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Shift in red fox, *Vulpes vulpes,* mating system associated with El Niño in the Bering Sea

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Abstract. Fifteen reproductive groups of red foxes were observed on Round Island, Alaska during five field seasons. Polygyny occurred among these foxes, correlated with abundant food resources. The predictions of the polygyny threshold model were supported, i.e. polygynous 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 the foxes), corresponding with the occurrence of El Niño in the Bering Sea. This change in food resources apparently caused red foxes to switch their diet from the most abundant to rarer prey species, and caused a shift from facultative polygyny to monogamy within this population.

The polygyny threshold model was first developed to expain 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 the benefits which include 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; Carey & Nolan 1975; Wittenberg 1976; Pleszczynska 1978).

Although monogamy is the predominant mating system among birds, it is rare among mammals, occurring in fewer than 3% of the species that have been studied (Kleiman 1977). Many canids, however, have been classified as `obligate monogamists' because the male's help is essential for capturing and delivering prey to a lactating female and her pups (Kleiman 1977). The time and energy a male expends in feeding one female's offspring will decrease the time and energy he can devote to a second female's offspring. Therefore, a male's help may be `depreciable' or non-shareable (Kleiman & Malcolm 1981). However, the mating systems of most wild canids are poorly known due to their typically secretive or nocturnal behaviour (Harrington et al., 1982).

The occurrence of El Niño (Wyrtki 1979; Cane 1983; Rasmusson & Wallace 1983) in the Bering Sea (Niebauer 1985) during 1982-1984 and the corresponding nesting failure of seabirds (Hatch 1987; L. Craighead & J. Oppenheim, unpublished data; D. L. Nysewander & J. L. Trapp, unpublished data; S. R. Johnson & J. S. Baker, unpublished data) provided a unique opportunity to document the effect of changing food resources on red fox reproductive groups and to test some of the predictions of the polygyny threshold model for a canid species. We 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.

METHODS

We observed reproductive groups of red foxes on Round Island, Alaska, U.S.A. (56°02'N 160°50'W), 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 the island are linked to the high production of coastal marine environments. However, this island study site provided a unique opportunity to monitor an entire population of approximately 30 adult foxes which were diurnally active, individually ear tagged and had no fear of human observers. Thus, it was

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possible to observe individuals directly through multiple pup-rearing seasons and to estimate the amount of parental care provided by all members of family groups.

Capture and Identification

Individually recognizable collars were put on foxes in 1980. This was done by threading the female portion of a Roto tag through a 0·25-inch (0·6 cm) wide nylon cable tie. The cable ties were then placed along the fox trails like snares. Fifteen collars were put on foxes using this method.

Beginning in 1981, individual foxes were marked with colour-coded ear tags. Twenty-seven adults were immobilized by firing darts from a Palmer Cap Chur pistol. Drug dosages were 1·5 ml Ketamine: Acepromzine in a ratio of 7:3. We sexed and weighed immobilized foxes and put a Roto-tag in each ear. The ear pinnae were punctured with a leather punch before the tagging.

Fifty pups were snared before they dispersed from their dens. Snares were made from 0·06-inch (0·15 cm) cable and were hung directly above each den (approximately 7·5 m) from an overhead line. The overhead line was elevated above the ground by tying the ends onto rock outcroppings (if available) or on to poles that were staked out away from the den. The snares were lowered to the ground by slackening one end of the overhead line when untagged pups came out of den holes. As pups ran through the den area 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 we were able to run into the den area and capture them.

Upon capture, pups were put into a nylon sack. They were sexed, weighed and ear tagged. Ear tags (Nasco sheep tags) were cut in half lengthwise so they did not extend beyond the tip of pup's ears. Pups were released within 5 min of capture.

Tag loss appeared to be very low. Of 27 ear-tagged adult foxes, we later observed only one fox with a single tag. (We were able to identify him by his second tag.) No pup lost a tag before 4 months of age (prior to dispersal); one pup lost a tag over the winter but she was identifiable by her second tag. We resighted all marked foxes at least once each season after they were ear tagged.

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

Observations

During each field season, we determined which dens were being used 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), we classified them as belonging to a reproductive group. After the active dens were identified, we observed the behaviour of foxes associated with the dens for a total of 858 h during the study. Observations were made during late afternoon and evening hours (1400-2000 hours, except during storms) from distances of 10-30 m. Individuals varied in the distance we could approach without altering their behaviour and we always adjusted our distances to the individuals we were watching.

We distinguished between reproductive females and female helpers in the following way: females that nursed pups were classified as reproductive. Females that did not nurse, but visited den sites regularly, delivered food and played with pups were classified as helpers. No nipples were visible on helpers when we 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

RESULTS

Nesting seabirds were the primary food source during summer months when the foxes were rearing young. Seabirds began arriving and nesting on the vertical rock cliffs in April. Nesting adults and chicks were both preyed upon and scavenged from the beaches during April-August, and reproductive foxes delivered the birds to their pups. During this period, adult foxes cached numerous seabird eggs in the tundra (primarily the largest eggs available, common murre, *Uria aalge*), but they

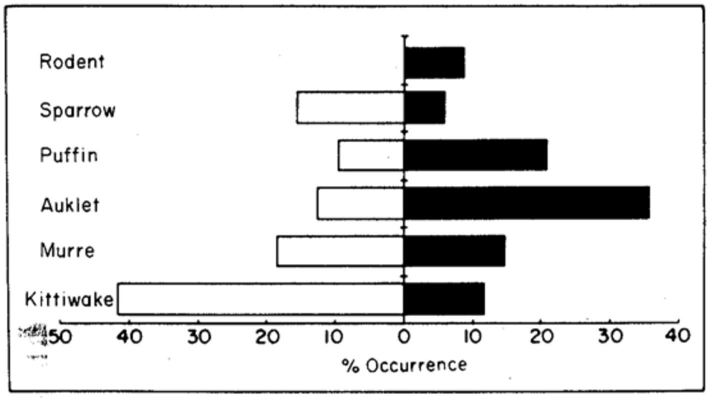

Figure 1. Seabird species that adults delivered to pups prior to and after the onset of ENSO conditions; $\chi^2=14{\cdot}7$, $P<0{\cdot}05$. □, 1980-1981 (N=31); ■, 1982-1984 (N=33).

rarely delivered eggs to their pups. By early Autumn (September), nestlings had fledged and seabirds abandoned their nests, so they were no longer available as prey for foxes. Our field observations were terminated in early fall each year, so we have no data on what the foxes ate during the harsh winter months. Presumably, they depended on their cached eggs, red back voles, *Clethrionomys rutilus,* that were abundant on the island, and walrus, *Odobenus rosmarus*, carcasses that were frequently washed onto the beaches.

Shift in Abundance of Food Resources

In 1977 approximately 142 000 seabirds successfully nested on the rock cliffs at Round Island (P. Arneson, unpublished data). The abundance of each species was approximately: 93 000 common murres; 43 000 black legged kittiwakes, *Rissa tridactyla*; 2000 pelagic cormorants, *Phalacrocorax pelagicus*; 1750 horned puffins) *Fratercula corniculata*; 1500 parakeet auklets, *Cyclorrhynchus psittacula*; 400 tufted puffins , *Fratercula cirrhata*; and 400 pigeon guillemots, *Cepphus columba*. This condition remained roughly unchanged through 1981 (C.J.Z., personal observation).

Beginning in 1982, kittiwakes and murres did not nest at Round Island and neither eggs nor chicks were evident from 1982 to 1984, although large numbers of adults were present. Red foxes switched the seabird species they delivered to pups when black legged kittiwakes and common murres failed to nest at Round Island (Fig. 1). During 1980-1981, reproductive foxes delivered primarily black legged kittiwakes (*N*=13 kittiwakes, 42% of the total deliveries) and common murres (*N*=6, 19%) to their pups. Following the kittiwake and murre nesting failure in 1982, parakeet auklets became the most frequently delivered food item to pups (*N*=12 auklets, 36% of the total deliveries), followed by horned and tufted puffins (*N*=7, 21%). Although the species of prey changed, the proportion of adults and chicks that were delivered to pups was similar between these two periods (50% adults and 44% chicks 1980-1981, *N*=36; 37% adults and 51% chicks 1982-1984, *N*=38).

Population Parameters

The total number of red foxes on Round Island (area= 3 km^2) was estimated to be 27-30 adults from 1980 to 1984 (Table 1). (These were the total number of marked individuals, and thus were minimum population estimates. However, unmarked foxes were seen only on nine occasions from 1982 to 1984.) The density of foxes on this island was about an order of magnitude greater than that reported for mainland populations (Ables 1975).

The proportion of reproductive adults within the population was very low (varying from 6 to 40% among years). An equal proportion of the male and female population did not breed; but in absolute numbers, there were more non-breeding females each year (Table I). Among non-breeders (> 1 year of age), 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
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Table I. Population structure: categories of non-breeders

	1980 (*N*=30)	1981 (*N*=28)	1982 (*N*=30)	1983 (*N*=28)	1984 (*N*=27)
Non-breeding den holders	1 pair (2)*	1 pair (2)	4 pairs (8)	3 pairs (6)	1 pair (2)
Floaters	63%(19)	43% (12)	63% (19)	57% (16)	63% (17)
Total non-breeding:					
Females		60% (10)	94% (17)	82% (14)	79% (11)
Males		60% (6)	91% (10)	82% (9)	77% (10)

N= total island population.
*No. in parenthesis is no. of individuals represented by that category.

any reproductive group or den site, but resided in small areas through which breeders regularly travelled.

Individual males and females appeared to restrict their movements to localized areas that they consistently scent marked. However, there was much overlap in areas used by floaters and by foxes from adjacent reproductive groups. Agonistic behaviour including fighting was observed, but because these areas were not exclusively occupied by individuals or even reproductive groups, the concept of home range (Burt 1943; Jewell 1966) rather than territory (Pitelka 1959) may be more appropriate.

Reproductive Groups

Fox pups were reared in six different den sites during the study, although the maximum number of active dens in any given year was five. Pups were first observed emerging from their dens in early June-early July during different years. Assuming 52 days gestation and 4-5 weeks lactation in the den before pups emerged (Macdonald 1980), courtship and mating must have occurred during February-March and pups were probably born in early-late May. Dispersal of juveniles began in early September, when adults delivered food to them infrequently and the young were seen making excursions further away from their dens. All of the marked juveniles in this study dispersed from their natal dens.

Fifteen reproductive groups were observed during the five-season study. Fourteen of the 15 observed groups had one male that delivered seabirds to the females and pups; one female raised a litter unassisted (the 'single female'). Five groups (33%) had two reproductive, nursing females (polygynous groups). The remaining nine groups (60%) had a single nursing female paired with a male (monogamous groups).

There are alternate explanations for the occurrence of two nursing females that may be unrelated to polygyny. For example, two females may have given birth, but one of them may have lost her litter (before or after birth), and she may have had induced lactation. The following evidence indicates that polygyny did occur: in three of five groups, we observed two females at separate dens approximately 0·2 km apart, each nursing pups. In two groups, the male foxes each delivered seabirds to two females in separate dens. (Helpers were never observed delivering birds to lactating females.) In both cases, the litter from the smaller den was subsequently moved to a larger communal den. We did not observe the adults move the litters, but in all cases the number of pups at each communal den totalled what had been observed at the two separate dens. In one group, a pup was tagged before it was moved to the communal den. In two groups, pups were visibly different in size, indicating one litter may have been younger. After pups were combined, we were unable to determine whether polygynous females nursed only their own pups, or indiscriminately nursed both litters.

Shift in Mating System

During 1980 and 1981, prior to the occurrence of El Niño and the seabird nesting failure, the majority of fox reproductive groups were polygynous (five of seven). Three of the seven groups (two polygynous, one monogamous) had a non-lactating female helper. The modal reproductive group size during 1980 and 1981 was three (range= 2-5) adult foxes. From 1982 to 1984, after the occur-

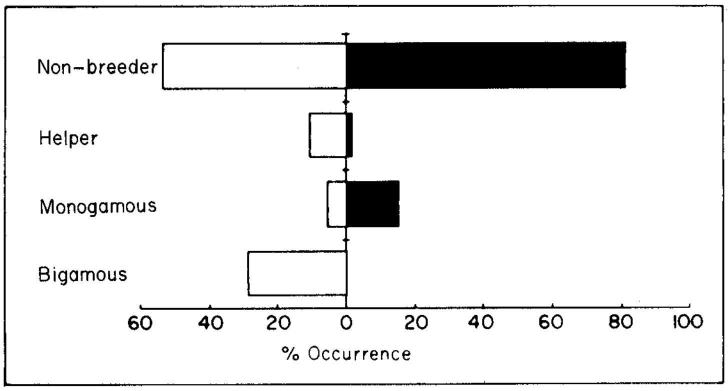

Figure 2. Annual reproductive status of adult females prior to and after the onset of ENSO conditions; $\chi^2= 18·3$, $P<0·005$. □, 1980-1981 (N=35); ■, 1982-1984 (N=50).

rence of El Niño, all pup-rearing groups (N= 8) were monogamous (Fig. 2). Only one of these groups had a female helper. The modal group size for this 3-year period was two adults (range =1·3). Reproductive group sizes were significantly different pre- and post-El Niño (Mann-Whitney *U*-test, $P<0·01$).

Prior to the reproductive failure of seabirds, polygynous females successfully reared as many or more pups as monogamous females, as predicted by the polygyny threshold model. (Polygynous and monogamous females cannot be compared after the seabird nesting failure because all females were monogamous.) We calculated reproductive success as the number of pups that survived to 1 year of age for groups that raised pups during 1980-1981. Eight polygynous females had a mean (±SE) of 2·2±0·27 pups/female survive to 1 year of age and two monogamous females had a mean (±SE) of 1·6±0·1 pups survive (NS, Mann-Whitney *U*-test). Thus, polygynous females had 1·4 times the reproductive success of monogamous females. Litter sizes of polygynous females were also somewhat larger ($\bar{X}$±SE =4·3±0·29, N=43 pups), although not significantly different from monogamous females ($\bar{X}$±SE=4·0±1·0, N=8 pups, Mann-Whitney *U*-test). Thus polygynous females 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. Polygynous males had a mean (±SE) litter size of 8·6±0·87, and a mean (±SE) of 4·4±0·84 pups surviving to 1 year of age; monogamous males had a mean (±SE) litter size of 4·0±1·0 ($P<0·05$, Mann-Whitney *U*-test) and a mean (±SE) of 1·6±0·1 pups survive ($0·1 < P < 0·05$, Mann-Whitney *U*-test).

A shift in the breeding status of six individual females that 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 polygynous female became monogamous; two other polygynous 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).

The Single Female

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 1 year (N=11 groups). Other foxes were frequently observed trespassing near this female's den. We 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 5 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 occassions male foxes remained at her den after she interacted aggressively with them. Her pups were observed being harassed by these males on two occasions.

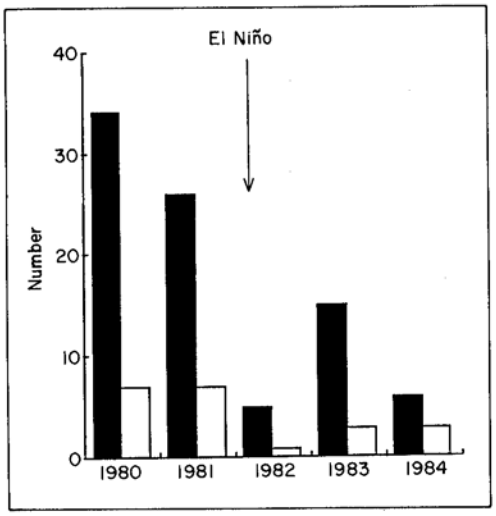

Figure 3. Total number of fox litters and pups on Round Island, Alaska each year. ■, number of pups; □, number of litters.

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 h that her pups received was less than half the number received per pup in all other groups (0·01/pup versus 0·03/pup, *N*=8 groups).

Decline in Productivity

In addition to the shift from polygyny to monogamy, fox productivity declined when seabird productivity declined. The proportion of non-breeding female foxes increased, and the number of litters (and pups) that were reared decreased (Fig. 3). Minimally, seven litters per year were reared in 1980-1981; only one, three and four litters were reared during 1982, 1983 and 1984, respectively. Mean (±SE) fox litter size was also significantly different: 4·25±0·27 in 1980-1981 and 3·5±0·71 in 1982-1984 ($P < 0{\cdot}01$, 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; $\chi^2 = 9{\cdot}5$, $P < 0{\cdot}005$).

DISCUSSION

In 1982, when the nesting failure of kittiwakes and murres began on Round Island, 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 with climatic effects in the arctic (Niebauer 1985). Niebauer (1985) found a significant relationship between El Niño and rising sea and air temperatures in the Bering Sea by correlating a 30-year time series analysis of atmospheric and oceanic parameters of the eastern Bering Sea to an index of ENSO activity in the south Pacific. The Aleutian 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).

The reproductive failure of Alaskan seabirds apparently caused a change in the diet of red foxes from the larger, most abundant prey, to smaller, less abundant prey, and caused the foxes to breed monogamously. Prior to the nesting failure, auklets and puffins (weighing 318 and 699 g on average, respectively; Dunning 1984) had comprised only 2·6 % of the total seabird population on Round Island, while kittiwakes and murres (weighing 407 and 993 g on average, respectively; Dunning 1984) comprised 95%. Kittiwakes and murres, nesting in colonies on exposed rock cliffs, may have been more vulnerable to fox predation when they were sitting on eggs and rearing young. Auklets and puffins on Round Island nested in rock crevasses and scree slopes. Thus, when the more abundant, larger, colonial species failed to nest, the diet of foxes switched to the less abundant, smaller species. Prior to the seabird nesting failure, five of seven fox groups had two lactating females indicating that polygyny in red foxes was correlated with food abundance. The predictions of the polygyny threshold model were supported, i.e. polygynous females had equal or better reproductive success than monogamous females. However, major climatic and oceanographic shifts, which resulted in seabird reproductive failure, apparently caused a shift from polygyny to monogamy in the red fox. A similar case of change of food availability was correlated with mating system shift in another red fox study. When the prey population of rabbits, *Oryctolagus cuniculus,* doubled, more than one red fox female per group bred in two of 10 dens in Sweden (von Schantz 1984).

Red fox group sizes on Round Island became smaller when seabirds became less abundant. The size of social groups in many carnivore species has been shown to increase seasonally with food abundance, e.g. coyotes, *Canis latrans* (Camenzind 1978; Bowen 1981; Bekoff & Wells 1982); wolves, *C. lupus* (Harrington et al. 1983); golden jackals, *C. aureus* (Macdonald 1979); brown hyenas, *Hyaena brunnea* (Owens & Owens 1978); and stripped hyenas, *H. hyaena* (Kruuk 1976; Macdonald 1978). These data support the predictions of the resource dispersion hypothesis (Macdonald 1983; Carr & Macdonald 1986) that a pair of carnivores may tolerate additional group members when there is abundant food resources, but may defend their territory against other group members when food resources are scarce. Similarly, it was proposed that during periods of low prey availability, yearlings and female wolves (subordinate pack members) had a greater tendency to dissociate themselves from packs and make more extraterritorial movements (Messier 1985). Data from our red fox study indicated that not only did group sizes become smaller when seabirds became less abundant, but the number of reproductive females per group also declined.

Food availability has also been correlated with productivity in other canid populations (Switzenberg 1950; Schofield 1958). Smaller litter sizes and/or fewer breeding females, and more unoccupied dens were found for red foxes during years of low vole abundance compared to vole peaks (Englund 1970; Kolb & Hewson 1980; Lindstrom 1982). By supplying food in an area of low vole abundance, the number of red fox litters became higher than expected from previous lows and from placental scar counts of nearby females (Lindstrom 1982). In von Schantz's (1984) red fox study, litter sizes were significantly smaller after the rabbit decline, although the number of litters did not change. 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).

Among carnivores, mating and progeny rearing are seasonally separated by as much as 2-3 months. Different constraints may operate during the mating season, during gestation, and during offspring rearing. When environmental constraints increase 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. By defending a constant territory size and altering group sizes according to food availability (Macdonald 1983; Carr & Macdonald 1986), any successfully reproducing foxes would tend to be monogamous with no helpers when environmental conditions were poor.

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. The area covered by the island fox, *Urocyon littoralis,* male was found to be three times greater during the winter when courtship and mating occur, while the home range of females remained the same (Fausett 1982). The movement patterns of both sexes suggested that island fox males were competing for various females by increased travelling, marking, and vocalizations, with limited aggression. There appear to be similarities between the island fox and Round Island red foxes during spring-fall: both species (living on islands) lack territories, have overlapping home ranges, and there are many non-breeding individuals (Laughrin 1977; Fausett 1982). Male red foxes on Round Island may behave similarly to island foxes during breeding, who have been seen in courtship behaviour with up to three different females, and successful males could mate with multiple females who cycled asynchronously.

Following mating, environmental conditions may determine how many carnivore females successfully give birth and how many abort or resorb fetuses. Offspring survivorship is difficult for adults to predict at the time of mating because reproductive effort must be committed several months prior to birth. The costs of lactation are typically greater than those of pregnancy (Randolph et al. 1977; Fedak & Anderson 1982). If conditions are not favourable for rearing offspring several months after conception, female carnivores may terminate reproduction in order to avoid the cost of lactation and ensure their own survival (see Goodman 1974). Forty-five per cent of female foxes on Round Island that had den sites did not successfully raise pups ('non-breeding den holders'). Apparently a high proportion of female foxes have reproductive failure; prenatal loss (ova that did not implant, lost embryos and resorbed fetuses) in other red fox populations were estimated to be 12-36% (Layne & McKeon 1956; Englund 1970). Foxes may adjust their litter sizes according to food supply by altering their ovulation rate (number of ova shed per female; Lindstrom 1982). After the occurrence of El 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 that survived to 1 year was similar (50% pup survival before El Niño, *N*=32; 43% pup survival after El Niño, *N*=21).

After birth, dominant canid females often monopolize reproduction by interfering with pup care of subordinate females (e.g. African wild dogs, *Lycaon pictus,* Frame et al. 1979; Malcolm 1979; captive red foxes, Macdonald 1980); or by killing the pups of subordinate females (e.g. African wild dogs, van Lawick 1973; captive dingoes, *Canis dingo,* cited by Macdonald & Moehlman 1982), and this may occur among Round Island females. When food resources are plentiful, a canid male's help may be less critical to reproductive females and/or female-female competition may be reduced and therefore more than one litter may successfully be reared in a group. Many non-breeding females may have mated as subordinate polygynous females, but only when there is ample food resources will the polygyny threshold be realized.

The poor pup survival by the single female fox can be interpreted in several ways. Her pups received infrequent food deliveries and were subject to more harassment and trespassing by other foxes than any other pups. These observations suggest that it is difficult for a female fox to rear pups successfully unassisted. Another interpretation is that male help was critical during this period when food resources were scarce, after the occurrence of El Niño conditions.

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 polygynously. It is unclear whether the behaviour 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 polygyny when food resources were abundant.

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