to monogamy within this population.

It has been suggested that fox groups may be composed of breeding females with their female offspring. My data indicates that female helpers were not offspring of the females they helped, and suggest that cooperative breeding in red foxes is not restricted to closely related individuals. Fox helpers inherited den sites and all group members benefited from cooperative breeding; therefore reciprocity or female cooperation may be involved.

There were no sexual differences in reproductive success for male and female red foxes, as predicted by sexual selection theory for a monogamous species. However, there was differential male mortality; breeding males had higher mortality rates than females and non-breeding males. Male biased mortality rates are usually related to polygyny and sexual dimorphism. Hypotheses are discussed that have been offered for this tendency in relation to red foxes.

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# CHAPTER I

# VARIATION IN GROUP SIZES AND MATING SYSTEMS AMONG CARNIVORES

## Literature Review:

Three classes of factors have been proposed to explain why social groups of carnivores evolved: 1) increased feeding efficiency in larger groups (Wyman 1967; Kruuk 1975), 2) decreased prey loss to competitors (Lamprecht 1978), and 3) greater protection of young from predators (Rood 1974; Rasa 1977). The size of canid social groups generally increase with difficulty of prey capture and relative prey size. The cooperatively hunting wolves (*Canis lupus* ), Cape hunting dogs (*Lycaon pictus*), and Indian dholes (*Cuon alpinus*) form the largest groups. There is a close relationship between the number of animals involved in a hunt and the prey species (Kruuk 1975). Up to 36 individuals sometimes occur in wolf packs (Rausch 1967), and they may hunt cooperatively to take down prey as large as moose (which weigh 500 kilograms) (Mech 1966). Cape hunting dogs live in packs of 2-40 individuals, and their prey consists primarily of gazelle and wildebeest (Kruuk 1972; Malcolm and Martin 1982). Foxes tend to be solitary or live in pairs, and they forage singly for small prey such as rodents, waterfowl (Sargeant 1972), insects, etc. Red foxes (*Vulpes vulpes*) sometimes occur in very small groups (2-5 individuals) (Macdonald 1979a), and examining the benefits of grouping in this species is particularly interesting since it must be independent of prey capture or defense of large prey items.

Studies of many carnivores have indicated that variation in social organization is related to characteristics of food resources. When food is clumped and economically defendable, coyotes (*C. latrans,* Bowen 1978, 1981; Bekoff and Wells 1982;

Camenzind 1978), golden jackals (*C. mesomelas,* Macdonald 1979b), Kalahari desert lions (M. J. Owens and D. D. Owens, pers. comm.), stripped hyenas (*Hyaena hyaena* , Macdonald 1978; Kruuk 1976) and brown hyenas (*Hyaena brunnea,* Owens and Owens 1978) increase group sizes. Coyotes tend to occur in smaller groups in the summer when preying on small rodents than in the winter when larger groups defend ungulate carcasses (Bekoff and Wells 1982). Golden jackals normally occur in pairs but they will feed in groups of 10-20 animals when they are fed at feeding sites (Macdonald 1979b). Brown hyenas become solitary foragers during the dry months when carcasses of prey species are dispersed and they form clans of about 13 hyenas during the rainy season when a large amount of carrion is available (Owens and Owens 1978, 1979). Kalahari desert lion prides disband and disperse when antelope are scarce; when prey densities increase, groups reform (Owens & Owens, pers. comm.). Badger (*Meles meles*) group size is correlated with the abundance of earthworms in badger territories (Kruuk and Parish 1982).

The mating systems of carnivores that live in groups are diverse. All canid species are thought to be monogamous; the male (and frequently other pack members) help hunt and deliver prey to one nursing female and her pups (Kleiman 1977). Regardless of the number of animals living in a group, usually only one canid female reproduces (Macdonald and Moehlman 1982; Zimen 1976; Rabb et al. 1967; Seal et al. 1979; van Lawick 1973; Macdonald 1979a; Malcolm & Martin 1982; Jonsingh 1982). In contrast, most other group living carnivores are not monogamous, but cooperatively raise the offspring of multiple females. Several adult female lions (*Panthera leo*) within a pride breed and rear cubs communally (Bertram 1975; Bygott et al. 1979; Packer & Pusey 1982), but provisioning by the male does not occur (Kleiman & Eisenberg 1973). In two species of the Hyaenidae, cubs of more than one female are reared in common dens. Spotted hyenas (*Crocuta crocuta*) live in clans of up to 80 individuals,

but adults do not deliver food to the cubs. Rather females nurse their offspring for up to one year after which time young hyenas accompany adults on hunts (Mills 1985; Frank 1986a, 1986b). Brown hyenas live in clans of up to 13 individuals, and both males and females provision cubs (Owens & Owens 1978, 1979, 1984). Among the Procyonidea, the coati (*Nasua nasua*) lives in female bands of two to five members with subadults of both sexes; males are solitary (Kaufman 1962). Breeding females occasionally share nests, and they nurse and groom all offspring indiscriminately (Russell 1979, 1983). Two species of the Viverridae that live in large groups have been studied extensively. Banded mongooses (*Mungos mongo*) live in packs ranging from six to 35 individuals of both sexes (Rood 1974) and several females produce litters. Dwarf mongoose (*Helogale parvula*) groups range in size from two to 27 animals (Rood 1980); but Rood concluded that only the litters of alpha females survive.

Similar to dwarf mongooses, the dominant female within canid groups does the majority of the breeding. During five years of a captive wolf study, only the dominant female bred (Zimen 1976; also Rabb et al. 1967). During seven years of an eight year study, only the dominant captive red fox female gave birth (Macdonald 1979a). During a ten year study, 20 of 26 litters were from the dominant Cape hunting dog female (Frame et al. 1979; Malcolm 1979). Only the dominant female bred in captive dingoes (*Canis dingo*) living in groups of 2-10 animals (Corbett, cited in Macdonald and Moehlman 1982). Dholes hunt in packs averaging 8.5 adults, and only the alpha pair breeds (Jonsingh 1982). In thirteen golden and silver-backed jackal (*C. aureus* and *C. mesomelas*) litters, offspring of both sexes were subordinate to parents and did not breed, but acted as helpers (Moehlman 1979, 1983).

Although the existing data clearly indicate that subordinate canids rarely breed, the mechanisms causing this phenomenon have not been identified. Evidence from captive wolf studies indicate that the majority of subordinate females are prevented from

reproducing by behavioral factors, not physiological suppression of gonadal cycles (Packard et al. 1985). Breeding attempts by subordinates can be prevented in four general ways.

1. Dominant females can prevent insemination by subordinates through intrasexual competition and aggression. Wolf pack members in captivity (especially the dominant female) obstruct attempted copulations between subordinate wolves (Zimen 1976; Rabb et al. 1967). Dominant male and dominant female Cape hunting dogs threatened and fought dogs of the same sex that tried to breed (Frame et al. 1979; Malcolm 1979). In captivity, subordinate dingo females were prevented from mating by the dominant female (Corbett, cited by Macdonald & Moehlman 1982).

2. Dominant females can interfere with pup care of subordinate animals. Dominant canids harass subordinate mothers causing them to neglect their pups. After a subordinate captive red fox female gave birth, the mother became "extremely nervous", frequently running around the enclosure carrying the pups. The dominant female in the enclosure visited the subordinate female's den occasionally, eliciting this behavior. All four pups died within eight days as a result of this treatment (Macdonald 1980). Subordinate wolf females which give birth often neglect their litters in favor of the dominant pairs litter (Altmann 1974). Of six Cape hunting dog litters that were from subordinate females, one survived; while five of nine litters from dominant females survived (Frame et al. 1979; Malcolm 1979). The males provided no food to the pups of one subordinate female. In another case, the dominant female prevented the males from feeding a subordinate female's litter. In captive dingoes, the dominant female will kill and eat the pups of the subordinate (Corbett, cited by Macdonald & Moehlman 1982). Similar infanticide was reported by a dominant female Cape hunting dog against the pups of a subordinate female (van Lawick 1973).

3. Males may not be attracted to subordinate females. Although subordinate captive female wolves all showed vaginal bleeding (indicating estrus), males usually showed no interest in them (Zimen, 1976).

4. There is some evidence that subordinates within groups may have delayed maturation or estrus may be suppressed. Ovulation is extremely rare in wolves up to two years old (Rausch 1967). Rausch examined 170 two year old wolves and found no scars from ovulation in the ovaries. However, the female wolf is capable of reproducing at ten months of age (Medjo & Mech 1976; Zimen 1976; Seal et al. 1979). Seal et al. (1979) observed a female wolf pup come into estrus after the alpha female died, while two subordinate sisters remained anestrus. Medjo & Mech (1976) suggested maturation may be delayed through social repression, poor nutrition, or some combination of both factors.

Red foxes may be an important comparison to other carnivores that have the capacity to forage as solitary scavengers or to form large groups under different ecological conditions. Foxes are solitary hunters and they are not known to forage or scavenge in groups. No previous study has been able to document how fox group sizes might vary with environmental conditions, or to determine what affect changes in group size might have on mating systems. However, due to their secretive behavior, direct observation of red foxes in the wild has never been conducted extensively. Past information about red foxes has been gathered from indirect methods, i.e., radio telemetry, trapping data and captive animal studies. I was able to overcome the limitations of previous fox studies by working on an island study site that lacked trees, brush, and other visual obstructions; thus, it was possible to directly observe an entire population of approximately 30 adult foxes which were diurnally active, individually marked with ear tags, and had no fear of human observers. This population of free

ranging foxes provided a unique opportunity to observe an undisturbed canid species in it's natural habitat.

## BIBLIOGRAPHY, CHAPTER I

Altmann, D. 1974. Beziehungen zwischen sozialer Rangordnung and Jungenautzucht bei *Canis lupus.* Zoologisher Garten N. F. Jena 44:235-236.

Bekoff, M. & Wells, M.C. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use and resource defense. *Z. Tierpsychol.* 60:281-305.

Bertram, B.C.R. 1975. Social factors influencing reproduction in wild lions. *J. Zool. Lond.* 177:463-482.

Bowen, W.D. 1978. Social organization of the coyote in relation to prey size. Ph.D. thesis, University of British Columbia, Vancouver.

Bowen, W.D. 1981. Variation in coyote social organization: the influence of prey size. *Can. J. Zool.* 59:639-652.

Brown, J.L. 1964. The evolution of diversity of avian territorial systems. *Wilson Bull.* 76:160-169.

Bygott, J.D., Bertram, B.C.R. and Hanby, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature* 282:839-841.

Camenzind, F.J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 in M. Bekoff, ed. Coyotes: Biology. Behavior, and Management. Acad. Press, New York.

Frame, L.H., Malcolm, J.R. Frame, G.W., and van Lawick, H. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti plains, Tanzania 1967-1978. *Z. Tierpsychol.* 50:225-249.

Frank, L.G. 1986a. Social organisation of the spotted hyaena. I. Demography. *Anim. Beh.* 35:1500-1509.

Frank, L.G. 1986b. Social organisation of the spotted hyaena. II. Dominance and reproduction. *Anim. Beh.* 35:1510-1527.

Jonsingh, A.J.T. 1982. Reproductive and social behavior of the Dhole (*Cuon alpinus*). *J. Zool.* 198:443-463.

Kaufman, J.H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorado Island Panama. *Univ. Calif. Publ. Zool.* 60:95-222.

Kleiman, D. G. 1977. Monogamy in mammals. *Q. Rev. Biol.* 52:39-68.

Kleiman, D. G. and Eisenberg, J. F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Beh.* 21:637-659.

Kruuk, H. 1972. The Spotted Hyena. Univ. of Chicago Press, Chicago.

Kruuk, H. 1975. Functional aspects of social hunting in Carnivores. Pages 119-141 in G: Baerends, C. Beer & A. Manning, eds. Function and Evolution in Behavior. Clarendon Press, Oxford.

Kruuk, H. 1976. Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). *E. Aft. Wildl. J.* 14:91-111.

Kruuk, H. and Parish, T. 1982. Factors affecting population density, group size, and territory size of the European badger, *Meles meles. J. Zool. Lond* 196:31-39.

Lamprecht, J. 1978. The relationship between food competition and foraging group size in some larger carnivores. A hypothesis. *Z. Tierpsychol.* 46:337-343.

Macdonald, D.W. 1978. Observations on the behaviour and ecology of the striped hyaena, *Hyaena hyaena,* in Israel. *Isr. J. Zool*. 27:189-198.

Macdonald, D.W. 1979a. "Helpers" in fox society. *Nature* 282:69-71.

Macdonald, D.W. 1979b. The flexible social system of the golden jackal, *Canis aureus. Behav. Ecol. Sociobiol.* 5:17-38.

Macdonald, D.W. 1980. Social factors affecting reproduction by the red fox, *Vulpes vulpes*. Pages 123-175 in E. Zimen, ed. The Red Fox, Symposium on Behavior and Ecology. Biogeographica 18, W. Junk, The Hague, The Netherlands.

Macdonald, D.W. & P.D. Moehlman. 1982. Cooperation, altruism, and restraint in the reproduction of carnivores. Pages 433-467 in P.P.G. Bateson & P.H. Klopfer, eds. Perspectives in Ethology . Plenum, New York & London.

Malcolm, J.R. 1979. Social organisation and communal rearing in the African wild dog. Ph.D. thesis, Harvard University.

Malcolm, J.R. & Martin, K. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav. Ecol. Sociobiol.* 10:1-13.

Mech, D.L. 1966. The wolves of Isle Royale. U.S. Natl. Park Serv. *Fauna* 7, 210 pp.

Medjo, D., and Mech, D.L. 1976. Reproductive activity in nine and ten month wolves. *J. Mamm.* 57:406-408.

Mills, M.G.L. 1985. Related spotted hyaenas forage together but do not cooperate in rearing young. *Nature* 316:61-62.

Moehlman, P.D. 1979. Jackal helpers and pup survival. *Nature* 277:382-383.

Moehlman, P.D. 1983. Socioecology of silverbacked and golden jackals (*Canis mesomelas* and *Canis aureus*). Pages 423-453 in J.G. Eisenberg & D.G. Kleiman, eds. Advances in the Study of Mammalian Behavior. American Society of Mammalogists.

Owens, M.J. & Owens, D.D. 1978. Feeding ecology and it's influence on social organization in Brown hyaenas (*Hyaena brunnea*) of the central Kalahari desert. *E. Afr. Wildl. J.* 16:113-135.

Owens, D.D. & Owens, M.J. 1979. Notes on social organization and behavior in Brown hyenas (*Hyaena brunnea*). *J. Mamm.* 60:405-408.

Owens, D.D. & Owens, M.J. 1984. Helping behaviour in brown hyenas. *Nature* 308:843-845.

Packard, J.M., Seal, U.S., Mech, D.L., Plotka, E.D. 1985. Causes of reproductive failure in two family groups of wolves (*Canis lupus*). *Z. Tierpsychoi.* 68:24-40.

Packer, C. and Pusey, A. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 296:740-742.

Rabb, G.B. Woolpy, J.H. & Ginsburg, B.E. 1967. Social relationships in a group of captive wolves. *Am. Zool.* 7:305-311.

Rasa, O. A. E. 1977. The ethology and sociology of the dwarf mongoose (*Helogale undulata rufula*). *Z. Tierpsychol*. 43:337-406.

Rausch, R.A. 1967. Some aspects of the population ecology of wolves, Alaska. *Am. Zool.* 7:253-265.

Rood, J.R. 1974. Banded mongoose males guard young. *Nature* 248:176.

Rood, J.R. 1980. Mating relationships and breeding suppression in dwarf mongoose. *Anim. Beh.* 28:143-150.

Russell, J.H. 1979. Reciprocity in the social behaviour of coatis, *Nasua narica.* Ph.D. thesis, University of North Carolina, Chapel Hill.

Russell, J.H. 1983. Altruism in coati bands; nepotism or reciprocity? Pages 263-290 in S. K. Wasser, ed. Social Behavior of Female Vertebrates. Acad, Press, New York.

Sargeant, A.B. 1972. Red fox spatial characteristics in relation to waterfowl predation. *J. Wildl. Mgt.* 36:225-236.

Seal, U.S. Plotka, E.D. Packard, J.M. & Mech, L.D. 1979. Endocrine correlates of reproduction in the wolf. 1. Serum progesterone, estradiol and LH during the estrous cycle. *Biol. Reprod.* 21:1057-1066.

van Lawick, H. 1973. Solo. Collins, London.

Wyman, J. 1967. The jackals of the Serengeti. *Animals* 10:79-83.

Zimen, E. 1976. On the regulation of pack size in wolves. *Z. Tierpsychol*. 40:300-341.

# CHAPTER II

## STUDY AREA

This study was conducted at Round Island, Alaska (56°02'N 160°50'W), which is located about 33 km. from the mainland in northern Bristol Bay (Fig. II. la). This 3 $km^2$ igneous island rises abruptly to 460 m. The cabin (that I lived in) is located on a .5 hectare flat, grassy (primarily *Calamagrostis canadensis*) plateau that is about 31 m above sea level. From the cabin site, approximately one third of the island is visible as a steep (eastern) slope that is composed of short tundra vegetation. The summit of the island is approximately a .5 hectare flat plateau that is entirely tundra (primarily *Empetrum nigrum, Spagnum* moss*, Vaccinium vitis idaea, Anemone narcissiflora, Rubus chamaemorus, Chrysanthenum articum, Salix alaxensis, S. reticulata*). From the summit, the eastern, western, and northern slopes of the island are visible. The west and northwest sides of the island are vertical rock cliffs that rise to 305 m elevation.

The rock cliffs provide nesting sites for several species of seabirds. Approximately 142,000 seabirds, including black legged kittiwakes (*Rissa tridactyla*), common murres (*Uria aalge*), pelagic cormorants (*Phalacrocorax pelagicus*), parakeet auklets (*Cyclorrhynchus psittacula*), horned puffins (*Fratercula corniculata*) and tufted puffins (*Lunda cirrhata*) nest during spring and summer on these rock cliffs (P. Arneson, pers. comm.). Many songbirds nest on the tundra slopes: primarily white-crowned sparrows (*Zonotrichia leucophrys*), golden-crowned sparrows (*Zonotrichia atricapilla*), tree sparrows (*Spizella arborea*), fox sparrows (*Passerella iliaca*) and lapland longspurs (*Calcarius lapponicus*). These birds are the main prey for foxes during spring and summer.

Two species of pinnipeds utilize the rocky beaches of the island as resting sites. Approximately 12,000 Pacific walruses (*Obodenus rosmarus*) and 500 Steller sea lions (*Eumetopia jubatus*) could be seen on the beaches during peak haul-outs. Many walruses die on Round Island or are washed ashore each summer and at least several carcasses were usually laying on the beaches where the foxes could scavenge them.

## Methods

The foxes on this island have never been trapped or hunted, and they have little fear of humans. Thus, I was able to monitor an entire population of approximately 30 adult foxes which were diurnally active, and which exhibited curiosity or boldness toward human observers. Direct observation of fox behavior was conducted by visually locating individuals on the tundra slopes and following them on foot.

### Capture and Identification.

Individually recognizable collars were put on foxes the first year of the study. This was done by threading the female portion of a Roto tag through a 1/4" wide nylon cable tie. The cable ties were then placed along the fox trails like snares. A large hole punched in the tip of the tie broke when the fox pulled on the collar. A stop was made (to prevent complete closure of the collar) by sewing dental floss through the tie and covering it with epoxy. Fifteen collars were put on foxes using this method. One adult fox was caught in a two meter by two meter enclosure made of chicken wire and was ear tagged with Roto tags. These techniques were not used after the first year because it was not possible to mark more than a portion of the individuals in the population with collars or enclosures.

After the first year of study, individual foxes were marked with color coded ear tags. Twenty seven adults were immobilized (Appendix I) by firing darts from a Palmer Cap Chur pistol. I modified the darts by filing the barbs on the needles down to

a small "nub". This modification allowed the needle to remain in the animal long enough to eject an ample amount of drug, but prevented it from dangling from the animal's leg and thus causing panic. Drug dosages were 1.5 cc Ketamine: Aceprornzine in a ratio of 7:3. This drug dosage was 50 per cent higher than that recommended for an animal the weight of a red fox (A. Franzman, pens. comm.). I found this to be the ideal dosage because some of the drug always back leaked when the filed barb caused the needle to fall off the animal prematurely. Ketamine immobilized a fox in 5-10 minutes and lasted 30-60 minutes, after which time a fox was again walking.

Before darting a fox, I spent variable amounts of time (generally one to four hours) habituating the animal to my close presence (7.5-15 m). I did not attempt a shot at more than 15 m. I aimed for the upper hindleg, and used only very short range charges. When struck by the dart, a fox ran away from the direction of impact, but none of the animals ever seemed to associate the shot with my presence. They usually ran 25-100 m. before stopping and resuming normal activity.

I sexed and weighed immobilized foxes and put a Roto-tag in each ear. The ear pinnae were punctured with a leather punch before the tag was put on.

Fifty pups were snared at their dens. Snares were hung from a line that was about 7.5 m. directly above each den. The lines were made from 1/16" cable and were elevated above the ground by tying the ends onto rock outcroppings (if available) or onto antennae poles that were staked out away from the den. Snares (also made of cable) were hung along these lines at about one-half meter intervals. The snares were lowered to the ground by slackening one end of the line when untagged pups came out of den holes. As pups ran through the den playing, their legs or feet would get caught in the snares. Tension on the line would prevent them from getting out of the snares until I was able to run into the den and capture them. When adults approached the den I lifted the snares out of the den by tightening the line.

Upon capture, pups were put into a nylon sac. They were sexed, weighed, and ear tags were put on. Ear tags (Nalco sheep tags) were cut in half lengthwise so they did not extend beyond the tip of pup's ears. Pups were released within five minutes of capture.

Tag loss appeared to be very low. Of 27 ear tagged adult foxes, I later observed only one fox with a single tag. (I was able to identify him by his second tag.) No pup lost a tag before four months of age (prior to dispersal); one pup lost a tag over the winter but she was identifiable by her second tag. Individuals may have varied in tag retention so that tag loss probability was highly correlated within individuals. However, I resighted all marked foxes at least once each season after they were ear tagged. Both foxes that were known to have lost one tag had punctured ear pinnae; in both cases, the ears were obviously torn where the tag had pulled out. In addition, I always carefully examined the ears of each fox that was immobilized and I never saw evidence of an old puncture wound

No fox (adult or pup) was ever handled more than once. Neither darting nor snaring seemed to alter their behavior or cause them to loose their boldness toward humans.

Observations.

I observed a total of 15 fox groups that were rearing pups during five field seasons from 1980-1984 (Appendix II). Pups were reared in six different den sites during the study (Fig. II.1b.), although the maximum number of active dens in any given year was five. Each field season, I determined which dens were actively being used and which ones were not by searching for signs of digging, bird parts, etc. Adult members of reproductive groups were identified by waiting at den sites or searching den vicinities. If adults visited the same den site regularly and assisted in rearing pups (i.e., delivered food items), I classified them as a belonging to a reproductive group.

After the active dens were identified, I observed the behavior of foxes associated with the dens for a total of 858 hours during the study. Observations were made during late afternoon and evening hours (1400-2000 h., except during storms) from distances of 10 to 30 m. Individuals varied in the distance I could approach without altering their behavior and I always adjusted my distances to the individuals I was watching.

A major concern was to distinguish between female helpers and reproductive females. Reproductive females were identified when I saw them nurse pups. Females that did not nurse were assumed to be helpers. In addition, no nipples were visible on helpers when I inspected them with binoculars at distances of 7.5-15 m., but nipples were visible at comparable distances on nursing females.

Quantitative estimates were obtained of the amount of parental care provided by all members of family groups. The number and species of seabirds delivered to pups, and the number of visits to the den by each member of a reproductive group were recorded. For comparison among dens, rates were calculated from the total number of seabirds and visits by each fox per one hour time period.

Non-breeding foxes were found by scanning the steep tundra slopes with binoculars (7X) or with spotting scopes (8-35X variable, zoom). The frequency of searching for foxes was dependent on weather conditions. Dense fog commonly formed as air masses rose from the ocean and passed over the top of the island. On days when visibility permitted, the eastern slope was scanned from the cabin site several times a day, and the remainder of the island was scanned from the summit at least once per day. During the five seasons, searches were made on a total of 396 days; viewing conditions were unsuitable on 80 days. The location of each fox sighting was converted to x-y coordinates using a 135 m. grid overlay on an aerial photograph of the island.

During the month of May, the majority of my effort was spent searching the slopes for tagged foxes, before vegetative growth began on the island and while visibility was unobstructed. Annual survival rates were determined from these individual fox resightings. If an individual was not seen during an entire field season, it was assumed that the animal did not survive the winter. The survival data should have low error because I never failed to see a fox one year and then resighted it the following season. Survival rates were calculated for four classes of individuals: "non-breeding den holders", "floaters", "breeders" and "pups". Non-breeding den holders were male/female pairs that regularly slept at den sites and chased intruders away, but with which pups were never seen. It is unknown whether these foxes did not mate, or whether the female's reproductive effort failed at some stage of development. "Floaters" were foxes that had no association with a den site or reproductive group (they never visited den sites or fed pups). These animals were usually resighted in the same general vicinity repeatedly; they seemed to occupy small areas that overlapped larger areas through which the breeders regularly traveled.

Statistical tests will be discussed as they appear in the text. Only non-parametric tests are used due to small sample sizes.

A major problem with the study is that observations were made during spring and summer only. Unfortunately, I was unable to observe behavior of the foxes during the winter season when they were mating, and when food resources were the least abundant.

Fig. II.1a. Location of Round Island, Alaska.

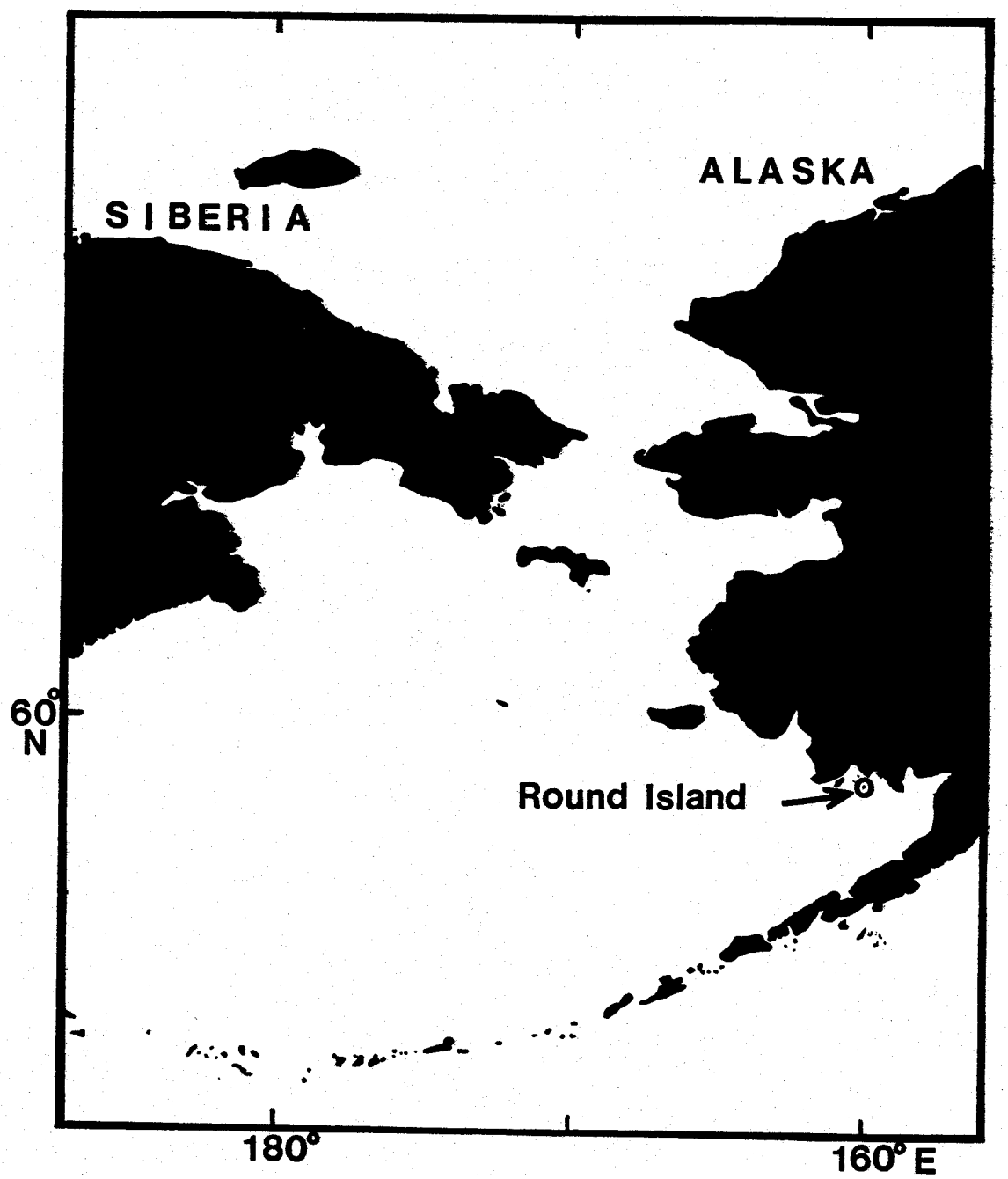
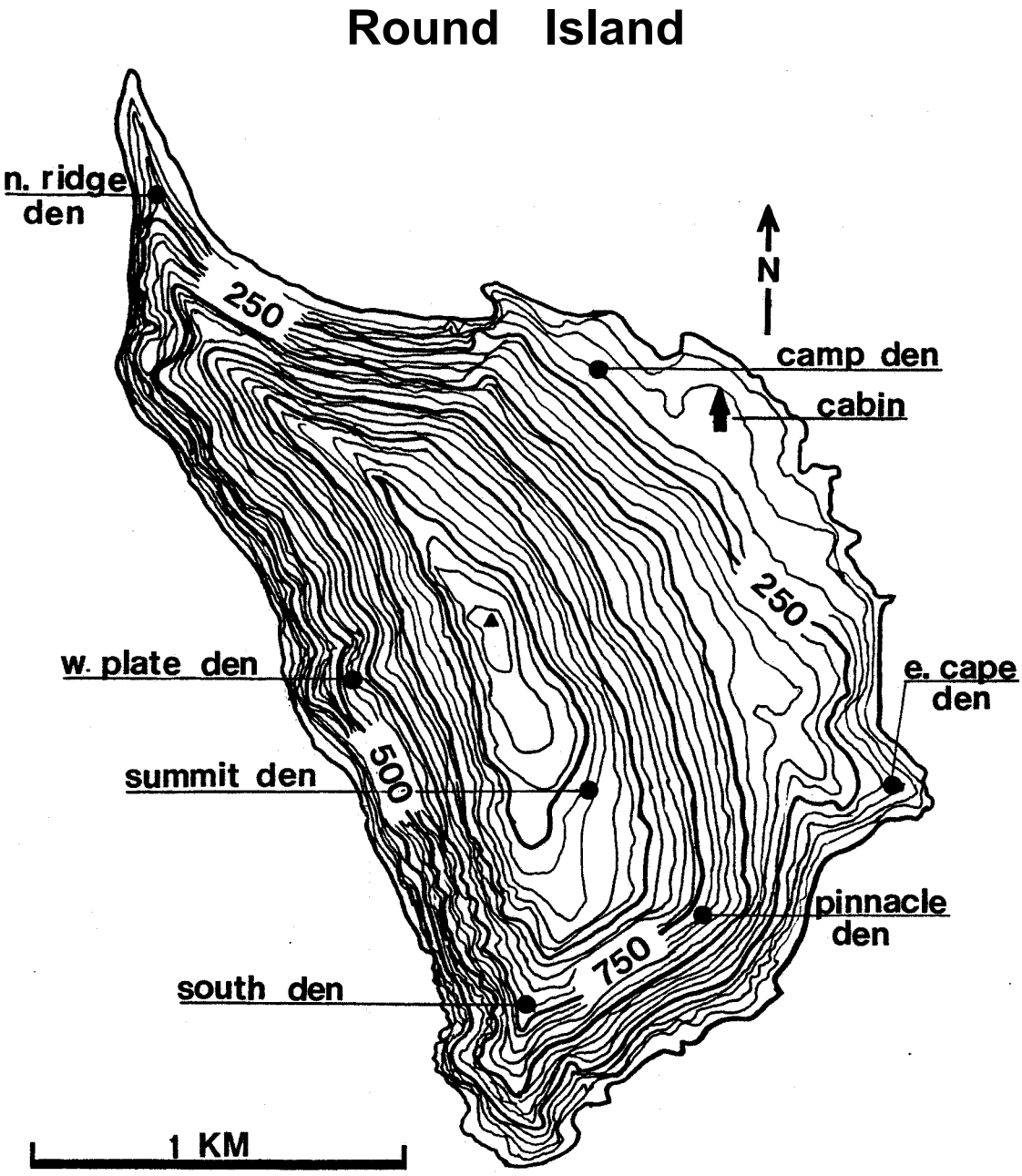


Fig. II.lb. Map of study site indicating location of fox dens.



# CHAPTER III
# DEVIATIONS FROM MONOGAMY IN THE RED FOX: A NEW PERSPECTIVE ON CANID MATING SYSTEMS

## I. Deviations From Monogamy in Canids.

Explanations for the evolution of monogamy in vertebrates are diverse. Monogamy has been defined in terms of association between a male-female pair (a sociographic unit) (Hinde 1976), exclusive mating, or solely in terms of biparental care (Wilson 1975). However, evidence suggests that male help is not essential for females to rear at least some offspring (Wittenberger & Tilson 1980). In addition, biparental care is only one type of cooperation that may be involved in monogamy; cooperative defense of a territory, or cooperative hunting may also be involved (Barlow 1984). It has been suggested that biparental care may be a consequence of monogamy, not a phylogenetic prerequisite (Wickler and Seibt 1983; Barlow 1984). Among many animals, male-female pairs remain together for many years but have no parental care (Wittenberger & Tilson 1980; Wickler and Seibt 1983); and even if males help care for offspring, the parents may each care for some of the young without staying together (Wickler and Seibt 1983). A more encompassing view of factors that promote monogamy (Wittenberger & Tilson 1980) includes: 1) A female cannot rear offspring without nonshareable male parental care (Kleiman & Malcolm 1981) because she needs help feeding or protecting the young. 2) Pairing with an unmated male is always better than pairing with a mated male. This is derived from the polygyny-threshold model (Verner 1964; Orians 1969). 3) Aggression by mated females prevents males from breeding with additional females even though the polygyny threshold is reached

(Wittenberger & Tilson 1980). 4) The quality and dispersion of food resources causes spacing of females, preventing polygyny (Kleiman 1977; Ralls 1977).

Monogamy is rare among mammals (Kleiman 1977); since the female mammal has internal gestation and is physiologically capable of providing for her offspring, the male is usually needed only for insemination. Kleiman (1977) suggested monogamy may take two forms, obligate and facultative. Facultative monogamy results when individuals occur at such low densities that only a single individual is available for mating. Obligate monogamy occurs when a female cannot rear offspring without help from the male (and other conspecifics). Canids were classified as "obligate monogamists" (Kleiman 1977) because the male (and frequently other pack members) help hunt prey and deliver meat to the nursing female and her young. Kleiman and Malcolm (1981) suggested that a canid male's help may be "depreciable" because the time and energy expended in feeding one female's offspring will decrease the effort that can be expended on a second female's offspring. Presumably, increased parental investment by males and other pack members results in increased pup survival. During the reproductive season, canids are unable to travel as far from the den as they do during other times of the year. It has been suggested that pack hunting canids would be restricted to a limited part of their hunting range for a longer period of time if they were raising two litters instead of one (Kleiman & Eisenberg 1973) unless the litters were perfectly synchronized in date of birth.

Among the pack living canids, non-breeding group members often postpone their own reproduction and assist monogamous pairs in raising offspring (Macdonald and Moehlman 1982; Zimen 1976; Rabb et al. 1967; Seal et al. 1979; van Lawick 1973; Macdonald 1979a; Malcolm & Martin 1982; Jonsingh 1982). Kin selection (Hamilton 1964) and reciprocity (Trivers 1971) have usually been invoked as the ultimate

(evolutionary) explanations for the occurrence of non-breeding group members (helpers) among canids.

I observed reproductive groups of red foxes on Round Island, Alaska from May through September, 1980-1984. The setting at Round Island (and perhaps other islands) may be rather atypical for foxes because food resources are very abundant during the summer months, and foxes living on islands are linked to production in the marine environment. However, this island study site provided a unique opportunity to monitor an entire population of approximately 30 adult foxes which were diurnally active, individually marked with ear tags, and had no fear of human observers. Thus, it was possible to observe directly individuals through multiple pup-rearing seasons and to estimate the amount of parental care provided by all members of family groups.

During the five season study a total of 16 family groups were located; 15 of these were observed closely. Fourteen of the 15 groups had one male which delivered seabirds to the females and pups; one female raised a litter unassisted (hereafter termed the "single female"). Five groups had two nursing females (henceforth referred to as "bigamous" groups). Three dens were determined to be bigamous by observing two females at each den nursing pups. Two other bigamous groups were located by following the male foxes; these two males each delivered seabirds to two females located in dens approximately .2 km apart, each nursing a litter of pups. In both cases, the litter from the smaller den was subsequently moved to a larger communal den. I did not observe the adults move the litters, but the number of pups at each communal den totalled what had been observed at the two separate dens. The remaining nine groups had a single nursing female paired with a male ("monogamous" groups).

Four of 14 groups had one or two non-lactating female "helpers" that assisted in rearing the pups. Two of the four bigamous groups had one and two helpers respectively, and two of the nine monogamous groups had a female helper. Males,

reproductive females, and helpers all brought food to and played with the pups, and scent marked the vicinity of their den sites.

Consistent with these results, deviations from monogamy have been observed in other canid studies. Thus, monogamy in canids does not appear to be a phylogenetic constraint, and obligate monogamy is probably an inappropriate term. There are reports of more than one pregnant female or multiple litters in some wolf packs. On Isle Royale a pack of 11-22 wolves included three breeding females (Jordan et al. 1967). Two female wolves gave birth in a Mt. McKinley National Park pack in 1972 (Haber 1977). Coyote groups have been observed in which two or more pairs of adults were thought to have given birth (Camenzind 1978; Gier 1975). The majority of fox species are thought to be monogamous; but there is additional evidence that red foxes sometimes form groups of several females and one male (Macdonald 1980; von Schantz 1981). Results of a radio telemetry study in England by Macdonald (1980) suggested that the mean adult family group size was 3.3. The occurrence of communal red fox dens (or polygynous associations) has been inferred on the basis of unusually large litter sizes, pups of varying sizes and weights, and the occurrence of multiple females in the vicinity of the same den (determined from radio telemetry fixes). The proportion of red fox groups that may have been polygynous has ranged between 2 and 20%: 11%, n=55 dens (Pils & Martin 1978); 2%, n=509 dens (Storm et al. 1976); 20%, n=5 dens (Macdonald 1980); 20%, n=10 dens (von Schantz 1981).

The conditions under which deviations from monogamy occur in canids are largely unknown. It has been suggested that factors leading to multiple litters in wolf packs may be temporary pack splitting that enables subordinates to "escape the sexual repression" of dominant wolves (Haber 1977), or the loss of an alpha female (Harrington et al. 1982).

II. Shift in Red Fox Mating Associated with El Niño in the Bering Sea

The polygyny threshold model was first developed to explain the evolution of avian mating systems (Verner 1964; Willson 1966; Orians 1969). This model predicts that the polygyny threshold is reached when a female pairing with an already mated male experiences reproductive success that is equal to or greater than a female pairing with an unmated male. The cost of sharing a male with a second female may be exceeded by benefits such as occupying a superior territory, mating with a superior male, or cooperatively rearing offspring with another female (Emlen & Oring 1977; Wittenberger & Tilson 1980). Shifts from monogamy to facultative polygyny among avian species have been documented under ecological conditions predicted by the polygyny threshold model (Martin 1971; Holm 1973; Wittenberger 1976; Carey & Nolan 1975; Pleszczynska 1978).

The occurrence of El Niño (Cane 1983; Rasmusson & Wallace 1983; Wyrtki 1979) in the Bering Sea (Niebauer 1985) during 1982-1984 and the corresponding nesting failure of seabirds (Johnson & Baker 1985; Craighead & Oppenheim 1982; Merculief, cited in Craighead & Oppenheim; Nysewander & Trapp 1984) provided a unique opportunity to document the effect of changing food resources on red fox (*Vulpes vulpes*) reproductive groups and to test some of the predictions of the polygyny threshold model for a canid species. I present data here suggesting that the nesting failure of seabirds, which comprise most of the summer diet of foxes on islands in the Bering Sea, resulted in a shift from facultative polygyny to monogamy in the red fox.

The red foxes at Round Island utilized nesting seabirds as their primary food source during summer months when they were rearing young. In 1977 approximately 142,000 seabirds successfully nested on the rock cliffs at Round Island (P. Arneson, unpubl. data). The abundance of each species was approximately: 93000 common

murres (*Uria aalge*), 43000 black legged kittiwakes (*Rissa tridactyla*), 2000 pelagic cormorants (*Phalacrocorax pelagicus*), 1750 horned puffins (*Fratercula corniculata*), 1500 parakeet auklets (*Cyclorrhynchus psittacula*), 1500 parakeet auklets, 400 tufted puffins (*Lunda cirrhata*), and 400 pigeon guillemots (*Cepphus columba*). This condition remained roughly unchanged through 1981 (pers. obs.).

In 1982, large scale oceanographic changes occurred in the Bering Sea associated with the El Niño-Southern Oscillation (ENSO). The periodic appearance of abnormally warm surface water off the coasts of Chile, Equador and Peru (ENSO) has been correlated to climatic effects in the arctic (Niebauer 1985). Niebauer (1985) found that El Niño was correlated to rising sea and air temperatures in the Bering Sea by correlating 30 years time series analysis of atmospheric and oceanic parameters of the eastern Bering Sea to an index of ENSO activity in the south Pacific. The Aleution Low apparently deepens and moves south and east, resulting in southerly flow from the North Pacific northward over the Bering Sea following an ENSO event (Niebauer 1985).

Associated with these oceanographic changes, kittiwakes and murres did not nest at Round Island during 1982-1984 and neither eggs nor chicks were evident, although large numbers of adults were present. This failure in bird production was documented 100 KM NNW of Round Island at Cape Peirce, Alaska (58$^{o}$ 35' N 161$^{o}$ 45' W) in 1984 (Johnson & Baker 1985) and on the Pribilof Islands (southern Bering Sea, Alaska) during 1982-1984 (Johnson & Baker 1985; Craighead & Oppenheim 1982; Merculief, cited in Craighead & Oppenheim 1982). Widespread mortality of black legged kittiwakes, short-tailed shearwaters (*Puffinus tenuirostris*) and other colonial nesting seabirds occurred in many areas of Alaska in 1983-1984, correlated with warmer than normal surface water temperature in the Bering Sea (Nysewander &

Trapp 1984). Nesting failure of black legged kittiwakes appears to have been caused by starvation of adult birds which abandoned nests (Nysewander & Trapp 1984).

Red foxes switched the seabird species they delivered to pups when black legged kittiwakes and common murres failed to nest at Round Island (Fig. III.1). During 1980-1981, reproductive foxes delivered primarily black legged kittiwakes and common murres to their pups. Following the kittiwake and murre failure in 1982, parakeet auklets became the most frequently delivered food item to pups, followed by horned and tufted puffins. Prior to El Niño, auklets and puffins had comprised only 2.6% of the total seabird population on Round Island, while kittiwakes and murres comprised 95%. Thus foxes switched their hunting efforts from the most abundant species to rare species.

During 1980-1981 (prior to El Niño), the majority of fox reproductive groups were bigamous. Five of seven pup rearing groups had two lactating females and one male, and three of the seven groups (two bigamous, one monogamous) had a non-lactating female helper. The modal reproductive group size during 1980-1981 was three (range=2-5) adult foxes. Following the onset of ENSO conditions in 1982, all pup rearing groups became monogamous (Fig. III.2). From 1982-1984, eight fox groups all consisted of one lactating female and a male, and only one group had a female helper. The modal group size for this three year period was two adults (range=1-3). Reproductive group sizes were significantly different between these two periods (Mann Whitney U test, $p<.01$). The reproductive failure of Alaskan seabirds following the Bering Sea El Niño apparently caused red foxes to switch prey species, and to breed monogamously.

Prior to the occurrence of El Niño, bigamous females successfully reared as many or more pups as monogamous females, as predicted by the polygyny threshold model. (Bigamous and monogamous females cannot be compared after El Niño

because all females were monogamous.) I calculated reproductive success as the number of pups that survived to one year of age, for groups that raised pups during 1980-1981. Eight bigamous females had a mean of 2.2 pups/female survive to one year of age and two monogamous females had a mean of 1.5 pups survive (n.s., Mann Whitney U test). Thus, bigamous females had 1.4 times the reproductive success of monogamous females. Litter sizes of bigamous females were also somewhat larger ($x=4.3$), although not significantly different from monogamous females ($x=4.0$, Mann Whitney U test). Bigamous females thus had equal or better reproductive success than monogamous females despite sharing a male's help. Males with two mates were more than twice as successful as males with one mate. Bigamous males had a mean litter size of 8.6, and a mean of 4.5 pups surviving to one year of age; monogamous males had a mean litter size of 4 ($p<.05$, Mann Whitney U test) and a mean of 1.5 pups survive ($.1<p<05$, Mann Whitney U test).

The optimal mating system for promoting the reproductive interests of males and females often differ (Orians 1969; Trivers 1972). However, in this study both sexes benefited by mating bigamously. It is unclear whether the behavior of male or female foxes determined the mating system. However, regardless of whether male-male competition, female choice, or female-female competition was the driving force, the reproductive success of both sexes was increased by bigamy.

In addition to the shift from bigamy to monogamy, fox productivity declined when seabird productivity declined. The proportion of non-breeding female foxes increased, and the number of litters (and pups) which were reared decreased (Fig. III.3). Minimally, seven litters per year were reared in 1980-1981; only one, three, and four litters were reared during the respective years of 1982-1984. Mean fox litter size was also significantly different: $4.25\pm.94$ in 1980-1981 and $3.5\pm2$ in 1982-1984 ($p<.01$, Mann Whitney U test). Non-breeding females increased from 53% of the

female population in 1980-1981 (n=36) to 84% in 1982-1984 (n=49)(Chi Sq test, $X^2$=9.5, p<.005).

A shift in the breeding status of six individual females which were members of pup rearing groups both before and after the food shift provides evidence that the reproductive changes were not due to variation among individuals or demographic shifts in the fox population at Round Island through time. Between 1981 and 1982, one bigamous female became monogamous; two other bigamous females did not successfully give birth; one monogamous female became a helper; and two helpers remained at their den sites as the only female but did not raise pups (the original breeding females moved to new dens) .

A reduction in food availability has been correlated with smaller group sizes and a decline in productivity (i.e., smaller litter sizes and/or fewer breeding females) in other canid populations (von Schantz 1984; Bekoff & Wells 1982; Bowen 1980; Camenzind 1978; Harrington et al. 1983). However, no previous canid study has documented the frequency of occurrence of deviations from monogamy, or correlated such deviations with environmental parameters. This study established that bigamy in red foxes was correlated with food abundance. The predictions of the polygyny threshold model were supported, i.e., bigamous females had equal or better reproductive success than monogamous females. However, major climatic and oceanographic shift, which resulted in seabird reproductive failure, apparently caused a shift from facultative polygyny to monogamy in the red fox.

Fig. III.1. Seabird species that adults delivered to pups prior to and after the onset of ENSO conditions; Chi Sq=14.7, p<.05.

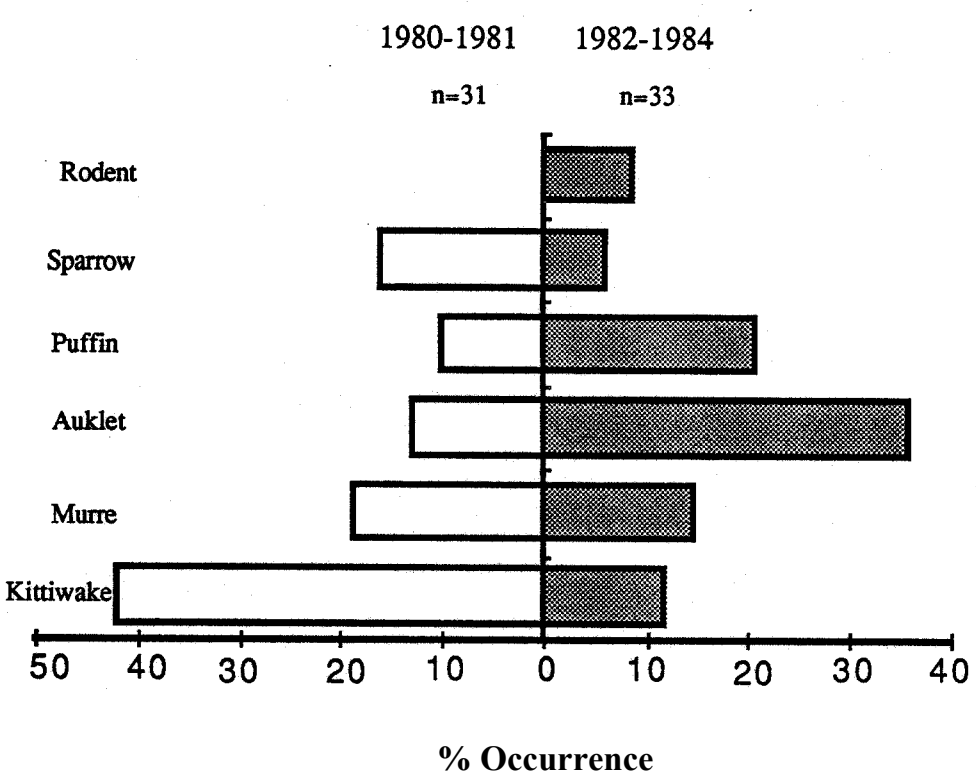


Fig. III.2. annual reproductive status of adult females prior to and after the onset of ENSO conditions; Chi Sq=18.3, p<.005.

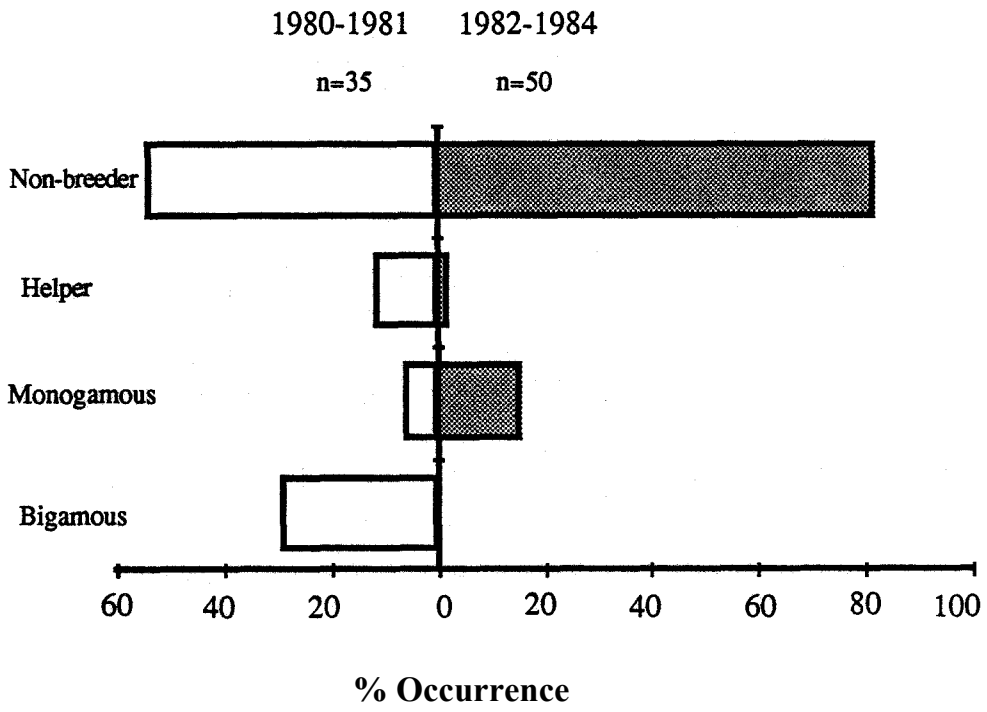
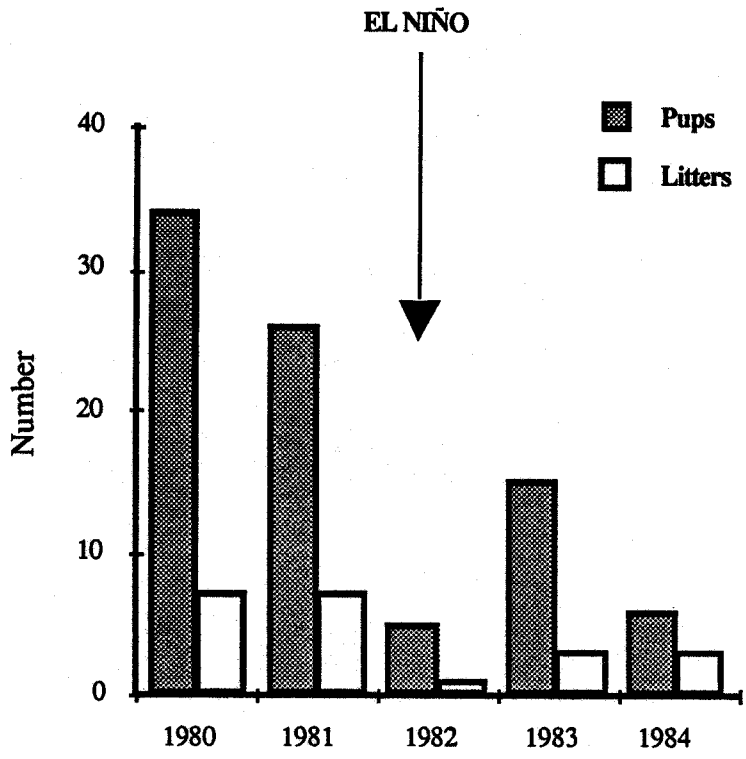


Fig. III.3. Total number of fox litters and pups on Round Island each year.



## CHAPTER III, BIBLIOGRAPHY

Altmann, S. A., Wagner, S. S. & Lenington, S. 1977. Two models for the evolution of polygyny. *Behav. Ecol. Sociobiol.* 2:397-410.

Barlow, G.W. 1984. Patterns of monogamy among teleost fishes. *Arch. Fisch Wiss.* 35:75-123.

Bekoff, M. & Wells, M. C. 1982. Behavioral budgeting by wild coyotes: the influence of food resources and social organization. *Z. Tierpsychol.,* 60:281-305.

Bowen, W. D. 1980. Variation in coyote social organization: the influence of prey size. *Can. J. Zool.* 59:639-652.

Cane, M. A. 1983. Oceanographic events during El Niño. *Science* 222:1189-1195.

Camenzind, F. J. 1978. Behavioral ecology of coyotes on National Elk Refuge, Jackson, Wyo. Pages 267-294 in M. Bekoff, ed. Coyotes: Biology. Behavior. and Management. Acad. Press, New York.

Carey, M. & Nolan, V. Jr. 1975. Polygamy in Indigo buntings: a hypothesis tested. *Science* 190:1296-1297.

Craighead, L. & Oppenheim, J. 1982. Population estimates and temporal trends of Pribilof Island seabirds. Unpubl. ms., Arctic Biol. Res., Ak.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197:215-223.

Gier, H. T. 1975. Ecology and social behavior of the coyote. Pages 247-262 in M.W. Fox, ed. The Wild Canids. Van Nostrand Rheinhoid, New York.

Haber, G. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. thesis, University of British Columbia, Vancouver.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. *J. Theor. Biol.* 7:1-52.

Harrington, F. H., Paquet, P. C., Ryon, J. and Fentress, J. C. 1982. Monogamy in wolves: a review of the evidence. Pages 209-222 in F. H. Harrington and P. C. Paquet, eds. Wolves of the World. Perspectives of Behavior. Ecology, and Conservation. Noyes Publ., Park Ridge, New Jersey.

Harrington, F. H., Fritz, S. H. & Mech, D. L. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. *Behav. Ecol. Sociobiol.* 13:19-26.

Hinde, R. 1976. On describing relationships. *J. Child Psychol. Psychiatry* 17:1-19.

Holm, C. H. 1973. Breeding sex ratios, territoriality; and reproductive success in the red-winged blackbird (*Agelaius phoeniceus*). *Ecol.* 54:356-365.

Johnson, S. R. & Baker, J. S. 1985. Productivity studies. Pages 171-231 in S.R. Johnson, ed. Population Estimation Productivity & Food Habits of Nesting Seabirds at Cape Peirce and the Pribilof Islands. Bering Sea, Ak. Rept. by LGL Ecological Research Assoc., Ins. to MMS, Anch., Ak.

Jonsingh, A. J. T. 1982. Reproductive and social behavior of the dhole (*Coon alpinus*). *J. Zool.* 198:443-463.

Jordan, P.A., Shelton, P.C., and Allen, D.L. 1967. Numbers turnover, and social structure of the Isle Royale wolf population. *Am. Zool*. 1:233-252.

Kleiman, D. G. 1977. Monogamy in mammals. *Quart. Rev. Biol.* 52:39-68.

Kleiman, D. G. and Eisenberg, J. F. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Beh.* 21:637-659.

Kleiman, D. G. & Malcolm, J. R. 1981. The evolution of male parental investment in mammals. Pages 347-387 in P.J. Gubernick & P.H. Klopfer, eds. Parental Care in Mammals. Plenum Publ. Corp.

Macdonald, D. W. 1979. Helpers in fox society. *Nature* 282:69-71.

Macdonald, D. W. 1980. Social factors affecting reproduction in red foxes. Pages 123-175 in E. Zimen, ed. The Red Fox. Symposium on Behavior and Ecology. *Biogeographica* 18, W. Junk, The Hague.

Macdonald, D. W. and Moehlman, P. D. 1982. Cooperation, altruism, and restraint in the reproduction of carnivores. Pages 433-467 in P.P.G. Bateson & P.H. Klopfer, eds. Perspectives in Ethology. Plenum, New York & London.

Malcolm, J. R. & Martin, K. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav. Ecol. & Sociobiol.* 10:1-13.

Martin, S. G. 1971. Polygyny in the bobolink: Habitat quality and the adaptive complex. Ph.D. thesis, Oregon State University.

Niebauer, H. J. 1985. Southern oscillation/El Niño effects in the eastern Bering Sea. Pages 116-118 in W.S. Wooster & D.L. Fluharty, eds. El Niño North: Niño Effects in the Eastern Subarctic Pacific Ocean. Washington Sea Grant Program, Univ. of Washington.

Nysewander, D. R. & Trapp, J. L. 1984. Widespread mortality of adult seabirds in Alaska August-September 1983. Unpubl. ms., U.S. Fish & Wildl. Serv., Anch., Ak.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589-603.

Pils, C.M. and Martin, M.A. 1978. Population dynamics, predator prey relationships and management of the red fox in Wisconsin. Technical Bull. No. 105. Dept. of Nat. Res., Madison, Wisconsin.

Pleszczynska, W.K. 1978. Microgeographic prediction of polygamy in the lark bunting. *Science* 201:935-937.

Rabb, G.B., Woolpy, J.H. & Ginsburg, B.E. 1967. Social relationships in a group of captive wolves. *Am. Zool.* 7:305-311.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Am. Nat.* 111:917-938.

Rasmusson, E. M. & Wallace, J. M. 1983. Meteorological aspects of the El Niño southern oscillation. *Science* 222:1195-1202.

Seal, U. S., Plotka, E. D., Packard, J. M. & Mech, L. D. 1979. Endocrine correlates of reproduction in the wolf: I. Serum progesterone, estradiol, and LH during the estrous cycle. *Biol. Reprod.* 21:1057-1066.

Storm, G.L., Andrews, R.D., Phillips, R.L., Bishop, R.A., Siniff, D.B. and Tester, J.R. 1976. Morphology, reproduction, dispersal, and mortality of Midwestern red fox populations. *Wildl. Monogr.* No. 49.

Trivers, R.L. 1971. The evolution of reciprocal altruism. Q. *Rev. Biol.* 46:35-57.

Trivers, R.L. 1972. Parental investment and sexual selection. Pages 136-179 in B. G. Campbell, ed. Sexual Selection and the Descent of Man. 1871-1971. Aldine, Chicago.

van Lawick, H. 1973. Solo. Collins, London.

Verner, J. 1964. Evolution of polygamy in the long-billed marsh wren. *Evol.* 18:252-261.

von Schantz, T. 1981. Female cooperation, male competition, and dispersal in the red fox, *Vulpes vulpes. Oikos* 37:63-68.

von Schantz, T. 1984. Non breeders in the red fox: a case of resource surplus. *Oikos* 42:59-65.

Wickler, W. & Seibt, U. 1983. Monogamy: an ambiguous concept. Pages 33-50 in P.P.G. Bateson, ed. Mate Choice. Cambridge Univ. Press.

Willson, M. F. 1966. Breeding ecology of the yellow-headed blackbird. *Ecol. Monogr.* 36:51-77.

Wilson, E.O. 1975. Sociobiology The new synthesis. Belknap Press, Cambridge, Mass. 697 pp.

Wittenberger, J. G. 1976. Habitat selection and the evolution of polygyny in bobolinks (*Dolichonyx oryzivorus*). Ph.D thesis, University of California, Davis.

Wittenberger, J. F. & Tilson, R. L. 1980. The evolution of monogamy: hypotheses and evidence. *Ann. Rev. Ecol. Syst.* 11:197-232.

Wyrtki, K. 1979. The response of sea surface topography to the 1976 El Niño. *J. Phys. Oceanogr.* 9:1223-1231.

Zimen, E. 1976. On the regulation of pack size in wolves. *Z. Tierpsychol.* 40:300-341.

# CHAPTER IV

# RED FOX HELPERS INHERIT DEN SITES: EVIDENCE FOR RECIPROCITY

## Introduction

Helpers, or individuals other than the parents that provide care for young, have been observed in over 120 mammalian species (most often primates, proboscideans, and canids) and in over 150 avian species (Reidman 1982; Brown 1978). The occurrence of helping behavior is often associated with production of few offspring that require intensive parental investment, and small groups of related animals. Ecological correlates of helping behavior include utilization of food resources that require cooperative foraging strategies (e.g., large prey or isolated, unpredictable food sources), or utilizing scarce breeding resources (food, mates, or breeding sites) that limit the reproductive options of young animals (Reidman 1982).

Cooperatively breeding organisms with helpers have provided important tests for the theories of kin selection (Hamilton 1964) and reciprocity (Trivers 1971; Axelrod and Hamilton 1981). The theory of reciprocity suggests that an individual may incur a short term cost in order to benefit another if the act is likely to be reciprocated in the future. The concept of kin selection requires that altruistic behavior be directed towards related individuals; an individual increases it's "inclusive fitness" (Hamilton 1964) by increasing it's own reproductive success and also that of related individuals. Studies of cooperatively breeding avian species (Rowley 1978; Woolfenden 1975; Emlen 1981; Ligon & Ligon 1978, Ligon 1981; Koenig 1978) have led to the suggestion that kin selection may have been "an additive factor contributing to the evolution of helping behavior, not a cause of group living" (Koenig and Pitelka 1981). Among the family

Canidae, non-breeding members of groups often provide food or protection to another individual's offspring (Macdonald and Moehlman 1982; Moehlman 1979, 1983; Bekoff and Wells 1982). Canid helpers have frequently been assumed to be older siblings, and kin selection has often been invoked as the evolutionary basis for alloparenting (Macdonald and Moehlman 1982; Moehlman 1979, 1983; Bekoff and Wells 1982; Malcolm and Martin 1982; Macdonald 1979, 1980; von Schantz 1981, 1984). However, attempts to distinguish between the hypotheses of kin selection and reciprocity have been confounded in most previous studies by the uncertainty of kinship coefficients among members of canid social groups. Most workers have only been able to infer relatedness among their subject animals (but see Bekoff and Wells 1982; Moehlman 1979, 1983; Frame et al. 1979).

Red foxes were traditionally thought to be a solitary, monogamous canid (Kleiman 1977). However, recent evidence suggests that multiple females (1-5) may use the same area, or live in a "group territory" which is shared with one male (Macdonald 1979, 1980; von Schantz 1981, 1984). It has been suggested that extra females living within such territories may be "helpers" (Macdonald 1979, 1980), but there have been no observations that they actually provide any assistance in rearing pups (outside of captivity; Macdonald 1980). Non-breeding females have been observed visiting the den of a breeding female and playing with pups (Macdonald 1980); but no prey items were delivered. Von Schantz (1981, 1984) concluded (from radio telemetry fixes) that non-breeding females that lived within a breeding female's territory did not function as regular helpers because they visited the litters only occasionally. Instead, he suggested non-breeding females may be "insurance backup" (Ernlen 1978) for breeding females by adopting pups in the event of the mother's death. Both Macdonald (1979, 1980) and von Schantz (1981, 1984) concluded that non-

breeding females were increasing their inclusive fitness by helping and adopting offspring of relatives.

Here I present data suggesting that helpers may reduce hunting requirements for breeding foxes. In addition, I suggest that cooperative breeding among red foxes may benefit all group members, irrespective of kin relations.

## Results

### Helpers and Other Non-breeding Adults in the Population

Fifteen reproductive groups were observed during the five season study. Four of 14 groups had helpers that brought food to and guarded the pups. (Two nursing females were observed in one group, but it was not known whether any helpers belonged to the group.) All helpers were non-lactating females. Three groups had one helper, and one group had two helpers.

The proportion of reproductive adults within the population was very low (varying from 6% to 40% among years, Table IV.1). In addition to helpers, a large proportion of non-breeding adult foxes (>1 year of age) were present in the population each year (Table IV.2). Among non-breeders, a small proportion defended den sites (i.e., chased away intruders) and regularly slept at dens although no pups were ever seen ("non-breeding den holders"). The remaining non-breeding adults were "floaters". Floaters had no association with any reproductive group but resided in small areas through which breeders regularly traveled.

### The Role of Helpers

#### Assistance at the Den

Helpers brought food to young and protected pups. I measured assistance in providing food by recording the per cent of total prey delivered and the per cent of

visits to den sites. This allowed me to determine whether helpers reduced the work required of parents in rearing offspring.

Helpers delivered significantly fewer prey items to pups than did reproductive females or males (Table IV.3), but there was a great deal of individual variation. The proportion of the total prey items (per group) that helpers contributed varied from 6% to 25% among groups. Helpers may have reduced hunting requirements for reproductive females. Females without helpers delivered birds at a significantly higher rate (.11 birds/hour) than did females with helpers (.06 birds/hour, n=59 birds, $.05<p<.1$ Wilcoxon ranked signs test). However, reproductive females visited their dens significantly more frequently than males or helpers (Table IV.3). Helpers made from 8% to 50% of the total den visits among group members. In one group, the helper visited the den more frequently than the reproductive female or the male, and fed the pups more frequently than the female. The two remaining helpers (for whom such data are available) fed pups and visited the den less frequently than other group members.

Reproductive Success

The presence of helpers correlated with increased reproductive success. Groups with helpers had higher pup survival than groups without helpers. (An equal proportion of groups with and without helpers were bigamous, thus this factor was constant.) Prior to the onset of El Niño conditions (from 1980-1981) litter sizes of groups with helpers (x=4.2, range=3-5) did not differ from those of groups without helpers (x=4.0, range=3-5). However, the proportion of marked pups that survived to one year of age was 1.6 times higher for groups with helpers (.6, n=15 pups) than for groups without helpers (.375, n=16 pups).

An alternate explanation for the correlation between helpers and increased reproductive success is that older, more experienced foxes had helpers. Thus, helpers may be correlated with the age of parents (Lack 1968; Brown 1978; Brown & Balda

1977). The age of most breeding foxes in this population was unknown, therefore this factor cannot be assessed.

## Factors that Influenced Helping Behavior

One advantage of helping for non-breeding females was eventual/subsequent inheritance of the breeding female's territory. Each of three surviving helpers acquired the den site at which they had helped after the breeding female either moved to a new den or died (Fig. IV.1). (Two of the five helpers observed during this study were not seen again after the year they helped, and were assumed to have died.) Each surviving helper gave birth to at least one litter after being a "non-breeding den holder" for 1 to 3 years (in that interval they defended their den site, but did not successfully breed). In contrast, of 29 females that had never served as helpers, only three were able to acquire territories and successfully breed. Therefore, female helpers significantly increased their reproductive success. Females that helped may have been older, more experienced foxes, and this may have correlated to their ability to become helpers.

Emlen (1984) suggested that four factors may influence whether a non-breeding individual will remain as a helper or leave and attempt to breed on it's own: 1) the risks of dispersal, 2) the probability of acquiring a suitable territory, 3) the probability of finding a mate, and 4) the probability of successfully reproducing. The risk of dispersing from the natal den site on Round Island was low for a red fox. The annual survival rates of "floater" foxes were not significantly different from any other class of animal ($X^2$=1.3, $p<.3$), except breeding males (which had significantly higher mortality rates than any other males, Table IV.4). The probability of acquiring a territory was extremely low however. During the study, eleven males acquired a territory and seven attained breeding status; eight females acquired a territory and six attained breeding status. The number of territories on average which became available

per year was 11/5 or 2.2 for a male; and 8/5 or 1.6 for a female. The probability of successfully reproducing was the proportion of the den holders with mates that raised pups each year. For males this proportion was .5; for females .45.

I calculated the probability that an animal would survive and reproduce successfully in year x+1, given that it did not reproduce in year x. All foxes are included in this calculation except breeders, i.e., non-breeding den holders, floaters, and helpers. Foxes that were alive in year x, but did not survive to year x+l are included in order to account for the probability of survival. Five males that did not breed in year x (i.e., they did not assist in rearing pups) were able to successfully reproduce in year x+l, while 48 males were not. Using the same criteria, seven females successfully reproduced in year x+1 that had not reared pups the previous year, and 57 females did not. Thus, the probability that a male who did not reproduce in year x would survive and reproduce in year x+1 was .09; for females this value was .11.

## Were Female Group Members Related?

I followed the lineages of foxes for five years. At the end of the fifth pup rearing season, no *known* offspring or sisters had cooperatively reared pups as helpers or bigamous mothers. Only one female younger than five years of age became reproductive. She paired monogamously when three years old.

Associations among members of reproductive groups never endured beyond one season (Fig. IV.1). Such short term associations were caused by several factors.

1) Female members of reproductive groups regularly switched den sites from year to year. Half of the surviving female breeders moved to new dens between years (n=8). Two pairs of bigamous females survived, and one of these females moved to a new den in each case. One helper-breeding female pair survived; the breeding female

moved to a new den and the helper did not move. Helpers were the only females that did not switch den sites during the study.

2) High mortality of breeding males resulted in one season pair bonds. Mortality rates were calculated as the per cent of individuals dying from year x to year x+1 (Table IV.4). Breeding males had significantly higher mortality rates than all other adult males (67%, n=9 vs. 32%, n=44; $X^2$=3.9, p<.05), and significantly higher mortality rates than breeding females (29%, n-14, $X^2$=3.2, .05<p<.10). Only once did both members of a male-female pair survive to the following year (n=9 pairs). In this case, the female subsequently became the helper for her previous mate. Similar, lack of stability among red fox pairs was documented by Neiwold (1980) who radio tracked 150 red foxes over a five year period and found that no male-female association endured longer than one breeding season.

3) No female or male offspring remained in their natal territory or served as helpers (n=50 marked pups; 46% survived as yearlings). On six occasions, yearling females were seen traveling through their natal den site. On five of these occasions they were aggressively chased away (four times by the mother); during one observation the mother tolerated her daughter at the den for several hours.

## Discussion

It has been suggested that fox groups may be composed of breeding females with their female offspring (Macdonald 1979, 1980; von Schantz 1981, 1984; Neiwold 1980). However, if floaters are present within a population, they could be a major source of error in radio telemetry studies showing helpers and female "groups". Floaters on Round Island commonly lived in areas as close as .2 km from den sites. Yet they never entered den sites, or interacted with the adults that were rearing pups.

My data indicate that red fox helpers at Round Island were not offspring of the breeding females they helped, thus suggesting that factors other than kin selection may be involved. Several factors indicate that female group members within the Round Island population were not next of kin. The helpers of bigamous trios should (on average) be less closely related to breeders they help than should helpers of monogamous pairs (Koenig & Pitelka 1981), unless the bigamous females are sisters. Another factor that would further decrease the average genetic relatedness between helpers and breeders is short term pair bonding between adults (Emlen 1981; Koenig & Pitelka 1981). Due to the short term associations between bigamous females, helpers and breeding females, and male-female pairs, and the occurrence of polygynous trios, it is unlikely that female group members were closely related in this population.

These data suggest that cooperative breeding in red foxes is not necessarily restricted to closely related individuals, and other factors may be of equal or greater importance. My data suggests that reciprocity or female cooperation may also be involved. Fox helpers inherited den sites, suggesting it is to their advantage to feed and help rear another foxes' pups, whether they are related or not, because they may subsequently attain breeding status. Therefore, helping could be considered to be reciprocal altruism (Trivers 1971; Axelrod and Hamilton 1981) and may increase a female foxes' fitness by increasing the probability that she will successfully breed. Females which shared a male and mated bigamously had equal or better reproductive success than females which paired monogamously (see Chapter III). Because bigamous females benefited from communal pup rearing, this behavior pattern may have evolved as a result of female cooperation (Altmann et al. 1977) or reciprocity between females. The cooperative female choice model (Altmann et al. 1977) for the evolution of polygyny predicts that the addition of another breeding female to a reproductive group will improve the fitness of all females. My data supports the

prediction of this model that females sharing a male may benefit from cooperative interactions within the group such as assistance in rearing young.

The evolution of cooperative breeding can result from one or more possible benefits for helpers (Brown 1978): 1) immediate benefits, such as increased survival (Vehrencamp 1978); 2) indirect benefits from kin selection; and 3) delayed, direct benefits by eventually succeeding to breeding status (Ligon & Ligon 1978; Woolfenden 1981; Koenig & Pitelka 1981; Emlen 1982a, 1982b; Wiley & Rabenold 1984). More than one source of selection is likely to influence the evolution of cooperative breeding in any species. My data suggests that all group members benefit from cooperative breeding, and therefore reciprocity or female cooperation may have importantly influenced social evolution in canids.

Figure IV.1.

Geneologies of Round Island red foxes, 1980-1984. Each fox occupies a single line through time, and movement into new den sites is indicated by a diagonal line.

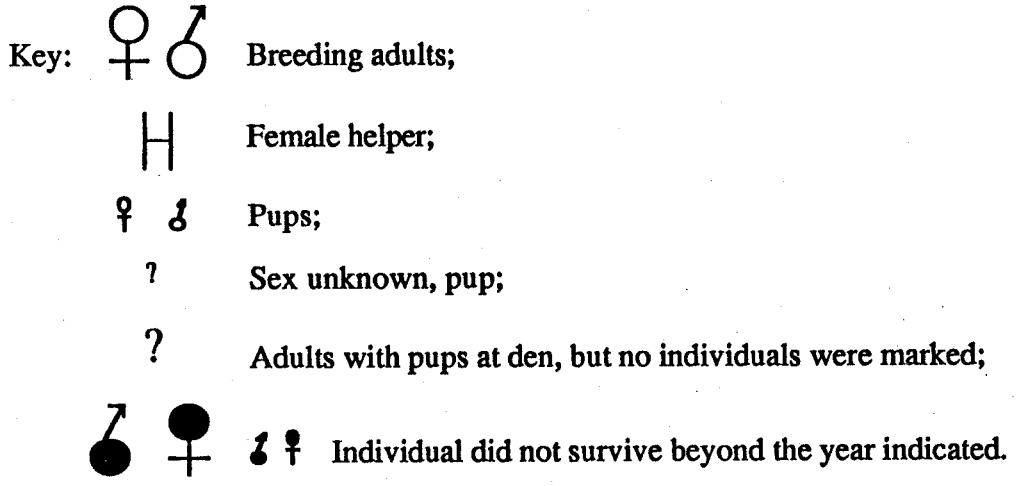


Fig. 1
**Geneologies of Round Island red foxes**

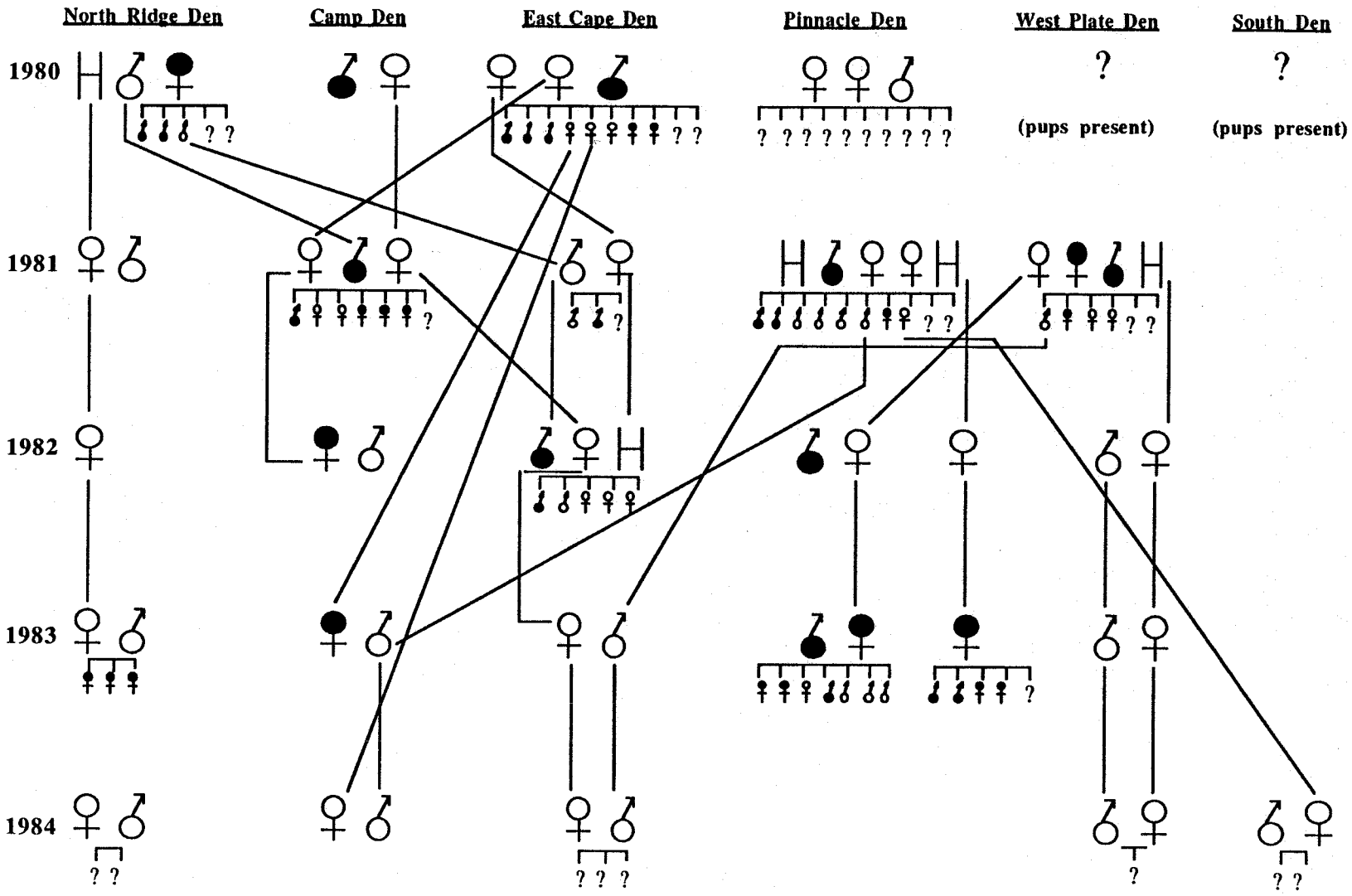


Table IV.1

Population structure of Round Island red foxes: proportion of non-breeding adults in the population, 1980-1984

| Year | Adult Population | % Reproductive Adults | | % Non-breeding Adults | |
|---|---|---|---|---|---|
| | | Females | Males | Females | Males |
| 1980 | 30 | > = 40% | > = 40% | > = 40% | > = 23% |
| 1981 | 27 | 40% | 40% | 60% | 60% |
| 1982 | 30 | 6% | 9% | 94% | 91% |
| 1983 | 28 | 18% | 18% | 82% | 82% |
| 1984 | 27 | 21% | 23% | 79% | 77% |

Table IV.2

Population structure: categories of breeders and non-breeders (n=total island population; # in parenthesis = # individuals represented by that category).

| | 1980 | 1981 | 1982 | 1983 | 1984 |
|---|---|---|---|---|---|
| | n=30 | n=27 | n=30 | n=28 | n=27 |
| Non-breeding den holders | 1 pair (2) | 1 pair (2) | 4 pairs (8) | 3 pairs (6) | 1 pair (2) |
| Floaters | 53% (19) | 44% (12) | 63% (19) | 61% (16) | 70% (17) |
| | | Breeding Groups | | | |
| Monogamous | | 1 (2) | | 3 (6) | 4 (8) |
| Monogamous w/Help | 1 (3) | | 1 (3) | | |
| Bigamous | 2 (6) | 1 (3) | | | |
| Bigamous w/Help | | 2 (9) | | | |

Table IV.3

Rate of food deliveries and visits to den by members of reproductive groups.

| | Mean # seabirds/12 hours | Mean # visits/12 hours |
|---|---|---|
| | n=135 seabirds | n=325 visits |
| Males | 1.02 (range=0-1.6) | 1.8 (range=1-2.2) |
| Females | .95 (range=.5-1.7) | 2.6** (range=1.8-3.4) |
| Helpers | .34* (range=.2-.5) | 1.7 (range=.2-.3.9) |

* Kruskal Wallis $X^2$=6.3, p<.05

**Kruskal Wallis $X^2$=2.7, .05<p<.1

Table IV.4

Annual Survival Rates

| | Males | Females |
|---|---|---|
| Floaters | .67 (n=36) | .58 (n=19) |
| Non-breeding den holders | .75 (n=8) | .80 (n=10) |
| Breeders | .33 (n=9)* | .71 (n=14) |
| Pups | .46 (n=24) | .46 (n=26) |
| Helpers | | .75 (n=4) |

* Value is significantly lower than breeding females, $X^2$=3.2, .05<p<.10; and significantly lower than all other adult males (non-breeding den holder and floaters), $X^2$=3.9, .02<p<.05.

## BIBLIOGRAPHY, CHAPTER IV

Altmann, S.A. Wagner, S.S. & Lenington, S. 1977. Two models for the evolution of polygyny. *Behav. Ecol. Sociobiol.* 2:397-410.

Axelrod, R. & Hamilton, W.D. 1981. The evolution of cooperation. *Science* 211:1390-1396.

Bekoff, M. & Wells, M.C. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use and resource defense. *Z. Tierpsychol.* 60:281-305.

Brown, J. L. 1978. Avian communal breeding systems. *Ann. Rev. Ecol. Syst.* 9:123-155.

Brown, J. L. & Balda, R. P. 1977. The relationship of habitat quality to group size in hall's babbler (*Pomatostomus halli*). *Condor* 79:312-320.

Emlen, S.T. 1978. The evolution of cooperative breeding in birds. Pages 245-281 in J. R. Krebs and N. B. Davies, eds. Behavioural Ecology: an Evolutionary Approach. Blackwell, Oxford.

Emlen, S.T. 1981. Altruism, kinship, and reciprocity in the white-fronted bee-eater. Pages 217-230 in R.D. Alexander & D.W. Tinkle, eds. Natural Selection and Social Behavior. Chiron, New York.

Emlen, S.T. 1982a. The evolution of helping behavior. I. An ecological constraints model. *Am. Nat.* 119:29-39.

Emlen, S.T. 1982b. The evolution of helping. II. The role of behavioral conflict. *Am. Nat.* 119:40-53.

Emlen, S.T. 1984. Cooperative breeding in birds and mammals. Pages 305-339 in J.R. Krebs & N.B. Davies, eds. Behavioral Ecology: an evolutionary approach. Blackwell, Oxford.

Frame, L.H., Malcolm, J.R., Frame, G.W. & van Lawick, H. 1979. Pack dynamics of African wild dogs (*Lycaon pictus*) on the Serengeti plains, 1967-1978. *Z. Tierpsychol.* 50:225-249.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. I, II. *J. Theor. Biol.* 7:1-52.

Kleiman, D.G. 1977. Monogamy in mammals. *Q. Rev. Biol.* 52:39-68.

Koenig, W.D. 1978. Ecological and evolutionary aspects of cooperative breeding in Acorn woodpeckers of central coastal California. Ph.D. thesis, University California, Berkeley.

Koenig, W.D. & Pitelka, F.A. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pages 261-280 in R.D. Alexander & D.W. Tinkle, eds. Natural Selection and Social Behavior. Chiron, New York.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Ligon, J.D. 1981. Demographic patterns and communal breeding in the green woodhoopoe, Phoeniculus purpureus. Pages 231-243 in R.D. Alexander & D.W. Tinkle, eds. Natural Selection and Social Behavior. Chiron, New York.

Ligon, J.D. & S.H. Ligon. 1978. Communal breeding in green woodhoopoes as a case for reciprocity. *Nature* 276:496-498.

Macdonald, D.W. 1979. "Helpers" in fox society. *Nature* 282:69-71

Macdonald, D.W. 1980. Social factors affecting reproduction by the red fox, *Vulpes vulpes*. Pages 123-175 in E. Zimen, ed. The Red Fox. Symposium on Behavior and Ecology. *Biogeographica* 18, W. Junk, The Hague, The Netherlands.

Macdonald, D.W. & P.D. Moehlman. 1982. Cooperation, altruism, and restraint in the reproduction of carnivores. Pages 433-467 in P.P.G. Bateson & P.H. Klopfer, eds. Perspectives in Ethology . Plenum, New York & London.

Malcolm, J.R. & Martin, K. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav. Ecol. Sociobiol.* 10:1-13.

Moehlman, P.D. 1979. Jackal helpers and pup survival. *Nature* 277:382-383.

Moehlman, P.D. 1983. Socioecology of silverbacked and golden jackals (*Canis mesomelas* and *Canis aureus*). Pages 423-453 in J.G. Eisenberg & D.G. Kleiman, eds. Advances in the Study of Mammalian Behavior. American Society of Mammalogists.

Neiwold, F.J.J. 1980. Aspects of the social structure of red fox populations: a summary. Pages 185-194 in E. Zimen, ed. The Red Fox. Symposium on Behavior and Ecology. *Biogeographica* 18, W. Junk, The Hague, The Netherlands.

Reidman, M.L. 1982. The evolution of alloparental care and adoption in mammals and birds. *Q. Rev. Biol.* 57:405-435.

Rowley, I. 1978. Communal activities among white-winged choughs *Corcorax melanorhamphus*. *Ibis* 120:178-197.

Rowley, I. 1981. The communal way of life in the Splendid Wren Malurus splendens. *Z. Tierpsychol.* 55:228-267.

Trivers, R.L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46:35-57.

Vehrencamp, S.L. 1978. The adaptive significance of communal nesting in groove-billed anis (*Crotophaga sulcirostris*). *Behav. Ecol. Sociobiol.* 4:1-33.

von Schantz, T. 1981. Female cooperation, male competition, and dispersal in the red fox, *Vulpes vulpes. Oikos* 37:63-68.

von Schantz, T. 1984. 'Non-breeders' in the red fox *Vulpes vulpes* : a case of resource surplus. *Oikos* 42:59-65.

Wiley, R.H. & Rabenold, K.N. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evol.* 38:609-621.

Woolfenden, G.E. 1975. Selfish behavior of Florida scrub jay helpers. Pages 257- 260 in R.D. Alexander & D.W. Tinkle, eds. Natural Selection and Social Behavior. Chiron, New York.

Woolfenden, G.E. 1981. Selfish behavior by Florida scrub jay helpers. Pages 257-260 in R.D. Alexander & D.W. Tinkle, eds. Natural Selection and Social Behavior, Blackwell, Oxford

# CHAPTER V

# GROUP SIZE AND REPRODUCTIVE SUCCESS IN RED FOXES

## Introduction

The term "cooperative breeding" refers to reproductive groups that have more than two adults helping care for young (Emlen & Vehrencamp 1983). Cooperative breeding is rare among birds and mammals. Adults other than the parents provide care for young in over 300 species of birds, some rodents, and in numerous mammalian carnivores including mustelids (European badger, *Meles meles;* Neal 1977), at least 7 canid species, lions (*Panthera leo,* Bertram 1975; Bygott et al. 1979; Packer & Pusey 1982), hyaenids (Brown hyaenas, *Hyaena brunnea* Owens & Owens 1979), and viverids (dwarf mongooses, *Helogale parvula,* Rood 1980; and banded mongooses, *Mungos mongo,* Rood 1974, 1978) (see review by Emlen 1984).

Cooperative breeding can take two forms: groups with non-breeding helpers (monogamy with helpers), or groups with more than one breeding female ("communal" breeding, or polygyny) (Emlen 1984). Most canid species are monogamous with helpers (Zimen 1976; Rabb et al. 1967; Seal et al. 1979; van Lawick 1973; Macdonald 1979a, 1980; Malcolm & Martin 1982; Jonsingh 1982), as are many avian species (Brown 1978). Monogamy and helpers in both canid and avian species are thought to result from the fact that their altricial young require non-shareable male parental care (Kleiman 1977; Kleiman & Malcolm 1981). However, breeding groups that are polygynous with helpers occur in several avian species (Koenig 1978; Rowley 1978; Councilman 1977), in mongooses (Rood 1974, 1978, 1980), and in red foxes (see Chapter III). Thus, red foxes provide a unique opportunity to contrast some of the

costs and benefits of helpers and polygyny for a canid species with those of avian species.

Emlen (1982a, 1982b) suggested that these two forms of cooperative breeding, helping and communal breeding, should be viewed as opposite ends of a continuum and he developed two models to explain the evolution of such breeding systems. 1) The ecological constraints model (Emlen 1982a) predicts that the frequency of helpers should increase with environmental harshness and the difficulty of becoming a successful breeder. During harsh seasons the costs of dispersal increase, breeding options are more constrained and offspring are predicted to stay home. 2) The helper-breeder conflict model (Emlen 1982b) suggests that breeders and helpers will attempt to bias reproduction in their own favor, and the reproductive status of female group members may change through time. Shifts from helping to polygyny and vice versa are predicted to occur depending on environmental conditions and social interactions between the females. This model predicts that polygyny should occur only when there is a per capita benefit from group living, and factors constraining reproduction are minimal, i.e., the subordinate can disperse and successfully breed on it's own. In such circumstances, it is to the subordinate female's advantage to stay in the group only if she can breed. A dominant female will allow the subordinate female to breed only if she is likely to disperse otherwise. If factors constraining reproduction are high, the dominant female should have "leverage" to induce the helper to stay in the group without allowing her to breed.

In contrast to Emlen's (1982a) ecological constraints model, Macdonald (1983) proposed a "resource dispersion hypothesis" for carnivores. He suggested that a pair of carnivores may defend a territory that is large enough to support them during years of low food abundance. During years of high food abundance, territory size may remain constant, but additional group members may be tolerated within the territory.

Thus, Macdonald's (1983) model predicts that group sizes should decrease with environmental constraints, while Emlen's (1982a) model predicts that group sizes should increase with environmental constraints.

In this Chapter, I will compare data from red foxes to data from avian studies to test the predictions of Emlen's (1982a, 1982b) models (which were proposed for both birds and mammals). I will discuss whether the red fox data supports the predictions of Macdonald's (1983) resource dispersion hypothesis or Emlen's (1982a) ecological constraints model.

## Methods

I will present an analysis of the differential reproductive success and subsequent survivorship of pups for groups of red foxes. Although the appropriate measure of reproductive success is the number of individuals which successfully become breeders, an approximation of this value that will be used is the number of young which survive to one year of age. Reproductive success (RS) per reproductive female and per capita will be calculated and used to test the hypothesis that individuals gain from the presence of others. In groups with two breeding females, the number of surviving pups from that group will be divided by two to calculate RS per reproductive female. To calculate per capita RS, the number of surviving pups will be divided by the number of adults in each group (mothers + helpers + the male). Litter size will be the number of pups that first emerge from the den, at approximately four to six weeks of age. Litter size per reproductive female and per capita will be calculated in a manner similar to pup survival.

## Results

### Group Size

The size frequency distribution of 14 fox groups during five pup rearing seasons (Fig. V.1) was characterized by a mode of two (a pair) and a mean of 2.6. One group was eliminated from this calculation because only a minimum estimate was obtained: two nursing females were observed, but whether any helpers belonged to the group was unknown. The largest proportion of individuals lived in groups of two; however the size of the group in which the average animal lived (="typical group size", Jarman 1974) was 2.9 (n=36 individuals).

Red fox groups on Round Island may also be categorized by the number of nursing females and the number of helpers in a group. Fourteen of the observed 15 reproductive groups had one male which delivered seabirds to the females and pups; one female raised a litter unassisted (the "single female"). Five groups had two nursing females and one male (henceforth referred to as "bigamous" groups); the remaining nine groups had a single nursing female and a male ("monogamous" groups). The modal number of nursing females per group was one and the mean was 1.4.

Four of 14 groups had one or two non-lactating female "helpers" that brought food to and guarded the pups. Two of four bigamous groups had one and two helpers respectively, and two of the nine monogamous groups had one female helper.

### Group Size and Reproductive Success

The reproductive success of groups is analyzed by non-parametric correlation techniques in Table V.1. Larger groups did not produce larger litters, but they did have more pups survive per adult fox. On the basis both of per reproductive female and per

capita, group size varied positively and significantly with the number of pups that survived to one year of age (henceforth referred to as "pup survival")

The number of pups that survived to one year of age was also correlated with litter size (Table V.2). ($r^2$=.74 for litter size; $r^2$=.67 for group size, Spearman rank correlation.) It appears that litter size had a greater influence on number of pups that survived than did group size, but both were significant. Stepwise multiple regression was used to estimate the relative importance of these variables (Table V.3). The first variable entered was litter size which accounted for 41% of variance in pup survival. Group size accounted for 20% of variance in pup survival.

## Yearly Variation

Yearly variation in weather, food or other ecological conditions could be an important source of variability. However, group sizes varied significantly among years, thus confounding my analyses of interannual variation in pup survival. Red fox groups were smaller during years of low food availability. During 1980-1981 seabird productivity was high on round Island and mean fox group size was 3.4. After the occurrence of El Niño in the Bering Sea in 1982, seabird productivity declined and the mean fox group size declined to two (Mann Whitney U test, $p<.01$). This the differences in litter size and pup survival among years and the differences due to changes in group size cannot be separated. Fox productivity was related to seabird productivity. When seabirds failed to nest at Round Island (during 1982-1984), the number of litters, litter sizes, and the number of reproductive females declined (see Chapter III). However, the percentage of pups which survived to one year of age did not change significantly (50% pup survival pre El Niño, n=32; 44% survival post El Niño, n=16; $X^2$=.2, $p<.7$. Three pups that died from infanticide are excluded from the post El Niño sample).

Litter size and pup survival were each analyzed by Kruskal Wallis (non-parametric) ANOVA for yearly variations (Table V.4). Litter size varied significantly among years. However, there was no significant yearly variation in the number of pups that survived to one year of age.

## Advantages of Large Group Size

To test whether large groups might have higher pup survival due to increased prey fed to pups, the rate of food deliveries per pup is plotted against group size (Fig. V.2). The rate of deliveries was calculated from the total number of seabirds that all adults in each group brought to their den. There was no correlation between group size and delivery rate per pup. Furthermore, the rate of food delivery per pup did not vary with litter size (Fig. V.3); each pup received approximately the same number of prey items regardless of the number of littermates or the number of adults. Thus, it appears that adults adjusted their feeding efforts according to the number of pups in a group, not according to the number of adults. Viewed from the perspective of adults, food delivery rate was negatively correlated with adult group size (Fig. V.4) Thus it may have been energetically beneficial for adults to be in large groups when raising pups.

Another potential benefit of large groups might be that an adult would be present at the den site a higher proportion of time. The rate of visits that adults made to dens was calculated in a manner similar to the rate of food deliveries, i.e., the total number of visits was standardized to a one hour time period. There was a significant positive correlation between group size and frequency of adult visits (Fig. V.5).

An observation made at Round Island indicate that other adults may be a threat to fox pups and therefore it might be beneficial for group members to be at dens to protect pups. Infanticide appeared to be the cause of death of one litter in 1983. Three ear tagged pups were found dead outside of the den entrance at approximately six

weeks of age. Canine teeth marks were found that had punctured the lungs; the wound was hemorrhagic indicating that it was the cause of death and not inflicted post mortum. After that date, a new female took over the den site and the mother of the pups was not seen again. This observation suggests that pups may benefit from protection against other foxes by having adults present at the den more frequently.

An alternate hypothesis is that older, more experienced parents belong to larger groups. Thus, large group size may be correlated with age of parents (Lack 1968; Brown 1978; Brown & Balda 1977). The age of most breeding foxes in this population was unknown, therefore this factor cannot be assessed.

## The Role of the Male

A single female raised a litter of five pups unassisted by any male in 1983. She was the only reproductive fox whose young all failed to survive to one year (n=11 groups). Other foxes were frequently observed trespassing near this female's den. I defined an intrusion as a visit to a den site by a fox that was not a member of that reproductive group. A total of 15 intrusions were observed at all fox dens where pups were reared during five years. Seven of the 15 intrusions were into this den during one summer. She was the only fox that was unable to chase intruders away: on three occasions male foxes remained at her den after she interacted aggressively with them. Her pups were observed being harassed by these males on two occasions. Harassment involved a male lying at the den entrance and preventing pups from emerging out of the den, and a male actively chasing the pups into the den. In addition, her pups were fed less frequently than pups at any other den. The mean number of seabirds per hour that her pups received was less than half the number received per pup in all other groups (.01/pup vs a mean of .03/pup, n=7 groups). This observation suggests that it is difficult for a female fox to successfully rear pups unassisted.

## Dominance Interactions Among Female Group Members

There were distinct differences in the social interactions between helpers and breeding females, and between bigamous females. Interactions were observed whenever two females were at the den simultaneously; they never arrived together, but often one female entered the den site while another was either sleeping there or interacting with pups (grooming or playing with them). In all four cases, helpers were subordinate to reproductive females and always greeted them submissively when they encountered one another at the den (n=9 interactions). A submissive display involved the following behaviors: crouching low to the ground, putting the ears back against the head, and wagging the tail furiously while making screaming vocalizations (Macdonald 1977a). In contrast, females which denned communally never greeted one another submissively; no dominance was evident between these four pairs of bigamous females (n=22 interactions). When two reproductive females encountered one another at a den, they typically looked at each other and then continued their previous activity with no visible change in behavior.

## Discussion

Several models have been proposed to predict ecological and social factors that might promote cooperative breeding (Emlen 1982a; Macdonald 1983), and to determine if it will take the form of non-breeding helpers or multiple females that share reproduction and communally rear young (Emlen 1982b) (Table V.5).

*Helper-breeder conflict model.* Emlen's (1982b) helper-breeder conflict model predicts that polygyny should occur only when there is a per capita benefit from group living, and factors constraining reproduction are minimal. If conditions are favorable so that a subordinate female can disperse and successfully breed, she is predicted to

stay in the group only if she is allowed to reproduce. Only when a subordinate female is likely to disperse will a dominant female let her to breed. If factors constraining reproduction are high, the dominant female should be able to monopolize reproduction and the helper will not have the option of dispersing. The Round Island fox data does not support the predictions of this model. Although there was a reproductive benefit from grouping, factors constraining reproduction were high (see Chapter IV). Thus, Emlen's (1982b) model would predict the occurrence of helpers, but not bigamy in this population. This model was proposed for both birds and mammals; I will compare data that have been collected from avian species with my fox data to test the applicability of this model.

The per capita benefits of grouping to reproductive success appear to be very different for red foxes than for avian species. In 15 species of birds, most did not increase per capita reproductive success as group size increased (Koenig 1981). Rather, most monogamous female birds produce more offspring than do conspecifics that nest with another female (Koenig 1981). In contrast, my data indicates that bigamous red fox females had equal or better reproductive success than monogamous females (Chapter III). Red foxes gained directly from group living by increased per capita reproductive success with increasing group size. Since all individuals benefit from group living, there/should have been no "conflict" between helpers and breeders.

Differences between the effects of group size on reproductive success of red foxes and avian species may be related to different factors constraining these organisms. One constraining factor is the risk of dispersal, or probability of survival if an animal leaves it's natal (familiar) territory. The annual survival rates of "floater" foxes were not different from those of foxes which had den sites (Table IV.4); therefore this does not appear to have been a constraining factor. However, Koenig & Pitelka (1981) proposed that a constraint on avian species might be the unavailability of

marginal habitat into which they could disperse. They suggested that group members among birds were "forced" to live in groups in order to maintain access to a localized and limited resource. Most avian species tend to be specialized feeders, and they can survive only in a narrow range of habitats (F. Pitelka, pers. comm.). In contrast, most carnivores can survive on a broad range of food items: vegetable matter, insects, carrion, or various size prey species. Thus, carnivores may have the option of either living in groups or living solitary, depending on the availability of food resources. Brown (1978) suggested that for avian species, communal living combined with territoriality might increase survival during the non-breeding season. Increased survival might be attained by improvements to the territory (i.e., elaborately covered sleeping nests or food storage) that is used throughout the year. The data from red foxes on Round Island does not support the hypothesis of forced grouping that was suggested for birds; rather grouping appears to be mutually beneficial for all fox group members when food resources are sufficient.

Another constraining factor, the probability of successfully reproducing, may differ for avian species and foxes. On Round Island the probability that a female fox would successfully reproduce if she had not done so the previous year was very low (.11, Chapter IV), and the annual proportion of females which successfully gave birth was also low (6%-40%, Table IV.1). Most communally breeding birds also occur in "saturated" habitats where the probability of acquiring an available nest site is low (Brown 1978). However, a high proportion (45%) of female foxes which had den sites did not successfully raise pups. Apparently a high proportion of female foxes become pregnant, but subsequently abort or resorb fetuses. Pre-implantation loss (lost ova) in one red fox population was reported to be 36% (n=104) for yearlings and 33% (n=141) for adult females, and post-implantation loss (lost embryos) was 16% (n=245) for yearlings and 12% (n=347) for adults (Englund 1970). Prenatal loss (ova that did

not implant and resorbed fetuses) in another red fox population was estimated to be 16-32% (Layne & McKeon 1956).

Among carnivores, mating and progeny rearing are seasonally separated by as much as two to three months, unlike that of most avian species. Different constraints may operate during the mating season, during gestation, and during offspring rearing for carnivores. Offspring survivorship is much more difficult for adults to predict among carnivores than among avian species because reproductive effort must be committed several months prior to birth. When juvenile survivorship varies annually, and is unpredictable prior to breeding, adults should maximize their own survival and reproduce at a low rate (Hirschfield & Tinkle 1975). The costs of lactation are typically greater than those of pregnancy (Randolph et al. 1977; Fedak & Anderson 1972). If conditions are not favorable for rearing offspring several months after conception, female carnivores may terminate reproduction in order to avoid the cost of lactation and insure their own survival (put a "cost ceiling on reproduction", Goodman 1974).

*Ecological Constraints Model vs. Resource Dispersion Hypothesis.* Emlen's (1982x) ecological constraints model predicts that the frequency of helpers should increase with the severity of environmental constraints; i.e., when conditions are unfavorable it is more risky to disperse, breeding options are limited, and offspring are predicted to remain in their natal territory. Data from many avian species support this prediction (Emlen 1984).

In contrast to Emlen's (1982a) model, Macdonald's (1983) "resource dispersion hypothesis" predicts that a pair of carnivores may tolerate additional group members during years of abundant food resources, but may defend their territory against other group members when food resources are scarce. The size of social

groups in many carnivore species has been shown to increase seasonally with food abundance, e.g., coyotes (Bekoff & Wells 1982; Bowen 1981; Camenzind 1978), Kalahari desert lions (Owens & Owens, pers. comm.), brown hyenas (Owens & Owens 1978), badgers (Kruuk & Parish 1982), stripped hyenas (Macdonald 1978; Kruuk 1976), and golden jackals (Macdonald 1979b). This red fox study indicated that group sizes became smaller when seabirds became less abundant, and the number of reproductive females per group may also be related to food abundance. Thus, data from carnivore studies support Macdonald's (1983) resource dispersion hypothesis, not Emlen's (1982a) ecological constraints model.

Hunting technique and size of prey may influence whether carnivore group members disperse or are forced to remain together during periods of scarce food resources (Harrington et al. 1983). Emlen (1984) suggested that the "obligate nature" of sociality in pack living canids may force them to remain in groups. Macdonald and Moehiman (1982) suggested that the canid species living in smaller groups, i.e., foxes, jackals, and coyotes, may benefit facultatively from helping behavior that is more obligatory among group hunting canids such as wolves, dholes and Cape hunting dogs. Correlations between group size and litter size among canids are not consistent across genera, and indicate that food resources influence the effect that canid helpers have on pup survival. Increased number of helpers in blackbacked and golden jackals (*Canis mesomelas* and *C. aureus*) were associated with significantly greater pup survival through 14 weeks of age (Moehlman 1979), but food resources were apparently plentiful throughout this study. Among coyotes, neither litter size nor the number or percentage of pups that survived to 5-6 months of age were significantly correlated with the number of adults, although there were positive trends (Bekoff & Wells 1982). The correlation between the number of adults in a pack and pup survival in Cape hunting dogs was positive, but not significant (Malcolm and Marten 1982).

When prey became scarce, Cape hunting dog yearlings were given access to prey before pups, and yearlings stole food from pups. Where prey were scarce among wolves, litter size and pack size were inversely correlated Where prey were abundant, wolf pack size and litter size were positively related (Harrington et al. 1983). Thus, when conditions are favorable, all canids may tolerate additional group members which help provision young. As food availability declines, the canids living in smaller groups may disperse (or be evicted by the resident pair), but the pack hunters may remain together and sacrifice pup survival to insure survival of yearlings (Malcolm 1979; Harrington et al. 1983).

The advantages of living in large groups (other than to increase hunting efficiency) have been investigated in some canid species. In silver backed jackals, the feeding rate to pups increased with group size and helpers contributed 18-32% of the observed regurgitations (Moehlman 1983). Coyote helpers did not appear to provide much food to pups. Bekoff & Wells (1982) concluded that coyote helpers resulted in pups being left alone less frequently. When left alone, pups were susceptible to harassment and possible predation by other coyotes. Camenzind (1978) reported that two coyote litters were destroyed, apparently by intruding coyotes from adjacent territories. Similarly, Macdonald (1977b) reported a case of cannibalism on a red fox litter by an adult from an adjacent territory.

*Formation and dispersal* of fox groups. Red fox helping behavior differs from that of other canid species in several ways: 1) all fox helpers are female; among coyotes, jackals, Cape hunting dogs, and wolves, both sexes help; 2) the number of helpers in fox groups rarely exceeds one; multiple helpers are common in other canid groups; 3) the proportion of groups that have helpers appears to be much lower in fox populations than in other canid populations (red foxes: 27%, n=14 (this study); Cape

hunting dogs: 88%, n=17 (Malcolm & Martin 1982); silver backed jackals: 63%, n=19, golden jackals: 75%, n=8 (Moehlman 1979; 1983); wolves: 63%, n=24, 75%, n=12 (Harrington et al. 1983).

Multiple red fox females might occur in reproductive groups when winter food resources are abundant and groups remain intact. More female foxes ovulate when food is abundant (Lindstrom 1982), and males could have the opportunity to mate with an additional female. Bigamy may occasionally occur when females that share a territory are unable to dominate one another and monopolize reproduction. Some females might fail to ovulate or terminate their reproductive effort, and they might help raise another female's pups that occur within their territory. Helping behavior has recently been reinterpreted as "parenting behavior" (from Williams 1966) that can be exhibited by an individual toward another individual's offspring (Jamieson 1986; Price et al. 1983) as occurs in cases of brood parasitism (Payne 1977), after a helper looses it's own offspring (Brown 1978; Brown and Brown 1980; Perrins 1979), and when a strange male helps after experimental removal of the parental male (Weatherhead and Robertson 1980). The mechanism may be a basic stimulus-response interaction that adults exhibit in the presence of vocalizing young (Price et al. 1983; Jamieson 1986; Woolfenden and Fitzpatrick 1984). In one reported case, a female fox which had been pregnant but failed to give birth, subsequently adopted another female's litter when the mother disappeared (von Schantz 1981). However, reproductive or hormonal conditioning is not necessary for adults to exhibit parenting behavior (Eisner 1960). Thus, fox helpers may occur simply because groups remain intact when there is sufficient food, and not all females successfully reproduce. Selection for helping behavior is based on the assumption that there is a cost to helping (Brown 1978; Emlen 1984). If reproducing is not an alternative, then selective pressure against helping may be very weak (Price et al. 1983), and selection for helping may be strong in red foxes

because of den site inheritance. There was no evidence for reduced survival or reduced likelihood to breed as a result of helping in foxes. Price et al. (1983) obtained similar findings for Darwin's finches (*Geospiza scandens*).

When environmental constraints increase so that adult survival becomes threatened during years of low food availability, foxes may: 1) exclude additional group members (including helpers) from their territory, at the risk of lower offspring survival; and 2) eventually forego reproduction and abort or resorb fetuses. Under these conditions, any successfully reproducing foxes would tend to be monogamous with no helpers. Defending a constant territory size and altering group sizes according to food availability may allow foxes to "hedge their bets" (Stearns 1976) and to "track environmental conditions" (Boyce and Daley 1980). After the occurrence of E1 Niño in 1982 (with the simultaneous decrease in prey availability), the number of reproducing females declined and litter sizes became smaller, but the percentage of pups which survived to one year did not change significantly. Lindstrom (1982) suggested that foxes may adjust their litter sizes according to food supply by altering their ovulation rate (number of ova shed per female). The Round Island data suggests that foxes may benefit by reducing reproductive output during periods of declining food availability.

Table V.1

Correlation of Reproductive Success versus Group Size

| | Spearman Rank Correlation | Probability |
|---|---|---|
| Per Reproductive Female | | |
| Litter size | .37 | .13 |
| Pups @ one year | .56 | .03 |
| Per Capita | | |
| Litter size | .24 | .41 |
| Pups @ one year | .525 | .099 |

Table V.2

Litter Size versus Number of Pups at One Year

| | Spearman Rank Correlation | Probability |
|---|---|---|
| Per Group | .80 | .002 |
| Per Capita | .39 | .24 |
| Per Reproductive Female | .66 | .02 |

Table V.3

Stepwise linear regression analysis with number of pups surviving to one year of age as dependent variable.

| | Entry Order | Partial Regression Coefficient | Partial Correlation Coefficient | Increase in $r^2$ |
|---|---|---|---|---|
| Litter size | 1 | .74 | .64 | .41 |
| Group size | 2 | .67 | .58 | .20 |

Table V.4

Reproductive Success and Yearly Variation in Conditions

| | $X^2$ Kruskal Wallis ANOVA | No. of Groups | Probability |
|---|---|---|---|
| Per Group | | | |
| Litter size | 7.9 | 14 | .096 |
| Pups @ one year | 3.4 | 10 | .33 |
| Per Reproductive Female | | | |
| Litter size | 9.8 | 18 | .04 |
| Pups @ one year | 5.1 | 15 | .27 |
| Per Capita | | | |
| Litter size | 7.8 | 14 | .1 |
| Pups @ one year | 1.4 | 10 | .69 |

Table V.5

Ecological conditions promoting different types of cooperative breeding; predictions of two models.

| | Helper-breeder conflict model | | Resource dispersion hypothesis |
|---|---|---|---|
| | Effects of group breeding: | | |
| | Per capita benefit | Per capita detriment | |
| Severe environmental constraints | Helpers | Helpers | Group members (helpers) disperse |
| Weak environmental constraints | Polygyny | Monogamy | Group members (helpers) tolerated |

Fig. V.1. Frequency distribution of breeding group size of red foxes on Round Island, 1980-1984. a, Proportion of individuals living in groups of each size. b, Proportion of groups of each size.

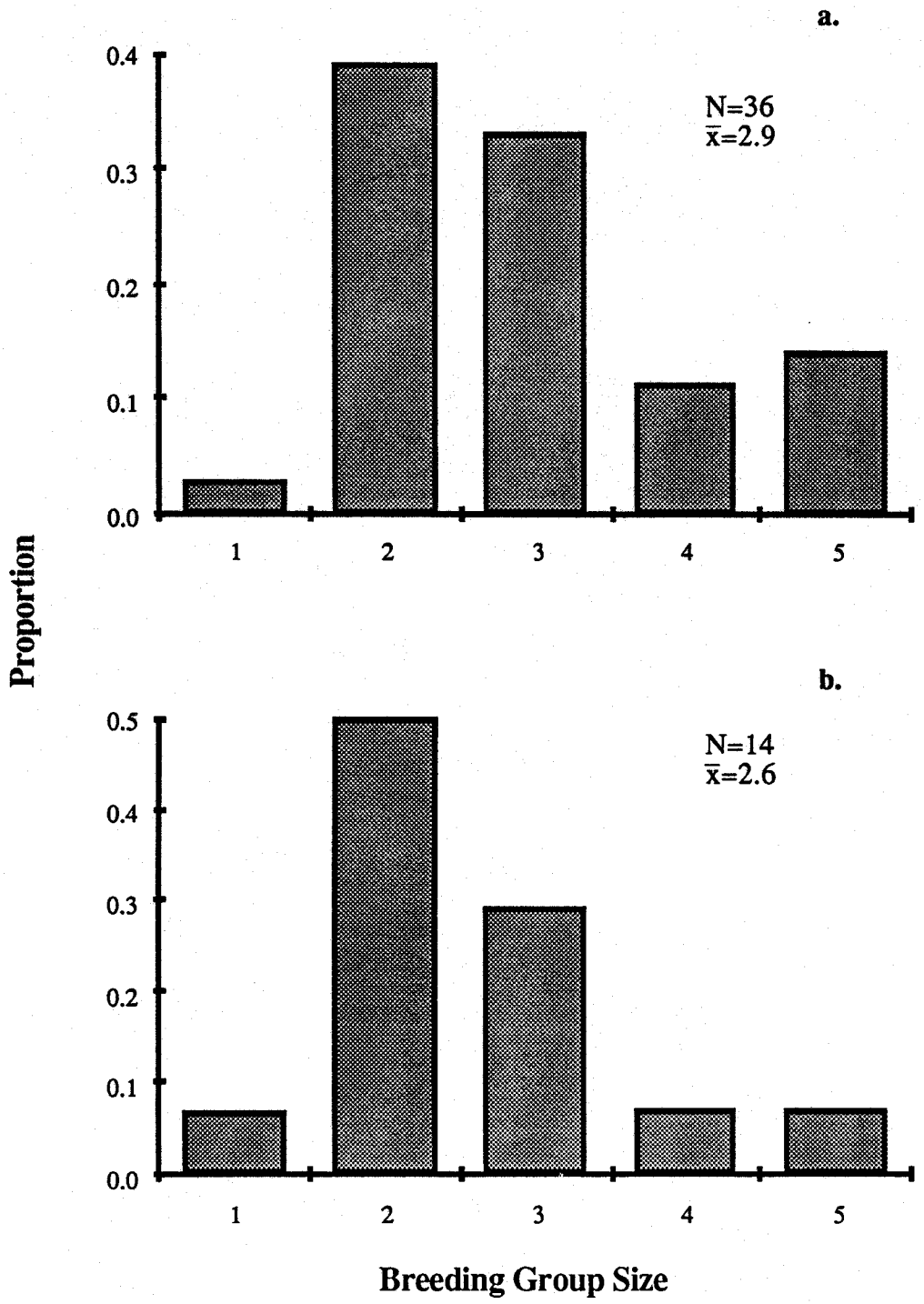


Fig. V.2. The effect of additional group members upon the amount of food brought to each pup. Data include 577 hours of observation taken on eight breeding groups. Feeding rate is calculated as the sum of prey items provided by all adults in each group per pup per hour.

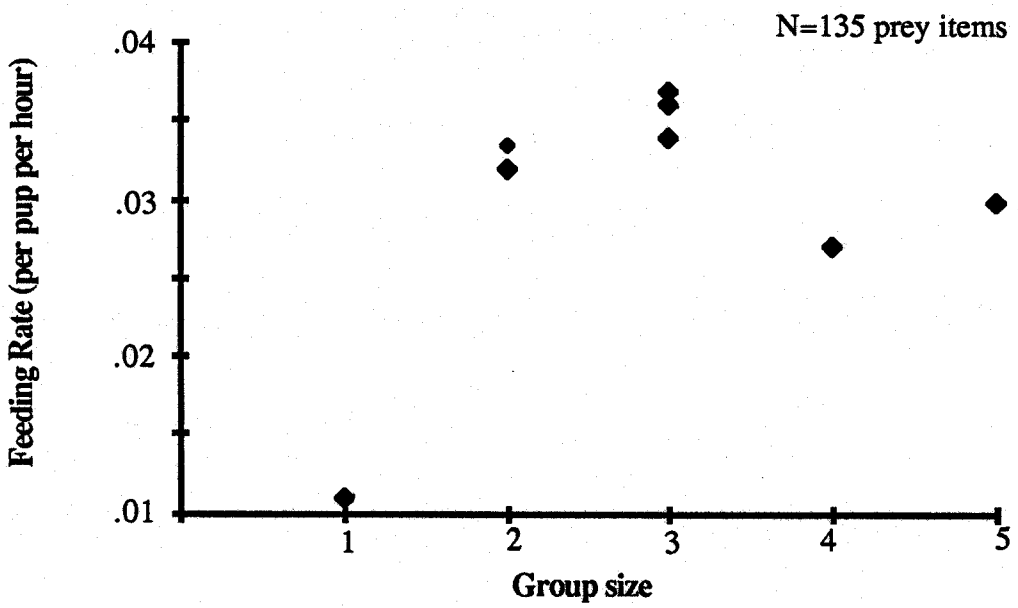


Fig. V.3. The effect of additional littermates upon the amount of food brought to each pup. Data points indicate the contributions of different group members to feeding the pups. Feeding rate is calculated as the number of prey items that were provided per pup per hour.

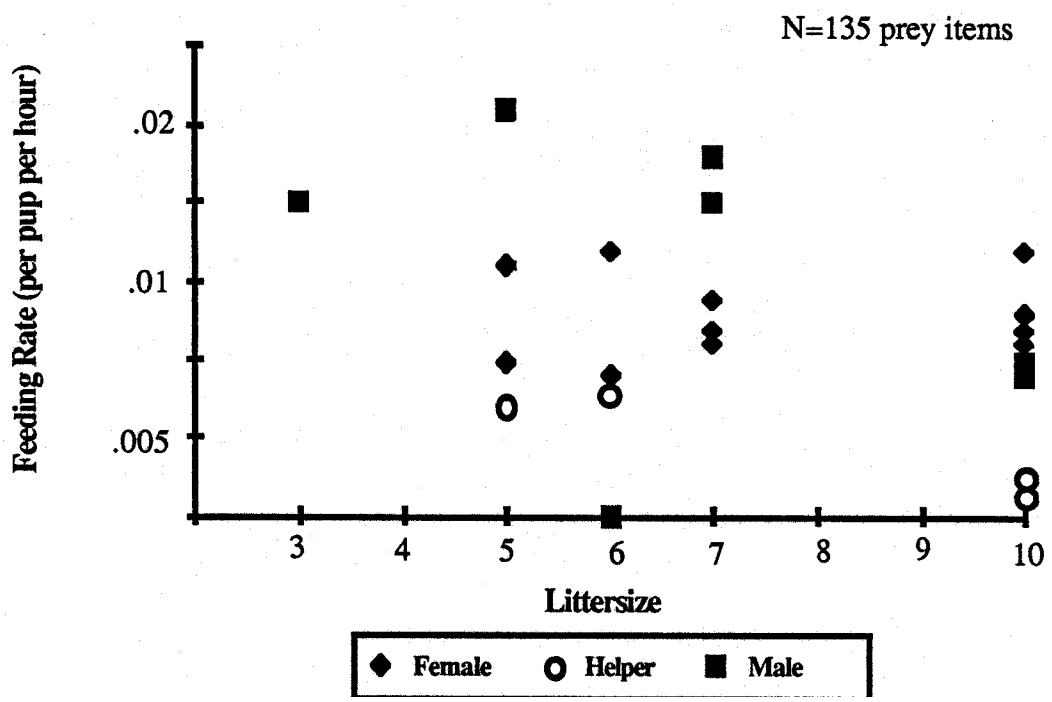


Fig. V.4. The effect of additional group members upon the amount of food each adult delivered to the pups. Data points indicate the contributions of different group members to feeding the pups. Feeding rate is calculated as the number of prey items that were provided per pup per hour.

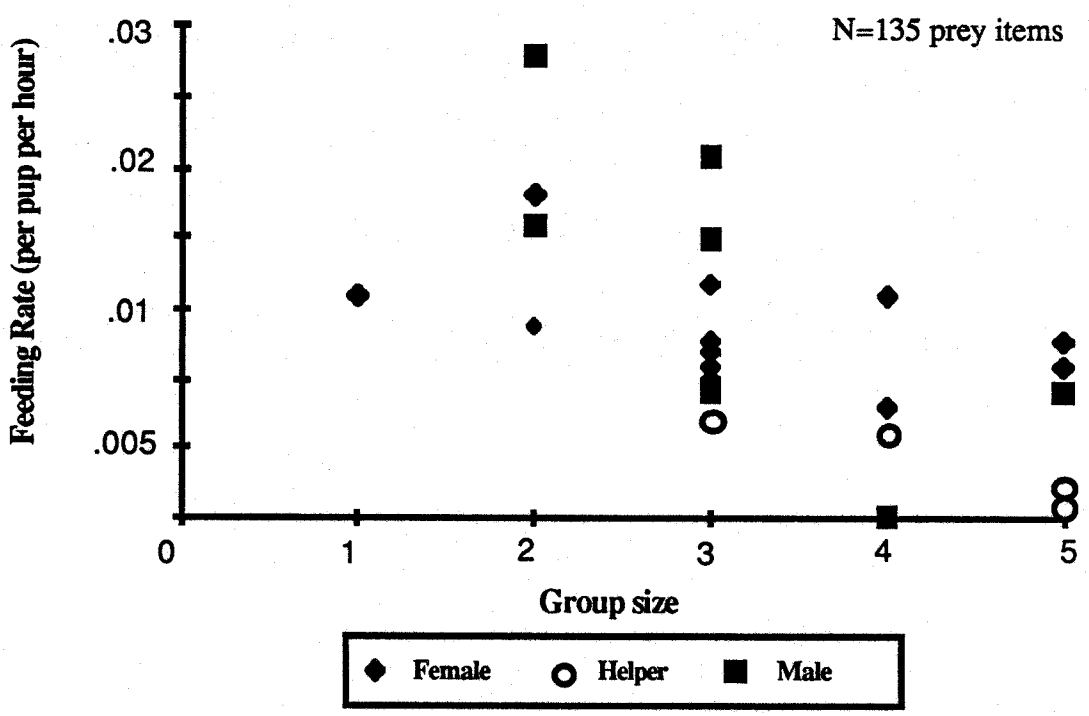
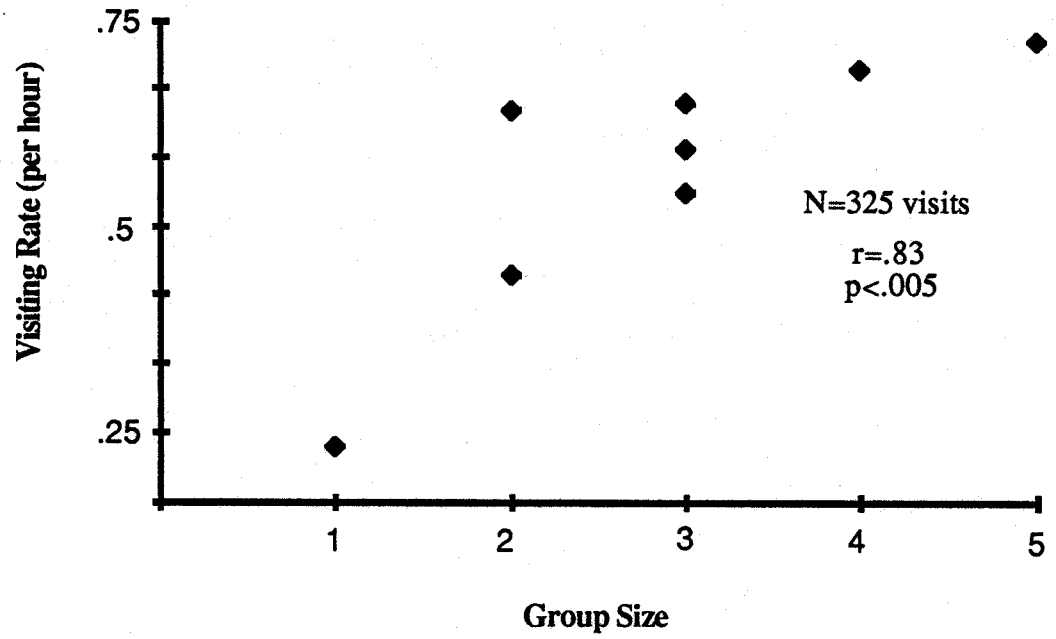


Fig. V.5. The effect of additional group members upon the frequency of visits to each den site. Data include 577 hours of observation taken on eight breeding groups. Visiting rate is calculated as the sum of visits from all adults in each group per hour.



## CHAPTER V, BIBLIOGRAPHY

Bekoff, M. & Wells, M.C. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use and resource defense. *Z. Tierpsychol.* 60:281-305.

Bertram, B.C.R. 1975. Social factors influencing reproduction in wild lions. *J. Zool. Lond.* 177:463-482.

Bygott, J., Bertram, B.C.R., & Hanby, J.P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature* 282:839-841.

Bowen, W.D. 1981. Variation in coyote social organization: the influence of prey size. *Can. J. Zool.* 59:639-652.

Boyce, M.S. and J.J. Daley. 1980. Population tracking of fluctuating environments and natural selection for tracking ability. *Am. Nat.* 115:480-491.

Brown, J.L. 1978. Avian communal breeding systems. *Ann. Rev. Ecol. Syst.* 9:123-155.

Brown, J.L. & Balda, R.P. 1977. The relationship of habitat quality to group size in hall's babbler (*Pomatostomus halli*). *Condor* 79:312-320.

Brown, J.L. & Brown, E.R. 1980. Reciprocal aid-giving in a communal bird. *Z. Tierpsychol.* 53:313-324.

Camenzind, F.J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 in M. Bekoff, ed. Coyotes, Biology. Behavior. and Management. Acad. Press, New York.

Councilman, J.J. 1977. Groups of the grey-crowned babbler in central southern Queensland. *Babbler* 1:14-22.

Eisner, E. 1960. The relationship of hormones to the reproductive behaviour of birds, referring especially to parental behaviour: a review. *Anim. Behav.* 8:155-179.

Emlen, S.T. 1982a. The evolution of helping behavior. I. An ecological constraints model. *Am. Nat.* 119:29-39.

Emlen, S.T. 1982b. The evolution of helping. II. The role of behavioral conflict. *Am. Nat.* 119:40-53.

Emlen, S.T. 1984. Cooperative breeding in birds and mammals. Pages305-339 in J.R. Krebs and N.B. Davies, eds. Behavioral Ecology. an evolutionary approach. Blackwell, Oxford.

Emlen, S. T. & Vehrencamp, S. L. 1983. Cooperative breeding strategies among birds. Pages 93-120 in A. H. Brush and G. A. Clark Jr., eds. Perspectives in Ornithology. Cambridge Univ. Press, Cambridge.

Englund, J. 1970. Some aspects of reproduction and mortality rates in Swedish foxes (*Vulpes vulpes*), 1961-1963 and 1966-1969. *Viltrevy* 8:1-79.

Fedak, M.A. & Anderson, S.S. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *J. Zool. Lond.* 198:473-479.

Goodman, D. 1974. Natural selection and a cost-ceiling on reproductive effort. *Am. Nat.* 113:735-748.

Harrington, F.H., Fritz, S.H. & Mech, D.L. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. *Behav. Ecol. Sociobiol.* 13:19-26.

Hirschfield, M.F. & Tinkle, D.W. 1975. Natural selection and the evolution of reproductive effort. *Proc. Nat. Acad. Sci.* 72:2227-2231.

Jamieson, I.G. 1986. The functional approach to behavior: is it useful? *Am. Nat.* 127:195-208.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.

Jonsingh, A.J.T. 1982. Reproductive and social behavior of the Dhole (*Cuon alpinus*). *J. Zool.* 198:443-463.

Kleiman, D.G. 1977. Monogamy in mammals. *Q. Rev. Biol.* 52:39-68.

Kleiman, D.G. & Malcolm, J. 1981. The evolution of male parental investment in mammals. Pages 347-387 in D.J. Gubernick & P.H. Klopfer, eds. Parental Care in Mammals. Plenum Publ. Corp., New York.

Koenig, W.D. 1978. Ecological and evolutionary aspects of cooperative breeding in Acorn woodpeckers of central coastal California. Ph.D. thesis, University California, Berkeley.

Koenig, W.D. 1981. Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *Am. Nat.* 117:421-443 .

Koenig, W.D. & Pitelka, F.A. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pages 261-280 in R.D. Alexander & D.W. Tinkle, eds. Natural Selection and Social Behavior. Chiron, New York.

Kruuk, H. 1976. Feeding and social behaviour of the stripped hyaena (*Hyaena vulgaris* Desmarest). *E. Afr. Wildl. J.* 14:91-111.

Kruuk, H. & Parish, T. 1982. Factors affecting population density, group size, and territory size of the European badger, *Meles meles. J. Zool. Lond.* 196:31-39.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Layne, J.N. & McKeon, W.H. 1956. Some notes on the development of the red fox fetus. *New York Fish and Game J.* 3:120-128.

Lindstrom, E. 1982. Population ecology of the red fox (*Vulpes vulpes*) in relation to food supply. Ph.D thesis, University of Stockholm.

Macdonald, D.W. 1977a. The behavioural ecology of the red fox, *Vulpes vulpes:* a study of social organisation and resource exploitation. D. Phil. thesis, Oxford.

Macdonald, D.W. 1977b. On food preference in the red fox. *Mammal Rev.* 7:7-23.

Macdonald, D.W. 1978. Observations on the behaviour and ecology of the striped hyaena, *Hyaena hyaena,* in Israel. *Isr. J. Zool.* 27:189-198.

Macdonald, D.W. 1979a. "Helpers" in fox society. *Nature* 282:69-71.

Macdonald, D.W. 1979b. The flexible social system of the golden jackal, *Canis aureus*. *Behav. Ecol. Sociobiol.* 5:17-38.

Macdonald, D.W. 1980. Social factors affecting reproduction by the red fox, *Vulpes vulpes*. Pages 123-175 in E. Zimen, ed. The Red Fox, Symposium on Behavior and Ecology. Biogeographica 18, W. Junk, The Hague, The Netherlands.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature* 301, 379-384.

Macdonald, D.W. & P.D. Moehlman. 1982. Cooperation, altruism, and restraint in the reproduction of carnivores. Pages 433-467 in P.P.G. Bateson & P.H. Klopfer, eds. Perspectives in Ethology. Plenum, New York & London.

Malcolm, J.R. 1979. Social organisation and communal rearing in the African wild dog. Ph.D. thesis, Harvard University.

Malcolm, J.R. & Martin, K. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behav. Ecol. Sociobiol.* 10:1-13.

Moehlman, P.D. 1979. Jackal helpers and pup survival. *Nature* 277:382-383.

Moehlman, P.D. 1983. Socioecology of silverbacked and golden jackals (*Canis mesomelas* and *Canis aureus*). Pages 423-453 in J.G. Eisenberg & D.G. Kleiman, eds. Advances in the Study of Mammalian Behavior. American Society of Mammalogists.

Neal, E.G. 1977. Badgers. Blandford Press, Dorset Englund.

Owens, M.J. & Owens, D.D. 1978. Feeding ecology and it's influence on social organization in Brown hyaenas (*Hyaena brunnea*) of the central Kalahari desert. *E. Afr. Wildl. J.* 16:113-135.

Packer, C. & Pusey, A. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature* 296:740-742.

Payne, R. B. 1977. The ecology of brood parasitism in birds. *Ann. Rev. Ecol. Syst.* 8:1-28.

Perrins, C.M. 1979. British Tits. Collins, London.

Price, T., Millington, S. & Grant, P. 1983. Helping at the nest in Darwin's finches as misdirected parental care. *Auk* 100:192-194.

Rabb, G.B. Woolpy, J.H. & Ginsburg, B.E. 1967. Social relationships in a group of captive wolves. *Am. Zool.* 7:305-311.

Randolph, P.A., Randolph, J.C., Mattingly, K. & Foster, M.M. 1977. Energy costs of reproduction in the cotton rat, *Sigmodon hispidus. Ecol.* 58:31-45.

Rood, J.P. 1974. Banded mongoose males guard young. *Nature* 248:176.

Rood, J.P. 1978. Dwarf mongoose helpers at the den. *Z. Tierpsychol.* 48:277-287.

Rood, J.R. 1980. Mating relationships and breeding suppression in the dwarf mongoose. *Anim. Behav.* 28:143-150.

Rowley, 1. 1978. Communal activities among white-winged choughs, *Corcorax melanorhamphus. Ibis* 120:178-197.

Seal, U.S. Piotka, E.D. Packard, J.M. & Mech, L.D. 1979. Endocrine correlates of reproduction in the wolf: I. Serum progesterone, estradiol and LH during the estrous cycle. *Biol. Reprod.* 21:1057-1066.

Steams, S.C. 1976. Life history tactis: A review of the ideas. *Q. Rev. Biol.* 51:3-47.

van Lawick, H. 1973. Solo. Collins, London.

von Schantz, T. 1981. Female cooperation, male competition, and dispersal in the red fox, *Vulpes vulpes. Oikos* 37:63-68.

Weatherhead, P.J. & Robertson, R.J. 1980. Altruism in the Savanah Sparrow? *Behav. Ecol. Sociobiol.* 6:185-186.

Williams, G.C. 1966. Adaptation and Natural Selection. Princeton Univ. Press, New York.

Woolfenden, G.E. & Fitzpatrick,, J.W. 1984. The Florida Scrub Jay: Demography of a, Cooperative-Breeding Bird. Princeton Univ. Press, New York.

Zimen, E. 1976. On the regulation of pack size in wolves. *Z. Tierpsychol.* 40:300-341.

# CHAPTER VI

# ESTIMATED SEXUAL DIFFERENCES IN REPRODUCTIVE SUCCESS AMONG RED FOXES

## Introduction

Since Darwin's *Descent of Man* (1871), numerous studies have predicted that lifetime reproductive success should be greater among males than among females. Sexual selection theory predicts that male reproductive success should increase with the number of mates obtained, while female reproductive success should not, and male reproductive success should have higher variance than that of females (Fisher 1930; Bateman 1948; Trivers 1972). Trivers (1972) argued that the intensity of intrasexual selection should increase as the ratio between male and female parental investment decreased. However, mathematical analysis supports Bateman's (1948) conclusion that higher variance in male vs female reproductive success is the only important cause of intrasexual selection (Wade 1979).

When parental care is given to offspring after fertilization, the sex which invests less should compete for mates, while the sex that invests more should be selective in accepting mates (Trivers 1972). Female mammals usually invest more in offspring than males due to gestation and lactation. The number of mates a male obtains is determined by his success in competition for females. Competition for mates is reduced in monogamous animals relative to polygamous animals because a male normally pairs with a single female. It has been suggested that differences between the sexes are a consequence of the mating system, i.e., sex differences are associated with polygyny (Darwin 1871; Trivers 1972). Among monogamous species, secondary sexual characters tend to be reduced or absent (Crook 1972; Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Harvey et al. 1978; Alexander et al. 1979). However,

intrasexual selection may still occur in monogamous animals when more males than females are available to breed. Such a situation could result from sex ratios biased toward males (Darwin 1871), or if more males than females were available to mate early in the breeding season (O'Donald 1972).

Reduced male survival is one important consequence of intrasexual selection. A female biased sex ratio may be indicative of reduced male survival. Sex differences in adult mortality rates are usually related to social system. In monogamous birds, there are fewer females, but in polygynous or promiscuous birds, there are fewer males (Mayr 1939). In seven species of pinnipeds, adult male mortality rates are higher than those of females (see Ralls et al. 1980; Johnson 1968); the extent of the difference appears to be related to the degree of polygyny (Stirling 1975). Among cetaceans, in three genera of odontocetes there appear to be increasing mortality rates in males that correspond with an increasing degree of sexual dimorphism, and presumably polygyny (Ralls et al. 1980). Adult mortality rates are equal in monogamous grey foxes and coyotes (Kleiman 1977).

Studies that have compared variance in reproductive success between the sexes within particular breeding seasons have found males to be more variable than females (Howard 1979; Sherman 1976; Payne 1979). Few studies have provided data on reproductive success from individuals within a population that were followed longitudinally through time to test these predictions over the life of individuals (but see Clutton-Brock et al. 1982). Here I present data on differences in reproductive success for males and females of a monogamous species. I present data suggesting there may be differential male mortality in this monogamous species and I will discuss the hypotheses that have been offered for this tendency.

# Results

## Female Reproductive Success

Twenty eight individual female foxes reached breeding age (one year) during the five years of this study. Thirteen females successfully reproduced; and I was able to determine pup survival for eleven of these females (Table VI.1). The cumulative number of pups that survived to one year of age (pup survival) after five breeding seasons varied from zero to six for each of these females. (Two females had litters the last year of the study; thus pup survival was unknown.) Mean pup survival among these eleven females was 2.7 ($s^2_{\bar{x}}$=5.0). The number of pups surviving to four months of age (just prior to dispersal) was calculated for all thirteen successfully reproducing females. A frequency distribution of these values indicates that a range of 0-12 pups were reared per female, with a median value of 5, and a mean of 5.3 ($s^2_{\bar{x}}$ =10.8). These females successfully reared one to three litters, with a median of one litter.

Fifteen of 28 females (54%) failed to produce any litters during the study, and 18 of 26 females (69%) failed to have any pups survive to one year of age (Fig. VI.1). Including non-reproductive females, mean pup survival to one year of age (RS) was 1.2 ($s^2_{\bar{x}}$ =3.7); mean number of pups surviving to four months of age was 2.5 ($s^2_{\bar{x}}$ =12.0).

## Male Reproductive Success

Male foxes shared a territory with a maximum of two reproductive females per year. A male was assumed to have fathered a litter of pups if he delivered food to that litter and visited the den site.

Fourteen of 26 males (54%) failed to produce any litters, and 17 of 23 males (74%) failed to have any pups survive to one year of age (Fig. VI.1). Twelve

males helped rear litters and were therefore assumed to have reproduced; I was able to determine pup survival for nine of these males (Table VI.1). Mean number of pups that survived for these nine males was 3.3 ($s^2_{\bar{x}}$ =7.0), with a range of 0-6. Mean number of pups that survived to four months of age (prior to dispersal) for the twelve successfully reproducing males was 5.75 pups ($s^2_{\bar{x}}$ =13.5), with a range of 1-12. Including data from fourteen non-reproductive males, mean pup survival was 1.3 ($s^2_{\bar{x}}$ =5.1); mean number of pups surviving to four months of age was 2.65 ($s^2_{\bar{x}}$ =14.4).

## Correlations With Reproductive Success

Among females that successfully reared litters, variation in the number of pups that survived to one year was correlated with both the number of litters they produced (which is equivalent to the number of years they reproduced; spearman's r=.89, p<.0002), and with litter size (fecundity; spearman's r=.87, p<.0004). The total number of pups reared to one year for females was best predicted by variation in the number of litters they produced, which accounted for 89% of the variance in reproductive success. For individual females, litter size and pup survival were significantly correlated (Table V.2).

Factors that influenced female fecundity were yearly variations in environmental conditions (Table V.4). Litter sizes were larger during seasons when seabirds, the primary prey item of these foxes, were abundant. During years that the seabirds failed to reproduce (associated with El Niño in the Bering Sea), litter sizes were smaller (Chapter III).

Factors that correlated with pup survival were group size, litter size, and paternal investment. Pup survival was positively and significantly correlated with the number of adult foxes in a reproductive group (Table V.1). The number of pups that

survived to one year of age was also correlated with litter size (Table V.2). One female successfully raised a litter of five pups to four months of age without any male's help. However, she was the only female whose pups all failed to survive to one year (n=11 groups).

For reproducing males, variation in reproductive success was correlated with the number of litters he helped rear (number of females he mated with; spearman's r=.62, .05<p<1). Litter size (fecundity of females with which he mated) was not a significant variable (spearman's r=.59, p<.13); nor was the number of years he reproduced (spearman's r=.46, p<.26).

## Sex Ratios and Mortality Rates

The adult sex ratio was female biased every year during this study (Table VI.2). However, the sex ratio of pups (when they first emerged from the den, at approximately five-six weeks of age) was close to 1:1 every year.

There were no significant sex differences in annual mortality rates among non-breeding foxes (including floaters and non-breeding den-holders; $X^2$=.02, p<.9), or among pups. However, breeding males had significantly higher over winter mortality than any other class of male (excluding pups, $X^2$=3.9, p<.05), or breeding females ($X^2$=3.2, .05<p<.1; Table IV.4). Among breeding males, bigamous males had higher rates of mortality than did monogamous males. Of five monogamous males, three survived and bred for a second season; of four bigamous males, none survived to the following year. These survival data are not significantly different (.15<p<.1, Fisher exact test), but the trend may suggest a real phenomenon

Females which reproduced did not have increased mortality rates over females that did not. There were no significant differences in mortality rates among females that reproduced compared to non-breeding females ($X^2$=.l, p<.8, Table IV.4). Bigamous

females did not have increased mortality rates (1 of 6 died=17%) compared to monogamous females (2 of 5 died=40%, Fisher exact test).

## Parental Care

There were no significant differences in the rates of food deliveries by reproductive females and males (Table IV.3). However, reproductive females visited dens significantly more frequently than males (Table IV.3). In five of eight groups females contributed more of the total feeding effort than did males; and in seven of eight groups reproductive females visited the den more frequently than males.

## Age of First Reproduction

Among thirteen known-age females (that were marked as pups and subsequently survived), only two successfully reproduced during the study. Both mated monogamously; one when three years old, and one when five years old.

Three females which first served as helpers and subsequently reproduced were ear tagged when they were adult helpers. Therefore, these females were at least one year old when they were marked. Two of these females were at least four years old when they mated monogamously, and one of them was at least three years old when she raised a litter unassisted by any male (the "single female").

Among twelve known-age males (using the same criteria), three became successful breeders. One male paired monogamously when he was one year old, and again the following season at two years of age (monogamously with a helper). Two other .males mated monogamously: one at three years, and one at four years of age.

One female was known to be at least five years old (she was an adult in 1980 when she was marked). This female was raising her third litter in 1984 (when the study terminated). No male had survived for longer than three years at the end of the

study, and no male had reproduced during more than two years. These data are consistent with the annual mortality rates indicating females may live longer and thus have more opportunities to reproduce.

Discussion

The differences in reproductive success for males and females were not significant among red fox breeders, nor among the entire population, including non-breeders. The mean number of pups that survived to one year of age for males was 1.3 ($s^2_{\bar{x}}$= 5.1), compared with a mean of 1.2 ($s^2_{\bar{x}}$ =3.7) for females (n.s., Mann Whitney U test). These results would be predicted by sexual selection theory for a monogamous species. Similarly, studies of polygynous species have confirmed the prediction that males are more variable than females in breeding success. In red winged blackbirds (*Agelaius phoeniceus,* Payne 1979), bullfrogs (*Rana catesbeiana,* Howard 1979), ground squirrels (*Spermophilus beldingi,* Sherman 1976), and red deer (*Cervus elaphus,* Clutton Brock et al. 1982), consistent data has been presented for polygynous species that males are more variable than females.

Breeding male red foxes had higher mortality rates than females, and the adult sex ratio was female biased every year of this study. Several factors have been suggested for differential male mortality rates: deleterious alleles on the single X chromosome of males, higher metabolic rates in males (Taber and Dasmann 1954), increased male susceptibility to nutritional stress (Widdowson 1976), greater tendency for males to emigrate (Greenwood 1980), and male-male competition for mates (Huxley 1938). 1 will discuss each of these hypotheses in relation to red foxes.

Trivers (1972) argued effectively against the unguarded X chromosome of males hypothesis because: 1) the distribution of differential mortality by sex is not predicted by a knowledge of which sex is heterogametic; 2) theoretical predictions of

the degree of differential male mortality that is expected due to the single X chromosome are far lower than those observed in many mammals; and 3) castrated human males and domestic cats have higher survival rates than normal individuals.

Taber and Dasmann (1954) suggested that differential male mortality rates of black-tailed deer fawns is caused by a higher metabolic rate than females. However, Moen (1973) reported that the existing data on metabolic rates in wild ruminants do not indicate any differences by sex. In many mammals (humans, rats, pigs, mink, chickens), females are less susceptible to nutritional stress (Widdowson 1976). When undernourished, females have higher survival rates than males, and they regain weight when fed adequately, whereas males do not. Similarly, Clutton-Brock et al. (1985) suggested that in sexually dimorphic species, males grow faster and for longer than females and thus require more food. However, all of these studies refer to the "adolescent growth period". I can reject this hypothesis for foxes because adolescent males do not have higher mortality rates than adolescent females.

Male biased dispersal is the most common pattern in mammals (Greenwood 1980). Emigration exposes males to risks (such as predation, food shortage, and interactions with strange conspecifics) that females avoid by remaining in their natal group. I can reject this explanation for the Round Island population of male foxes because all yearlings of both sexes left their natal territories.

Another explanation for differential male mortality rates is that larger body size and more conspicuous coloration in sexually dimorphic species tends to put males at an energetic disadvantage and draw attention of predators. This explanation does not apply to monomorphic foxes.

Male-male competition is usually associated with polygynous species. According to Trivers (1972), in species with minimal parental investment, sexual selection usually favors male adaptations that lead to high reproductive success at the

cost of male mortality. Triver's theory suggests that in moving toward monogamy, less effort is invested in male-male competition as more of the male's reproductive effort is directed toward parental investment.

Although the foxes were no more than bigamous, I found that bigamous males may have had higher mortality rates than monogamous males. Thus, bigamous males may invest more energy either in mating activities (e.g., defending two females) or in parental care while rearing two litters simultaneously. However, in spite of a survival cost for bigamous males, they still had higher reproductive success in one year than monogamous males had in two years (see Chapter III).

Mortality of breeding males in foxes suggests two hypotheses to account for this sexual difference in a monomorphic, typically monogamous species. 1) Male-male competition may be significant under conditions of high density. The form of male-male competition should be strongly influenced by the distribution in space of breeding females (Trivers 1972). The density of foxes on this island study site was an order of magnitude greater than that reported for mainland populations (Ables 1975). Monogamy tends to correlate with dispersed animals (Kleiman 1977), which would probably result in infrequent male-male competition. Under high density conditions, monogamous species may also compete to mate. 2) Even though the sex ratio was female biased, more males than females may have been ready to breed (O'Donald 1972). The majority of females in the population did not successfully raise litters, and these females may not have been receptive to males.

Female foxes had as much variance in reproductive success as males. Very few females successfully reproduced each year, and many individuals never reproduced during the study. Variance in fitness constrains the intensity of selection that can act on any trait (Arnold and Wade 1984). High variance in female reproductive success in a monomorphic, monogamous canid may provide some insights into the evolution of

reproductive suppression within canids. Red foxes represent one of the least social canids, and the pack hunting canids probably evolved from this primitive state (Kleiman and Eisenberg 1973). If foxes are characterized by a large proportion of non-breeders (and high variance in reproductive success), this may be a primitive trait that was a precursor to sociality. As canids became more social and began living in larger groups that remained together year round, there may have been severe competition for reproduction. If there was high variance among females in breeding success, there would have been great opportunity for selection (Arnold and Wade 1984), and adaptations that enabled females to monopolize reproduction would have spread quickly. There would have been high selective pressure for mechanisms that enabled the dominant animals in a group to monopolize reproduction and exploit other group members' help to insure survival of their litter. Thus, the pack living canids may have evolved complex mechanisms to prevent subordinate females from successfully raising offspring as a result of high variance in female reproductive success.

Table VI. 1

Variation in Reproductive Success

| | Successful Breeders Only | | | |
|---|---|---|---|---|
| | Females | | Males | |
| | Mean | Variance | Mean | Variance |
| Pups @ 4 months | 5.3 | 10.8 | 5.75 | 13.5 |
| Pups @ one year | 2.7 | 5.0 | 3.3 | 7.0 |

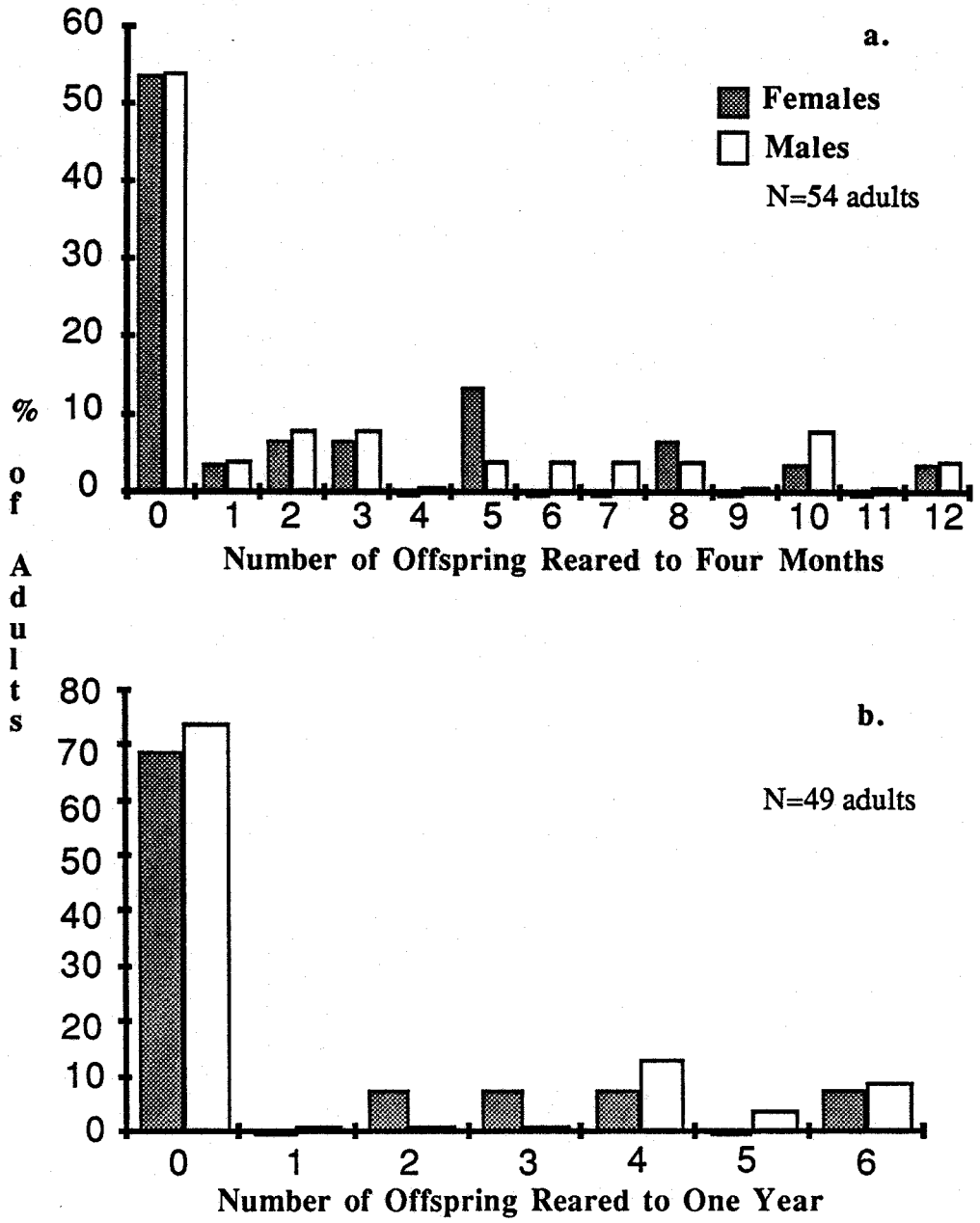
| | Entire Population, Including Non-reproductive Foxes | | | |
|---|---|---|---|---|
| | Females | | Males | |
| | Mean | Variance | Mean | Variance |
| Pups @ 4 months | 2.5 | 12.0 | 2.65 | 14.4 |
| Pups @ one year | 1.2 | 3.7 | 1.3 | 5.1 |

Table VI.2

Sex Ratio

| Year | Adult Males | Adult Females | Unknown | Male Pups | Female Pups | Unknown |
|---|---|---|---|---|---|---|
| 1980 | -- | -- | | 6 (.54) | 5 (.45) | 1 |
| 1981 | 10 (.38) | 16 (.62) | 1 | 10 (.5) | 10 (.5) | 6 |
| 1982 | 11 (.38) | 18 (.62) | 0 | 2 (.4) | 3 (.6) | 0 |
| 1983 | 11 (.39) | 17 (.61) | 0 | 6 (.43) | 8 (.57) | 1 |
| 1984 | 13 (.48) | 14 (.52) | 0 | -- | -- | 6 |

Fig. VI.1. a, Frequency distribution of the total number of pups reared to 4 months of age by adult red foxes on Round Island, 1980-1984. b, Frequency distribution of the total number of pups reared to one year of age by adults.



CHAPTER VI, BIBLIOGRAPHY

Ables, E. D. 1975. Ecology of the red fox in North America. Pages 216-236 in M. W. Fox, ed. The Wild Canids. Van Nostrand Reinhold Co., New York.

Alexander, R. D., J. L. Hoogland, R. D. Howard, M. Noonan, and P. W. Sherman. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. Pages 402-435 in N. A. Chagnon and W. Irons, eds. Evolutionary-Biology and Human Social Behavior: an anthropological perspective. North Scituate, Mass., Duxbury Press.

Arnold, S.J. and Wade, M.J. 1984. On the measurement of natural and sexual selection: theory. *Evol*. 38:709-719.

Bateman, A. J. 1948. Intra-sexual selection in Drosophilia. *Heredity* 2:349-368.

Clutton-Brock, T. H., P. H. Harvey, and B. Rudder. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* 269:797-799.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red Deer: behavior and ecology of two sexes. University of Chicago Press. 378 pp.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131-133.

Crook, J. H. 1972. Sexual selection, dimorphism, and social organisation in the primates. Pages 231-281 in B. Campbell, ed. Sexual Selection and the Descent of Man. 1871-1971. Aldine, Chicago.

Darwin, C. 1871. The Descent of Man, and Selection in Relation to Sex. Vol. 1, 2. Murray, London.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Oxford, Oxford Univ. Press.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Beh*. 28:1140-1162.

Harvey, P. H., M. J. Kavanagh, and T. H. Clutton-Brock. 1978. Sexual dimorphism in primate teeth. *J. Zool*. 186:475-486.

Howard, R. D. 1979. Estimating reproductive success in natural populations. *Am. Nat.*114:221-231.

Huxley, J. S. 1938. Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *Am. Nat.* 72:416-433.

Johnson, A. M. 1968. Annual mortality of territorial male fur seals and its management significance. *J. Wildl. Mgt*. 32:94-99.

Kleiman, D. G. 1977. Monogamy in mammals. *Q. Rev. Biol.* 52:39-68.

Kleiman, D. G. and J. F. Eisenberg. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Beh.* 21:637-659.

Leutenegger, W. and J. T. Kelly. 1977. Relationship of sexual dimorphism in canine size and body size to social behavioral and ecological correlates in anthropoid primates. *Primates* 18:117-136.

Mayr, E. 1939. The sex ratio in wild birds. *Am. Nat.* 73:156-179.

Moen, A. N. 1973. Wildlife Ecology, W. H. Freeman, San Francisco. 458 pp.

ODonald, P. 1972. Sexual selections by variations in fitness at breeding time. *Nature* 237:349-351.

Payne, R. B. 1979. Sexual selection and intersexual differences in variance of breeding success. *Am. Nat*. 114:447-452.

Rails, K., R.L. Brownell, Jr., and J. Ballou. 1980. Differential mortality by sex and age in mammals, with specific reference to the sperm whale. *Rep. Int. Whal. Comm.* (Special Issue 2).

Sherman, P. W. 1976. Natural selection among some group-living organisms. Ph.D. thesis, University of Michigan.

Stirling, I. 1975. Factors affecting the evolution of social behavior in the Pinnipedia. Pages 205-212 in K. Ronald and A. W. Mansfield. Biology of the Seal. Proceedings of a Symposium held in Guelph 14-17 August, 1972. Rapp. P-V. Reun. Cons. Int. Explor. Mer.

Taber, R. D. and R. F. Dasmann. 1954. A sex difference in mortality in young Columbian black-tailed deer. *J. Wildl. Mgmt*.18:309-315.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbell, ed. Sexual Selection and the Descent of Man. 1871-1971. Aldine, Chicago.

Wade, M. J. 1979. Sexual selection and variance in reproductive success. *Am. Nat.* 114:742-746.

Widdowson, E. 1976. The response of the sexes to nutritional stress. *Proc. Nutr. Soc.* 35:175-180.

# APPENDIX I

## DATES FOXES WERE IMMOBILIZED AND MARKED

| Date | Number of Foxes Ear-tagged |
|---|---|
| 1981 | |
| May 22 | 1 |
| May 24 | 2 |
| May 28 | 1 |
| May 30 | 1 |
| May 31 | 2 |
| June 3 | 1 |
| June 4 | 2 |
| June 6 | 1 |
| June 12 | 2 |
| June 17 | 1 |
| June 23 | 2 |
| July 8 | 1 |
| July 11 | 1 |
| Subtotal | 18 |
| 1982 | |
| May 20 | 1 |
| May 22 | 1 |
| May 28 | 1 |
| June 23 | 1 |
| September 14 | 1 |
| Subtotal | 5 |
| 1983 | |
| May 23 | 2 |
| May 26 | 1 |
| August 24 | 1 |
| Subtotal | 4 |

# APPENDIX II

## DATES IN TIE FIELD

Inclusive dates spent on the study site.

May 14, 1980 - September 21, 1980

April 29, 1981- September 6, 1981

May 5, 1982 - September 17, 1982

May 13, 1983 - August 31, 1983

July 4, 1984 - September 6, 1984 *

* Judy Sherbourne kindly collected tag resight data from May 22 - July 3 in 1984.