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DIFFERENTIAL INVESTMENT IN MATING BY RED FOXES

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I measured physical condition, body mass, age, and mass of gut contents for 330 red foxes, *Vulpes vulpes*, in an area of central Italy. Females were fatter than males ($P < 0.001$), and they were fatter in the southern part of the study area than in the northern part ($P < 0.001$). Males had the same fat level across the study area ($P > 0.887$). Large males ate less ($P = 0.069$) during mating season, and their condition deteriorated immediately afterwards ($P < 0.001$). Small males maintained their body fat during the breeding season ($P = 0.467$), even though superficial fat decreased slightly ($P = 0.069$). Adult males maintained body condition for longer periods and recovered more rapidly than yearlings. Neither mass of gut contents nor body-fat indices varied in the same periods for females ($P > 0.125$). This pattern of differential inter- and intrasexual investment in mating suggested alternative mating strategies in males. Large males may have spent less time hunting and more time searching for multiple mates and fighting with other males; small males may have saved energy guarding their mates and may not have attempted to mate with additional females. These findings suggest that not all red foxes are monogamous.

Key words: *Vulpes vulpes*, red fox, mating system, alternative strategies, body fat, body size

Differential reproductive success among individuals and random mutation are the core of evolutionary processes (e.g., Clutton-Brock, 1988). To maximize their mating success, individuals in a population may use alternative mating strategies. Different strategies may be favored in different environments, exist as mixed evolutionary stable strategies, or may be conditional on competitive ability (which in turn is determined by body size, strength, and experience—Krebs and Davies, 1981). As a result, body mass and age may determine different investment strategies for individuals.

In polygynous species, variance in lifetime reproductive success (and therefore investment in mating) is greater for males than females, and individuals with higher reproductive potential (e.g., larger males) gain more from a higher investment in mating (Clutton-Brock, 1988; Trivers, 1972). In monogamous species, both variance and investment are assumed to be more even between sexes. Analysis of differential in-

vestment in mating both between and within sexes may help in understanding the mating system of a species.

Red foxes, *Vulpes vulpes*, have been described as a monogamous species in earlier studies (Cavallini, 1996c), but results of recent studies suggest the presence of polygyny. Males may overlap home ranges of two females (Pouille et al., 1994); males move more widely immediately after the peak of mating season, apparently searching for additional mating (Cavallini, 1996b); and physical injuries among males (Duff and Hunt, 1995; White and Harris, 1994) peak during the mating season.

My objective was to quantify influence of sex, body mass, age and local variation on dynamics of fat reserves in a population of red foxes during the mating season. I hypothesized that, if monogamous, males and females should have similar patterns of fat depletion, but if facultatively polygynous, males should invest more heavily in mating; this would result in lower fat levels for

males (but not for females) during the mating season or immediately afterwards. If alternative mating strategies are present in the population, this would lead to large males (with better chances in competition) investing more heavily in reproduction than small ones; fat levels should therefore be more constant in small than in large males.

MATERIALS AND METHODS

The climate of the study region was Mediterranean, with mild winters and dry hot summers. Based on overall similarity among smaller administrative units (communes), the 2,448 km² study area was subdivided in four sections (in north to south order): 1) a coastal belt (50,054 ha) that was flat with a very high human population (>400 persons/km²), sparse woodlands (20 % of total area), and large cultivated areas (>50 %); 2) internal valleys (71,285 ha) that were mostly flat with a high human population (>200/km²), sparse woodlands (22%), and large cultivated areas (>50%); 3) coastal hills (41,200 ha; up to 400 m above mean sea level) with a low population (36/km²), large percentages of woodlands (38%), and cultivated fields (45%); and 4) southern hills (82,300 ha) that were up to 800 m in elevation with the lowest population density (33/km²), the highest proportion of wooded areas (51%) and least cultivated fields (33%).

Foxes were killed from January to May 1992 in the Province of Pisa (43°N, 10–11°E), central Italy, during predator control operations. Most foxes were shot using a variety of methods (battues, with dogs, at dens), but significant numbers were snared or poisoned. I did not perform post-mortem analyses to ascertain cause of death.

Foxes were collected from hunters within 6 h of death and were kept refrigerated in plastic bags (≤ 48 h, -2°C) until they could be weighed, measured, and dissected. Two indices were used: 1) subcutaneous fat index (on a 1–4 scale; 1 = fat absent or barely detectable, ≤ 0.5 mm thick; 2 = little fat on the sternum, ≤ 2 mm thick; 3 = thick fat on the sternum; 4 = almost continuous layer of fat over abdomen and thorax); and 2) logarithm of the mean perirenal fat index (mass of the kidney with surrounding fat divided by the mass of kidney; hereafter "lnKFT"—Cavallini, 1996a). Age was estimated by counting cementum annuli of a canine tooth, measuring

the pulpar cavity of the same tooth, and weighing the dried eye lenses of the fox (Cavallini and Santini, 1995a). Because of the small number of older foxes, animals were grouped in two age classes: yearlings (8–13 months old at the time of sampling, because most births took place around the end of April—Cavallini and Santini, 1995b) and adults (≥ 2 years old). In January–May, no foxes of intermediate ages were present (Cavallini and Santini, 1995a). Mean (± 1 SD) mass of males in the area was 5.75 kg \pm 0.95 (Cavallini, 1995). Large males were defined as those > 5.75 kg, whereas those weighing < 5.5 kg were defined as small. The cut-off points were chosen to have similar sample sizes in the two classes. In the study period (late winter and early spring), yearlings were nearly fully grown (Cavallini, 1995). Stomach and intestines were removed, opened, and their contents weighed (± 1 g). Mating period was determined by an analysis of male and female reproductive tracts. In the study area, fox mating started at the beginning of February and stopped at the end of March. Half of matings were between 22 February and 3 March, with a median date of 25 February (Cavallini and Santini, 1995b).

LOWESS smoothing was used to show the temporal trends of the data. LOWESS is more informative than other smoothing methods, because it does not presuppose any particular shape of the relation between X and Y (Wilkinson, 1990). Unfortunately, differences between lines cannot be tested directly; I therefore identified critical periods from the inspection of LOWESS plots and tested differences between periods using analysis of variance (ANOVA) followed by Tukey's multiple comparison test. Parametric statistics (univariate and multivariate general linear hypothesis; Wilkinson, 1990) were used for normally distributed variables (as determined by Lilliefors test; Wilkinson, 1990). Non-parametric statistics were used for non-normal and ordinal variables.

RESULTS

I collected 125 females and 205 males, but due to physical damage caused during collection, sample size was reduced for several variables. Females were fatter than males, but this difference was not constant across the study area (lnKFI versus sex and area-sex, $F = 14.4$, $P < 0.001$; area, $F =$

6.6, $P < 0.001$; sex by area, $F = 4.9$, $P = 0.003$; $n = 268$). Females from southern hills ($\ln\text{KFI} = 0.561 \pm 0.161$ SD; $n = 29$) were fatter than those from internal valleys (0.452 ± 0.144 , $P = 0.018$; $n = 59$), which in turn were fatter than those from coastal belt (0.292 ± 0.086 , $P = 0.026$, $n = 10$). Only within the coastal belt did females have the same fat as males (0.357 ± 0.107 , $P = 0.967$, $n = 12$). Males had the same distribution of fat levels across the whole study area ($P > 0.887$). In males, subcutaneous fat decreased until the end of the mating period but increased again afterward (Fig. 1a; Table 1). Perirenal fat followed the same trend (Fig. 1b; Table 1). For females, both subcutaneous and perirenal fat remained constant throughout the study period (Table 1).

Decrease in fat indices was not uniform among males. Adult males maintained average body condition for a longer period and recovered more rapidly than yearlings (Fig. 1c). This different pattern, however, did not result in a significant effect of age class on fat level variation among the three periods ($\ln\text{KFI}$ versus period and age class-period, $F = 4.7$, $P = 0.01$; age class, $F = 1.1$, $P = 0.29$; period by age, $F = 0.1$, $P = 0.85$; $n = 140$). Large males lost condition at the end of the mating period, recovering afterwards, but small males remained in constant condition ($\ln\text{KFI}$ versus period and body size class-period, $F = 4.6$, $P = 0.012$; body size, $F = 5.1$, $P = 0.026$; period by body, $F = 4.0$, $P = 0.02$; $n = 125$).

Gut contents of males followed a similar trend; large males had heavier gut contents before peak of mating than during the main mating period. After mating, gut contents increased again (Fig. 1d; Table 2). Decrease of mass of gut contents preceded that of fat indices (Fig. 1a, b, d). Small males had a more constant mass of gut contents (Fig. 1e; Table 2). Mass of gut contents of females did not vary significantly during the sampling period (Table 2). Due to strong covariance between body mass and mass of gut contents ($r^2 = 0.275$), small sample

size, and non-normality, I could not use ANOVA to analyze these data.

DISCUSSION

This study provided several indications for the occurrence of polygyny in red foxes. The dynamics of fat reserves were strikingly different for the two sexes; females showed local (but not temporal) variation, whereas the reverse was true for males. Local variation may be related to the need for females to accumulate energetic reserves for lactation (May–June in this area; Cavallini and Santini, 1995b). A locally rich food supply will be converted into fat by females but not males who may use it for growing larger or competing more effectively (e.g., Emlen and Oring, 1977). In North America, female red foxes are not fatter than males (Allen and Gulke, 1981).

Male red foxes ate less during the mating season, and their condition deteriorated immediately afterward. The delay may be due to inertia in depleting fat stores and to wider movements after the peak of estrus (Cavallini, 1996b). Changes were more evident for superficial fat depots, which are depleted first (Boertje and Stephenson, 1992) and expand faster than internal ones (Pond et al., 1994). Decrease in gut contents only approached significance, presumably because of the confounding factors of digestion, influenced by time elapsed from ingestion to sampling and small sample size (particularly the small number of foxes killed during the short mating season).

A decrease in body mass of males during the mating and breeding season also has been reported for red foxes from Switzerland (Lüps and Wandeler, 1983), Ireland (Fairley, 1970), and Wales (Lloyd, 1980). Condition of foxes also has been reported to deteriorate during breeding in Norway (Lund, 1959) and Scotland (Kolb and Hewson, 1980). These changes have been checked statistically only for the Scottish sample, where males were significantly leaner during January and February after the peak of the mating season.

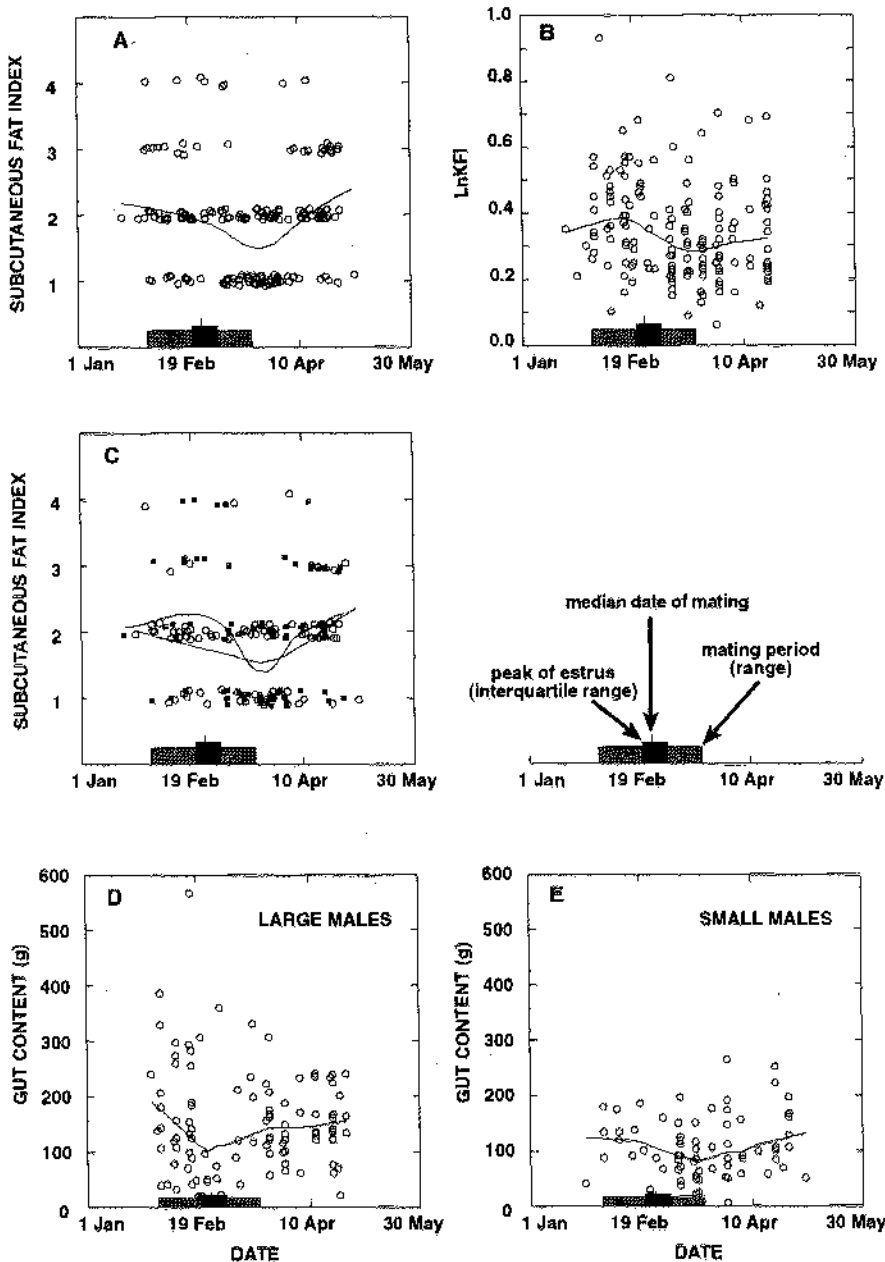


FIG. 1.—Temporal variation of fat indices and gut contents of male red foxes killed between January and May (mating and breeding season) in the Pisa Province, central Italy. The smoothing line is LOWESS (smoothing factor (F) = 0.5; Wilkinson, 1990). To prevent symbols from overlapping, a small amount of uniform random error was added to the location of each point (procedure JITTER; Wilkinson, 1990). A) Subcutaneous fat index from 1 = fat absent to 4 = continuous layer of fat of 168 males. B) Logarithm of the kidney fat index (LnKFI) of 164 males. C) Subcutaneous fat index of 162 males (82 yearlings, 80 adults); open symbols and the continuous line represent yearlings; black squares and the dashed line are adults. D) Mass of gut content (g) of 101 male red foxes larger than average (>5.75 kg). E) Mass of gut content (g) of 69 small male red foxes (<5.5 kg).

TABLE 1.—Temporal variation of indices of body condition mean \pm SD (logarithm of kidney fat index, lnKFI; subcutaneous fat index from 1 = fat absent to 4 = continuous layer of fat) of red foxes killed between January and May in the Pisa Province, central Italy. Periods are: before mating (January–22 February); late mating (9–31 March); after late mating (13 April to May). F indicates results of parametric ANOVA; H indicates results of Kruskal-Wallis test.

Sex	Index	Before mating	Late mating	After late mating	Statistic (d.f. = 3)	n
Females	lnKFI	0.436 \pm 0.145	0.495 \pm 0.154	0.425 \pm 0.148	F = 1.93, P = 0.15	91
	Subcutaneous fat	2.4 \pm 0.84	2.5 \pm 0.81	2.5 \pm 0.63	H = 0.27, P = 0.8	98
All males	lnKFI	0.399 \pm 0.143	0.301 \pm 0.140	0.336 \pm 0.145	F = 7.37, P = 0.001	145
	Subcutaneous fat	2.1 \pm 0.86	1.5 \pm 0.67	2.2 \pm 0.68	H = 27.05, P < 0.001	149
Large males (>5.75 kg)	lnKFI	0.404 \pm 0.151	0.295 \pm 0.133	0.391 \pm 0.152	F = 4.64, P = 0.013	79
	Subcutaneous fat	2.16 \pm 0.90	1.56 \pm 0.70	2.42 \pm 0.65	H = 16.78, P < 0.001	82
Small males (<5.5 kg)	lnKFI	0.337 \pm 0.108	0.304 \pm 0.143	0.259 \pm 0.104	F = 0.775, P = 0.467	47
	Subcutaneous fat	1.75 \pm 0.46	1.44 \pm 0.70	1.82 \pm 0.60	H = 5.34, P = 0.069	46

Several alternative hypotheses, not involving polygyny, can be formulated to explain the observed pattern, but they at present are unsupported by data: 1) decreased food availability—females, however, had constant mass of gut contents and maintained body condition in the same period, which makes this hypothesis unlikely; 2) lower diet quality—the diet, however, was similar across the whole study area (Cavallini and Volpi, 1996); 3) seasonal incidence of diseases (e.g., scabies, *Sarcoptes scabiei*—Lund, 1959)—this could not explain, however, rapid recovery of body fat after the mating season and absence of a

decrease in body fat for females and small males; and 4) the investment by males in hunting to provide food for cubs (suggested as a cause of weight loss by Fairley, 1970)—this was not consistent, however, with the pattern of fat loss observed in my study.

Investment in reproduction was not uniform among male foxes. Only large males showed a significant decrease in body fat after the peak of breeding, whereas small males maintained condition. This phenomenon has never been demonstrated for wild carnivora, although differential food intake has been reported for farmed blue foxes,

TABLE 2.—Temporal variation of mass of gut contents (g \pm SD) of red foxes killed between January and May in the Pisa Province, central Italy. Periods are: before mating (January–22 February); during mating (22 February–3 March); after mating (3 March–May). H indicates results of Kruskal-Wallis test.

Sex	Before mating	During mating	After mating	Statistic (d.f. = 3)	n
Females	143 \pm 83	102 \pm 42	112 \pm 64	H = 4.16, P = 0.125	120
Large males (>5.75 kg)	169 \pm 117	99 \pm 117	150 \pm 66	H = 5.34, P = 0.069	101
Small males (<5.5 kg)	125 \pm 44	85 \pm 54	104 \pm 58	H = 3.19, P = 0.202	69

Alopex lagopus (Korhonen and Niemela, 1993) and suggested for ursids (Coy and Garshelis, 1992). The pattern is comparable to that of several ungulates (e.g., Clutton-Brock et al., 1982) and the opossum, *Didelphis virginiana*, in which large males lose body mass during the mating season but mass of small males increases (Ryser, 1992).

I interpret my results as suggesting existence of size-dependent alternative mating strategies in red foxes; i.e., that larger-than-average males (with better chances of success in direct confrontation) spend less time hunting and foraging and invest more heavily in reproduction. They could move more, fight with other males, and try to mate with several females (Cavallini, 1996b; Saunders et al., 1993; White and Harris, 1994). Small males could be more prudent, minimizing metabolic expenses and continuing to feed regularly. In fact, the mating season is riskier for small males (White and Harris, 1994), which face higher risks from incursions by larger males in their home ranges. They could increase their guarding behavior to compensate for access to a lower number of females, according to the "make-the-best-of-a-bad-job" strategy (Krebs and Davies, 1981). This strategy has been suggested for the Egyptian mongoose, *Herpestes ichneumon*, in which a large male was polygynous but a small male monogamous (Palomares, 1993). Positive allometric effects of body size must therefore be taken into account when analyzing energy budget and possibly also ranging behavior (Saunders et al., 1993) of carnivores.

My results are in contrast to the view of the fox as a monogamous species (Moehlman, 1989). The increase of excursions outside their normal home range during the mating season (Saunders et al., 1993) or immediately after the peak of estrus (Cavallini, 1996b) also indicates a potential for polygyny. Polygyny might therefore occur not only within groups (Zabel and Taggart, 1989) but also between neighboring groups.

I therefore suggest that large male red foxes have higher reproductive success than small ones, but this should be tested by further research (e.g., using genetic markers).

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