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Fluctuating resources and the evolution of litter size in the arctic fox

Magnus Tannerfeldt and Anders Angerbjörn

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Fluctuations in essential resources cause a strong selection pressure on the ability to adjust parental investment accordingly. In the dog family, Canidae, variance in female prebirth investment is adjusted by litter size. The arctic fox, *Alopex lagopus*, is a small canid living on the northern tundras of the world. It has the largest known litter size in the order Carnivora, up to 18 young, and litter size is highly variable. We have analysed data from arctic fox populations throughout the species circumpolar range. In some areas, arctic foxes feed on strongly fluctuating populations of small rodents. In contrast, they have more stable food resources at bird cliffs and along coast lines. Food availability determines arctic fox litter and population sizes. A comparison between fluctuating and stable arctic fox populations showed that fluctuations are associated with large litter sizes. There were significant differences in litter size means, maxima and variances, as well as in placental scar count means. We have discussed five hypotheses on the determination of variation in litter size: one energetic, one genetic (based on density variation), one diet-determined, one based on reproductive allocation and one based on differences in reaction norms. Our findings suggest that litter size in the arctic fox is determined by the combined effect of immediate resource levels and the degree of resource predictability. We describe reaction norms that suggest how litter sizes result from adaptive plasticity within each of two genetic strategies where, according to the jackpot hypothesis, populations with unpredictable food resources generally have larger litter sizes. Within each genetic strategy, or reaction norm, litter sizes are adjusted through a number of plastic traits. These traits are influenced by nutritional limitations and include reduced ovulation rates, prenatal losses, and litter size reduction during the lactation period.

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In stable environments, litter size can be expected to approach an optimum resulting from a trade-off in life history traits (Lack 1947, 1948). In strongly fluctuating environments, however, trade-offs that influence life history strategies may have different optima in different phases of the fluctuations. This means that many traits experience changing selection pressures in time spans that are too short for adaptations to occur within each phase. Organisms can cope with such fast changes either by adopting an 'average optimum' or by developing plasticity in the trait (Gotthard and Nylin 1995). If the trait becomes plastic and the resulting norm of

reaction is genetically determined, this norm is subject to natural selection (Houston and McNamara 1992). The reaction norm may thus be optimised to the frequency and amplitude of environmental and population fluctuations. For litter (or clutch) size in fluctuating populations, there is evidence both for an 'average optimum' (Stearns 1992, Clutton-Brock et al. 1996) and for adaptive plasticity (Morris 1985, Price and Liou 1989, Roff 1992).

Important components of reproductive rate on the population level are age at maturity, proportion of females reproducing, number of litters per season, age

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structure and average litter size (e.g. Millar 1977). Individual litter sizes can be affected by a large number of variables such as maternal effects, habitat variance, population density and weather conditions. Many of these components exert their influence on litter size by affecting the food supply and thus amount of energy available for a breeding female (Lack 1954, Stearns 1992). In mammals, food availability affects ovulation and food stress has the strongest effect on lactating females (Bronson 1989). Effects on ovulation and prenatal losses have consequences on litter size at birth, while effects on lactation influence litter size at weaning. The relation between variation in litter size and food resources can be summarised under an 'energy limitation hypothesis'. There has also been an interest in effects of density variation on reproductive rate from a life history perspective (Pianka 1970, Stearns 1976, Pianka 1978, Charlesworth 1980). Stenseth et al. (1985) studied how stability in population density could be related to reproductive rate. Their 'density variation hypothesis' predicted that reproductive rate should increase with an increased variation in population density. An alternative to these two hypotheses is what we here will call the 'hormone turbo hypothesis', proposed by Lindström (1988). He suggested that reproductive hormones from prey individuals may be transferred to female predators and influence their litter sizes. Yet another hypothesis suggests that the total lifetime reproductive success of an animal is allocated differently according to environmental stability (the 'reproductive allocation hypothesis'). Under favourable conditions, large litters are born, which has a negative effect on subsequent reproduction (Stearns 1992). In stable, less favourable situations, animals are expected to produce smaller litters but with higher probability of future reproduction (Frafjord 1993). We propose a fifth hypothesis where reaction norms for litter size have evolved in response to different degrees of predictability in fluctuations of essential resources. According to this 'jackpot hypothesis', at a given resource level, animals from populations in fluctuating environments have larger litters than those from stable populations. Of these five, only the reproductive allocation hypothesis assumes a substantial cost of reproduction.

Predictable vs unpredictable environments

The size of fluctuating arctic fox populations is determined by corresponding fluctuations in the recruitment of young (e.g. Macpherson 1969, Bannikov 1970), which in turn is correlated with food availability (Macpherson 1969, Hersteinsson 1984, Angerbjörn et al. 1991, Tannerfeldt et al. 1994). Arctic foxes can utilise a wide variety of food resources, for example berries, insects, birds, fish, seal placentas, small mammals and reindeer (*Rangifer tarandus*) carcasses (Chese-

more 1968, Hersteinsson and Macdonald 1982, Fay and Stephenson 1989, Stickney 1989, Birks and Penford 1990, Nielsen 1991, Angerbjörn et al. 1994). In the arctic fox's holarctic range, productivity is generally low but food resources can be extremely abundant in small patches and during short time periods. The dominant pattern in these resource fluctuations is determined by lemming (*Lemmus* and *Dicrostonyx* spp.) and vole (*Clethrionomys* and *Microtus* spp.) population peaks, where prey is superabundant every three to five years and otherwise scarce (e.g. Hansson and Henttonen 1985, Stenseth and Ims 1993). Although this pattern is surprisingly regular, there is considerable variation around the mean periodicity (Hanski et al. 1993). Moreover, arctic foxes are short-lived in the wild and cannot expect to experience more than one peak event, if even that (Hiruki and Stirling 1989, Prestrud 1992a, Tannerfeldt and Angerbjörn 1996). Thus, this resource is unpredictable to arctic foxes and there should be a strong selection pressure to adjust reproductive investment to the rodent peaks. In other areas, arctic fox populations are sustained on more stable food resources. This occurs for example at bird cliffs and along coast lines, where food is abundant during the months of arctic fox reproduction (Hersteinsson and Macdonald 1982, Prestrud 1992b). Under these circumstances, food resource levels are more predictable than in rodent areas.

In the dog family, Canidae, females normally give birth to one litter per year and variation in age at maturity is low (Bekoff et al. 1981, Sheldon 1992). It has also been argued that for canids "the variance in female prebirth investment can only be adjusted by litter size" (Geffen et al. 1996). Intraspecific comparisons in Canidae have shown that litter size declines with decreases in prey abundance (Angerbjörn et al. 1995, Geffen et al. 1996). Arctic foxes (*Alopex lagopus* (L.)) can have up to 16 or 18 young, which is the largest known litter size in the order Carnivora, only matched by the large, social African hunting dog (*Lycaon pictus*) (Ewer 1973). When total litter weight, controlled for gestation time, is plotted against female weight, the arctic fox has the highest values among the Canidae (Geffen et al. 1996). Most females mate in their first or second year (Macpherson 1969, Hersteinsson 1984, Hall 1989, Prestrud 1992a). Adult yearly mortality is 33–60% in a wide range of habitats (except for the age class 7–8 yr in Iceland, with 17%; Hersteinsson 1984, Hiruki and Stirling 1989, Prestrud 1992a, Tannerfeldt and Angerbjörn 1996). Litter size and the proportion of breeding females are main determinants of reproductive rate in the arctic fox (Macpherson 1969, Bannikov 1970, Prestrud 1992a, Angerbjörn et al. 1995). These parameters are influenced by food availability in arctic and red foxes (*Vulpes vulpes*) (Macpherson 1969, Englund 1970, Lindström 1989, Hersteinsson 1992).

Litter size at weaning is equal to the number of ovulated eggs minus pre-weaning losses. Depending on the stage at which losses occur and the accuracy of the method used to determine them, these losses have been referred to by the partly overlapping terms pre-implantation, post-implantation, intra-uterine, pre-natal or losses during lactation. Only a few studies on foxes have penetrated the problem in detail and the data suggest the following sequence for red and arctic foxes. 1. Most females mate every year (Macpherson 1969, Hersteinsson 1992 on *A. lagopus*; Englund 1970 on *V. vulpes*). 2. Ovulation rates are related to food availability (Englund 1970, Lindström 1989 on *V. vulpes*). 3. Pre-implantation losses are related to food availability (Englund 1970 on *V. vulpes*). 4. The number of resorbed and aborted embryos is relatively constant (Englund 1970 on *V. vulpes*; Strand et al. 1995 on *A. lagopus*). 5. Whelping frequency is related to late winter food availability, possibly due to intra-uterine loss of complete litters (Macpherson 1969, Angerbjörn et al. 1991 on *A. lagopus*; Lindström 1989 on *V. vulpes*). 6. Litter size at emergence is related to late winter food availability (Angerbjörn et al. 1995) and summer food availability (Hall 1989, both on *A. lagopus*). 7. Juvenile survival is related to summer food availability (Tannerfeldt et al. 1994 on *A. lagopus*).

In this paper, we address the question of how litter size in the arctic fox has evolved and is determined. The arctic fox exhibits a large intraspecific variation in litter size, where rodent and non-rodent eating arctic fox populations, respectively, are reported to have different reproductive strategies (Bræstrup 1941, Hersteinsson 1990, Frafjord 1993). We examine five hypotheses on litter size determination in relation to main food resources and discuss between-population differences in terms of reaction norms.

Hypotheses

The energy limitation hypothesis

This hypothesis suggests that litter size is chiefly determined by a female's energetic state. As we showed earlier, several studies on red and arctic foxes have demonstrated how ovulation rates and losses during pregnancy and lactation are influenced by food availability. Litter size reductions can be quite substantial in arctic fox populations, with up to 35% pre-weaning losses (Hersteinsson 1990). This seems to be a general mechanism in mammals (Bronson 1989). Energy expenditure can vary with a number of factors such as ambient temperature, territoriality, travel distances and reproductive effort. Energy intake can be affected by time spent on activities other than feeding, e.g. predator avoidance, territorial and reproductive behaviour, and by food availability (Morris 1998). For

breeding arctic foxes we suggest that the main factor affecting energy expenditure is litter size, whereas energy intake largely is determined by food availability, which can be equated with food abundance within the territory, with the exception of the superabundant food during lemming peaks. We will here focus on the central implication of the energetic hypothesis, viz. that litter size is directly related to female body condition and/or food availability.

The density variation hypothesis

The basis for the specific hypothesis is a theoretical work by Stenseth et al. (1985), where reproductive rate is expected to increase with increased variation in population density. The hypothesis suggests selection for increased reproductive output during increase phases. During population crashes, on the other hand, there should be a non-selective situation that leads to an overall selection for larger litters (Stenseth and Gustafsson 1985). Further, the increase phases are often longer (up to two years) than the crash phases (less than one year), which enhances this selection pressure. This hypothesis does not take food availability or other extrinsic factors into account. Selection in a cyclic population would thus produce genetic differences in reproductive rate compared to a stable population. The authors found support for this density variation model on litter size variation in microtine rodents (Stenseth and Gustafsson 1985, Stenseth et al. 1985; but see Hansson and Henttonen 1985). This should have wide applicability but has to our knowledge not been tested on any other animal group.

According to the hypothesis, arctic foxes in stable environments are prone to lose the ability to produce large litters. An alternative explanation for lower litter size maxima in stable populations is that selection favours a reduction in litter size variance rather than in litter size means. The hypothesis suggests a genetic difference in litter sizes between fluctuating and stable populations, as suggested for arctic foxes by Bræstrup (1941) and Frafjord (1993). Valberg Nordrum (1996) showed a low, but heritable, genetic response to selection for litter size in arctic foxes with 0.01 cub per year. Gene flow between populations must be minimal if a genetic dimorphism is to become fixed in one state in some populations and another state in other populations.

The hormone turbo hypothesis

Another explanation for population differences in litter size is that differences are caused by the type of diet, not the amount of food. Lindström (1988) found that in red foxes, there was a positive correlation between

mean litter size and vole spring densities, established already at the stage of follicle maturation. However, the best determinant of ovulation rate in January–February was not food availability in winter or early spring, but vole density in May, several months later. Also, there was no correlation between female fat deposits and subsequent ovulation rates. Lindström (1988) therefore suggested that red foxes can detect when rodent populations are increasing, through hormones associated with reproduction that are present in the prey's body. In strongly fluctuating rodent populations, especially in lemmings, increases in numbers are associated with a larger proportion of reproductive females in winter (e.g. Cockburn 1988). Fox females feeding on rodents from an increasing population would thus ingest a supernormal amount of reproductive hormones and might be stimulated to increase ovulation. A prerequisite is that the hormones are absorbed in a physiologically active form.

Lindström acknowledged that the effect, if present, could either be a mere physiological by-product in the foxes, or a selected trait to use these hormones as a cue for an increased reproductive effort. Hormones involved in reproduction are much the same for all mammals (Eckert 1983) and the foxes might therefore not be able to turn off their response. If hormones can be transmitted through the food web, the phenomenon should be general. An increase from 12 to 15–17 young in the arctic fox is equivalent to the fecundity increase of 30–40% observed in the red fox. However, the crucial question is whether ingestion of reproductive hormones in realistic amounts can affect ovulation rates in foxes. Further, the mechanism has to be demonstrated to act in natural populations. Onset of reproduction in the mountain vole (*Microtus montanus*) has been shown to be stimulated by the occurrence of a secondary plant compound, 6-MBOA (6-methoxybenzoxazolinone), in their food (Sanders et al. 1981). These voles feed on grass that becomes abundant after heavy rainfalls, which are unpredictable events. When the fresh grass emerges, it contains 6-MBOA. By responding to this compound, the mountain vole can time its optimal reproductive effort to the most resource-rich period. Also other species respond in a similar way to experimentally issued 6-MBOA (Bronson 1989). Likewise, reproduction in vervet monkeys (*Cercopithecus aethiops*) is correlated with the availability of acacia flowers, which are rich in flavonoids with estrogenic properties (Bronson 1989).

The reproductive allocation hypothesis

A fourth hypothesis explaining population differences in reproductive rates suggests that arctic foxes cannot produce large litters every year (Frafjord 1993). They then “have to choose between producing annual but

small litters or intermittent but large litters” (Frafjord 1993). This assumes a reproductive cost leading to a trade-off between current and future reproductive effort (Stearns 1992). If a fox produces four cubs in each of four years, this is equivalent to producing 16 cubs in the one peak year, given that survival rates and cub ‘quality’ are the same. The difference in means is presumably accentuated by the exclusion, in most calculations, of ‘litters of zero’ during rodent lows. A crucial assumption in this argument is that arctic foxes are not able to produce large litters for several consecutive years even if resources are abundant.

The jackpot hypothesis

In this hypothesis, litter size is a plastic trait that is adjusted to resource levels according to a norm of reaction, whose shape in each population is adapted to the degree of predictability in resource variation. If reproductive costs are small, maximum litter sizes should be larger in strongly fluctuating and unpredictable environments than in stable environments. Within each reaction norm, litter sizes are mainly determined by the level of resources, often food availability. Reproductive costs can be small, also with large litter sizes, because of the fine-tuned mechanisms of pre-natal litter size regulation in foxes (see above). Litter sizes are thus the result of influence from both resource levels and a population-specific genetic component.

Materials and methods

We have reviewed published data from arctic fox populations in the entire distribution range, and compared placental scar counts and litter sizes at weaning for stable and fluctuating populations. We then tested our results against predictions from five hypotheses on the determination of variation in litter size.

There are several problems in estimating litter sizes. Ovulation rates and pre-implantation losses are difficult to measure and intra-uterine litter size estimations in most arctic fox studies are made from placental scar counts. These have sometimes been equated with litter size at birth, but it has been demonstrated that losses between implantation and birth can be quite high (Strand et al. 1995). Litter size at birth is seldom recorded in wild foxes and the young are instead counted after emergence from the den. In this study, we have used placental scar counts and litter sizes around weaning as estimates of litter sizes. The difference between scar counts and litter sizes around weaning is the sum of losses from implantation to birth (post-implantation losses) and losses during lactation.

The age of counted young is important, since mortality may occur early and all young may not be found

Table 1. Arctic fox litter sizes around weaning, at 3–6 weeks of age. R = rodents in diet, No R = rodents absent or only occasionally eaten, Ru = Russia, Can = Canada. Asterisk (*) signifies anecdotal evidence, blank = figure not given in paper, ^{a)}In Bræstrup (1941), ^{b)}includes data from several other authors, ^{c)}in Bannikov (1970), ^{d)}excluded from calculations presented in Table 3.

Food	Site	Maximum	Mean	sd	N	Reference
No R	Iceland	10	4.2	1.5	309	Hersteinsson 1984
No R	Rat Island, USA	5	2.8		16	Berns 1969
No R	Commander Islands, Ru	12 ^{d)}				Lavrov 1932
No R	Mednyi Island, Ru	10 (12*)	6.4	1.4	17	Barabash-Nikiforov 1938
No R	West Greenland	8 ^{d)} (10*)				Fabricius 1788 ^{a)} and Müller 1906 ^{a)}
No R	Pribilof Islands, USA	11			22	Preble and McAtee 1923
No R	Svalbard (Spitzbergen)	8	5.3	1.7	35	Prestrud 1992a
No R	Svalbard (Spitzbergen)	8	5.8	1.6	5	Frafjord 1992
R	Wrangel Island, Ru	18	6.5		53	Dorogoi 1987 Chernyevski and Dorogoi 1981
R	Prudhoe Bay, USA	10	5.5	3.1	4	Underwood 1971
R	NWT, Canada	14	6.7	3.3	27	Macpherson 1969
R	Kildin Island, Ru	13	6.5	2.2	48	Lavrov 1932
R	Prudhoe Bay, USA		4.8		11	Fine 1980
R	Yugov Peninsula, Ru	16	7.8		117	Nasimovich and Isakov 1985 ^{b)}
R	Yamal, Ru		9.0 ^{d)}			Nasimovich and Isakov 1985 ^{b)}
R	Taymyr, Ru		5.0–6.5 ^{d)}			Nasimovich and Isakov 1985 ^{b)}
R	Yakutia, Ru	15 ^{d)}	4.0–4.8 ^{d)}		> 134	Nasimovich and Isakov 1985 ^{b)}
R	Hudson Bay, NWT, Can	12	7.6	3.5	9	Hall 1989
R	Sweden	16	6.3	3.3	164	Angerbjörn et al. 1995
R	Norway	13	11.2		5	Frafjord 1992
R	Jämtland, Sweden		6.7 ^{d)}		41	Ericson 1986
R	Finland 1964–74	12 ^{d)}	6.6 ^{d)}		10	Kaikusalo 1991
R	Finland 1985–91	5 ^{d)}	2.4 ^{d)}		28	Kaikusalo 1991
R	NWT, Canada	14	6.1		11	Speller 1972
R	Karska Tundra, Ru	22* ^{d)}	7.1 ^{d)}			Chirkova et al. 1959 ^{c)}
R	Herschel Island, Can	7	5.0		4	Smits et al. 1989
R	Norway	16 ^{d)}	6–8 ^{d)}			Collett 1912

(Bekoff 1989). This is especially important in denning species and litter sizes from the wild must be regarded as minimum numbers (Frafjord 1993, Angerbjörn et al. 1995). In the arctic fox, litter sizes are usually estimated at the age of 3 to 6 weeks, i.e. from emergence outside the den until cubs start to become wary and make longer excursions. The age at weaning varies from 5 to 9 weeks, apparently according to food availability, where limited food results in early weaning (Hersteinsson and Macdonald 1982, Garrott et al. 1984, Derefeldt 1996). The young gradually become independent during the month after weaning, but some cubs may even leave the den in their sixth week of life (Frafjord 1992). We have in this paper only used litter sizes that were determined in the first weeks after emergence, i.e. at 3 to 6 weeks of age, and equate them with litter sizes at weaning. Litter sizes are further best compared between populations with a similar age structure, since there may be age differences in reproductive performance. For the arctic fox, however, there are no differences between age classes in the number of placental scars (Macpherson 1969, Hall 1989, Hersteinsson 1992, Prestrud 1992a).

Arctic foxes are territorial, but just as red foxes they tend to increase group size at high densities (Macdonald 1983, Schantz 1984a, b, Lindström 1986, Hersteinsson

1992). Therefore females may share dens, leading to over-estimations of litter sizes. Frafjord (1991) observed that two arctic fox females jointly nursed what he, based on size differences, concluded to be two different litters (but see below). Arctic foxes have even been observed to pool litters that were born in separate dens (Ovsyanikov 1988, Angerbjörn unpubl.). Without a size difference in the cubs, such instances would normally be recorded as one large litter (Lavrov 1932, Frafjord 1993). Having said all this, an arctic fox female can still have up to 20 or even 25 implanted embryos (Macpherson 1969, Hammill 1983, Fay and Rausch 1992) and arctic fox litter sizes of 16–18 have been documented in many cases (Collett 1912, Nasimovich and Isakov 1985, Dorogoi 1987, Angerbjörn et al. 1995; Table 1). It has even been observed that embryos of two distinctively different size classes developed in the same uterus (P. Hersteinsson pers. comm.). Moreover, all field studies share the same problems, so there is no reason to assume a bias between rodent and non-rodent eating populations. Litters of one were excluded from the Swedish data set (Angerbjörn et al. 1995) because this category included dens where the number of cubs could not be counted. The expected true number of litters in this category was low and their exclusion is not likely to have had a significant impact on the results.

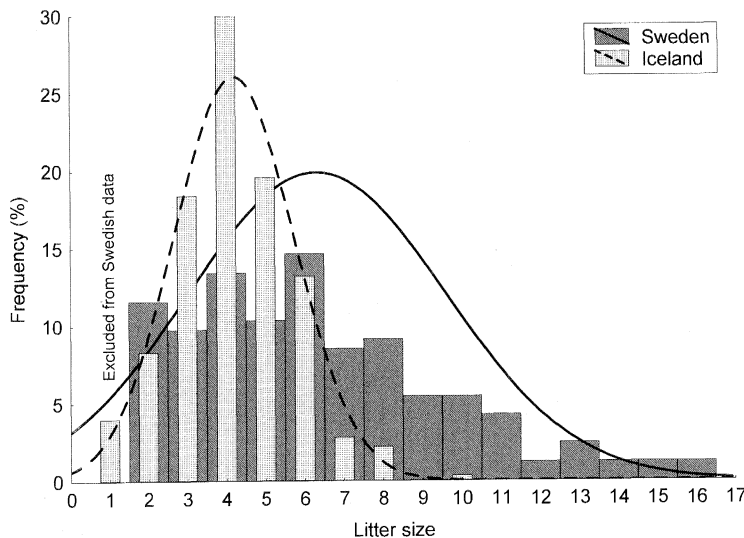


Fig. 1. Litter sizes around weaning and normal distribution in two arctic fox populations. The Swedish population feeds mainly on fluctuating populations of small rodents. The Icelandic population has more stable food supplies (Swedish data from Angerbjörn et al. 1995, Icelandic data from Hersteinsson 1984). Litters of 1 were excluded from the Swedish data set because this category included dens where the number of cubs could not be counted. The expected number of dens in this category was low and their exclusion is not likely to have had a significant impact on the results.

Results

We have compared litter size data on arctic fox populations feeding on rodents versus populations in non-rodent areas. An illustrative comparison can be made between the Swedish and the Icelandic arctic fox populations (Fig. 1). A large part of the arctic fox population in Iceland is coastal and feeds on wash-ups from the sea or on cliff-nesting birds (Hersteinsson 1984, Hersteinsson and Macdonald 1996). The total inter-year availability of these food resources is comparatively predictable. Litter sizes in coastal Icelandic arctic foxes varied between 1 and 10, with a median of 4 (mean 4.19, $N = 309$, Hersteinsson 1984). In contrast, arctic foxes in Sweden depend on voles and lemmings for breeding (e.g. Angerbjörn et al. 1995). This is a summer food resource that fluctuates widely between years (Stenseth and Ims 1993). In most years, only a few arctic fox litters are born, whereas when food is abundant, a very large proportion of the population breeds. The variance in litter size in the Swedish population was large, ranging from 2 to 16 cubs per litter, with a median of 6 (mean 6.31, $N = 164$, Angerbjörn et al. 1995). Differences in food availability and predictability thus seem to be reflected in the variation in litter size. Hersteinsson (1990) found a very similar pattern for placental scar counts in a comparison between the Icelandic and a Canadian population (Macpherson 1969).

There are no reports of litter sizes larger than 12 from areas without rodents, whereas there are several accounts of 16 and 18 cubs from the lemming areas of Scandinavia and Siberia (Collett 1912, Nasimovich and Isakov 1985, Angerbjörn et al. 1995) and litter sizes of 14 from North America (Macpherson 1969; Table 1). Because litter size estimation can be difficult, we have for weaned litter sizes only used studies where sample

sizes and investigation methods were given (Tables 1 and 2). Data from Finland were not included because of an unexplained, drastic drop in weaned litter sizes between 1974 and 1985 (Kaikusalo 1991, Kaikusalo and Angerbjörn 1995). Data in Ericson (1986) are included in Angerbjörn et al. (1995). There were significant differences in litter size means, maxima and standard deviation and in placental scar means (Table 3, Fig. 2). There is a risk that maximum values are positively related to sample sizes, but the trend was negative for placental scars and for weaned litter sizes the difference was even greater when studies with sample sizes smaller than 10 were excluded (Table 1; Mann-Whitney U -test, $p = 0.006$, $U = 0$, $N = 11$). For both litter size and scar counts, we tested the coefficients of variation (CV) for each population against that of every other population (Sokal and Rohlf 1981). There were neither any differences among CV of litter size (all $p > 0.45$), nor among CV of placental scar counts (all $p > 0.5$). To summarise so far, there seem to be two major reproductive strategies adopted by arctic foxes. One is to raise small litters every year and the other is to raise large litters intermittently, with small or no litters in most years. The former strategy is associated with coastal habitats, where birds and/or foods of marine origin are most important. The latter strategy is associated with a diet based on fluctuating rodent populations. What, then, is so special about rodents?

The energy limitation hypothesis

The following predictions are based on the assumption that the amount of energy available to fox females determines litter sizes.

Table 2. Placental scar counts in arctic foxes. Anthony (1991) and Hall (1989) did not mention distinguishing between dark and light scars. R = rodents in diet, No R = rodents absent or only occasionally eaten, Ru = Russia, Can = Canada. ^{a)}Our recalculation, ^{b)}in Bannikov (1970), blank = figure not given in paper.

Food	Site	Maximum	Mean	sd	N	Reference
No R	Iceland	9	5.4	1.6	289	Hersteinsson 1992
No R	Svalbard	11	6.4	1.9	102	Prestrud 1992a
R	Yukon Delta, USA		8.3	0.8	22	Anthony 1991
R	NWT, Can	21	10.6	3.1	118	Macpherson 1969
R	St. Lawrence Island, USA	20	11.5		77	Fay and Rausch 1992
R	Hudson Bay, NWT, Can		7.7	5.3	44	Hall 1989 ^{a)}
R	Karska Tundra, Ru		10.2			Chirkova et al. 1959 ^{b)}
R	Victoria I., NWT, Can	25	9.5	7.8	16	Hammill 1983

Prediction 1: *Within a population, the number of placental scars is positively correlated with winter food availability and/or female condition.*

In the relatively stable, 'non-rodent', Svalbard population, there were no inter-year differences in placental scar counts although mean "rump fat thickness" varied between years (Prestrud 1992a). In Canada, Hall (1989) did not find any correlation between the number of placental scars and a subcutaneous fat index. In another Canadian study, placental scar counts did not differ between years while winter food availability did, as indicated from gut contents (Macpherson 1969). The prediction was thus not supported.

Prediction 2: *Equally fat females from rodent and non-rodent areas have the same number of placental scars.*

When we compared two studies, conducted on Svalbard (Prestrud 1992a, Prestrud and Nilssen 1992) and in Canada (Hall 1989), we found that they contradicted this prediction. Although the range and distribution of an index of stored fat (Underwood 1971) were similar in the two populations, the number of placental scars differed ($p = 0.030$; Svalbard: mean = 6.4, sd = 1.9, $N = 102$; Canada, our recalculation: mean = 7.7, sd = 5.3, $N = 44$). However, a cautionary note must be made on this comparison since the fat index is subjective. Nevertheless, the Svalbard population had foxes with up to 40% of their body mass as fat and yet the maximum number of scars in the population was only

Table 3. Comparisons between arctic fox populations in areas with and without rodent prey, respectively. Data from Tables 1 and 2, (where figures denoted by ^{d)} were excluded). Placental scar counts and litter sizes around weaning were compared in Mann-Whitney U -tests.

		p	U	N
Placental scars	Means	0.046	0	8
	Maxima	0.083	0	5
	sd	0.350	2	6
Litter sizes	Means	0.047	10	16
	Maxima	0.013	7	16
	sd	0.014	0	9

11, compared to 14 in the Canadian study. The maximum number of scars in another Canadian population was 22 (Macpherson 1969). The energy limitation hypothesis was therefore not supported for placental scar counts.

Prediction 3: *Litter size is positively related to the energy available to fox females.*

Macpherson (1969) concluded that lemming abundance governed the survival of young cubs and thus weaned litter sizes. Hall (1989) found a good correlation between microtine numbers and litter sizes. Furthermore, in a long-term field experiment, litter sizes were larger at dens supplemented with food (Angerbjörn et al. 1995). The energy limitation hypothesis was supported for litter size.

The density variation hypothesis

If litter size is determined only by genetic differences related to fluctuations in population density, we make the following predictions.

Prediction 4: *The number of placental scars is higher for rodent foxes than for non-rodent foxes, in all phases of the rodent cycle.*

This was supported by an overall comparison (Table 3, Fig. 2b) and by Macpherson (1969), who found no differences between population phases. However, although Hall (1989) found no differences in scar count variation, there was an inter-year difference between means, with the highest numbers during a rodent peak and the following year. The density variation hypothesis was partly supported for scars.

Prediction 5: *Post-implantation losses are constant and variation in placental scar counts explains litter size variation.*

The reason is that the cost of losses is smallest early in pregnancy and selection should therefore favour early

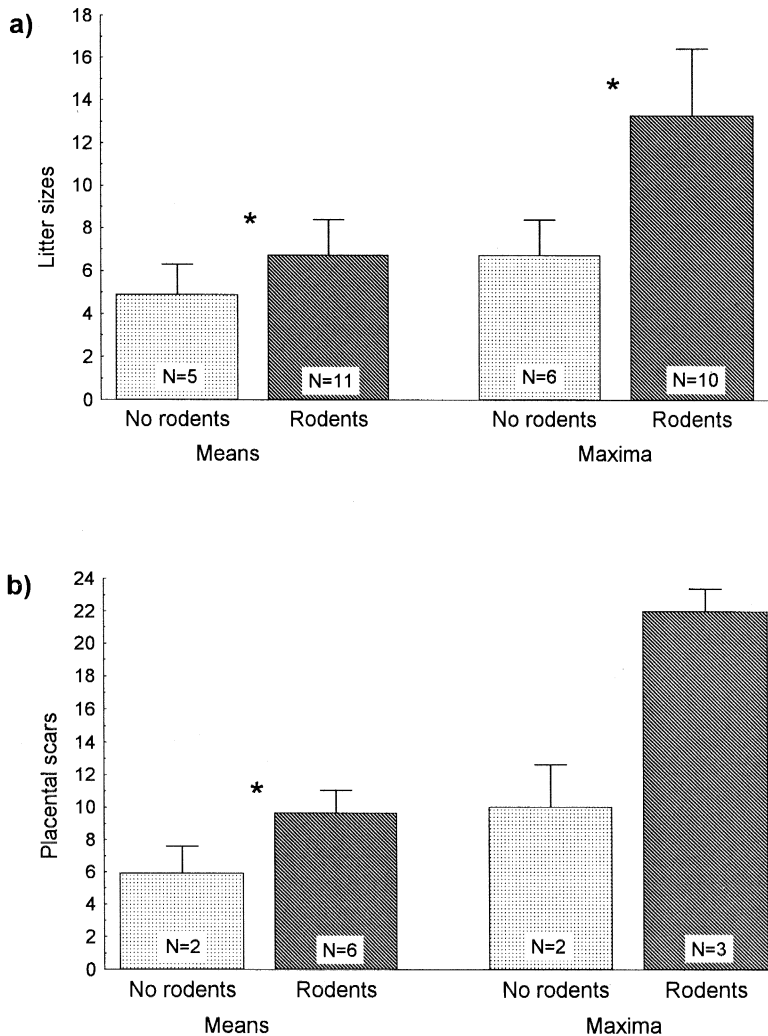


Fig. 2. Differences (+SE) between population means and maxima in a) arctic fox litter sizes at weaning, and b) placental scar counts, in relation to whether rodents were a substantial part of the diet or not; data from Tables 1–3. Significant differences, with $p < 0.05$, are denoted by an asterisk.

determination. It has been found that a constant proportion of arctic fox embryos was lost regardless of female resources (Frafjord 1992, 1993). Also for red foxes, post-implantation losses did not differ between years while litter sizes did (Englund 1970). In the latter study, it was shown that food availability determined ovulation rates, which in turn determined the number of placental scars. However, in Canadian arctic foxes, there were no significant inter-year differences in placental scar numbers while weaned litter size varied with rodent availability (Macpherson 1969). Other data have also indicated a poor correlation between scar counts and litter 22 sizes (Hall 1989). The prediction was thus only partly supported.

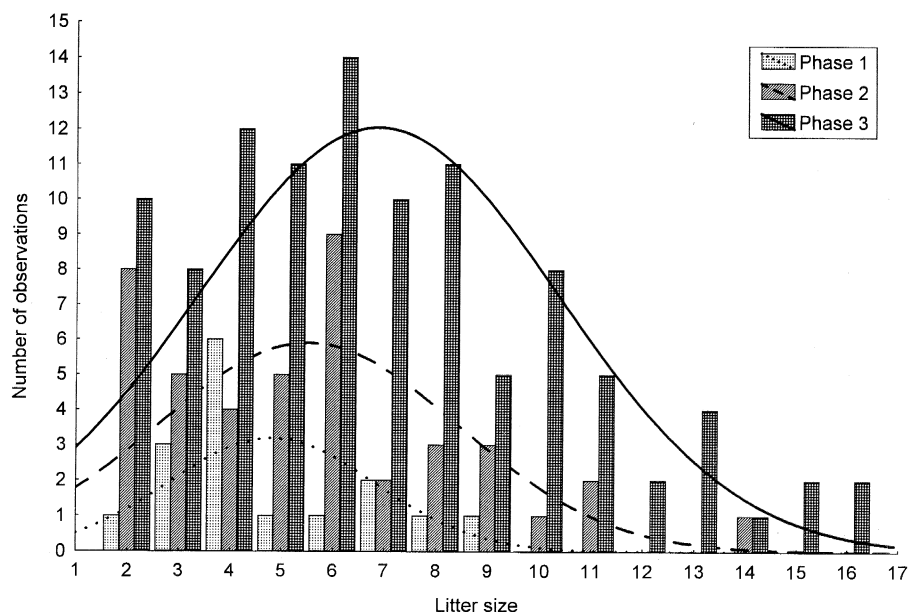
Prediction 6: *Litter size is larger for rodent foxes than for non-rodent foxes, in all phases of the population cycle.*

We have re-analysed the Swedish data (Angerbjörn et al. 1995) and classified years of low population density, including declines, as phase 1, increase years as phase 2 and peak years as phase 3. Years with no reproduction were excluded (Fig. 3). There was a difference in litter size between population phases 1 and 3, and the prediction was thus not supported (Table 4). The litters in phase 1 were equal to (compared to Hersteinsson 1992, $p = 0.16$) or smaller than (Prestrud 1992a, $p = 0.002$) those in non-rodent areas. Thus, the density variation hypothesis was not supported for litter size.

The hormone turbo hypothesis

The following prediction applies if reproductive hormones in the diet act to determine litter size.

Fig. 3. Litter sizes around weaning and normal distributions for Swedish arctic foxes (reanalysed from data in Angerbjörn et al. 1995), separated according to phase in the population cycle: 1) decline and low density years, 2) increase years, 3) peak years. Phases 1) and 3) were significantly different in means and variances (Table 4).



Prediction 7: *In rodent areas, the number of arctic fox placental scars is highest following winter reproduction of rodents.*

In other phases, the number of scars is lower with no differences between rodent and non-rodent areas. This was not supported, since the mean number of scars was high also in other phases of the rodent cycle (Macpherson 1969; for red fox: Englund 1970). In the data presented by Hall (1989), there were inter-year differences in placental scar counts, but the highest numbers occurred during rodent peak and decline phases, not during the increase phase. The prediction was not supported.

The reproductive allocation hypothesis

The hypothesis that arctic foxes are unable to produce large litters in several consecutive years generates the following prediction.

Prediction 8: *The reproductive effort, i.e. litter size, in one year affects reproduction in following years negatively.*

Arctic foxes on St. Lawrence Island implanted a large number of embryos every year (Fay and Rausch 1992). The figures for this population were among the highest of all (Table 2). Moreover, pregnancy rates were high (mean = 86.2% per year, $N = 94$) and did not differ between years. Ages of the studied animals were normally distributed and the oldest animal was 8 years old. Given a reasonably small migration to and from the island, and the fact that most arctic foxes start repro-

ducing in their first two years of life (Hersteinsson 1984, Hall 1989, Tannerfeldt and Angerbjörn 1996), this indicated that the same animals had large litters in several consecutive years. Our own data indicate that an individual's litter size in a given year is determined by food resources (Tannerfeldt and Angerbjörn 1996) and not by litter size the previous year or individual differences (multiple regression, litter previous year: $p = 0.25$, individual: $p = 0.20$, $R^2 = 0.13$, $N = 18$). Interestingly, Prestrud and Nilssen (1992) found that among females caught November–March, those that had reproduced the previous spring had less subcutaneous fat reserves than other females. This suggests a cost of reproduction, although it is not known if it actually affects subsequent breeding negatively. As mentioned earlier, Hall (1989) did not find any correlation between the number of placental scars and a subcutaneous fat index. It must be concluded that at present there is no evidence for a substantial cost of reproduction in the arctic fox.

The jackpot hypothesis

If litter size reaction norms are adapted to the degree of predictability in resource level fluctuations, the following predictions can be made.

Prediction 9: *The range of litter sizes is larger in unpredictable than in predictable environments.*

This was supported for weaned litter sizes since maximum values differed; for placental scar counts there was a strong tendency despite small sample sizes (Table 3, Fig. 2).

Table 4. Comparisons between weaned litter sizes in different population phases of the arctic fox population cycle in Sweden: 1) low density years, 2) increase years, and 3) peak years. Years with no reproduction were excluded. For means, there was neither an effect of county nor was the interaction term significant, but there were differences between the population phases (Two-way anova on square root-transformed data, phase: $p = 0.030$, $F_{2,155} = 3.59$; county: $p = 0.85$, $F_{2,155} = 0.16$). There were significant differences in litter size means (Newman-Keul post-hoc test) and variances, but not in coefficients of variation (corrected CV, Sokal and Rohlf 1981) between the peak (3) and low (1) population phases. Data reanalysed from Angerbjörn et al. (1995).

Pop. phase	Mean	sd	CV	<i>N</i>	Comparisons	<i>p</i> (mean)	<i>p</i> (sd)	<i>p</i> (CV)
1	4.8	2.0	42.32	16	1–2	0.33	0.11	0.67
2	5.5	2.9	53.03	43	2–3	0.15	0.19	0.58
3	6.9	3.5	50.84	106	3–1	0.04	0.01	0.64

Prediction 10: *Within populations, weaned litter sizes are adjusted by resource levels, but with equal resources, animals from unpredictable environments have more placental scars and larger weaned litters than those from predictable environments.*

If the norms of reaction differ, there is an interaction between the effects from immediate food availability and the resource predictability experienced by the population. As shown under predictions 3 and 6, litter size is positively related to food availability within populations. Under prediction 2 we showed that with equal resources, placental scar counts are higher in rodent eating fox populations. Comparing weaned litter sizes in the same populations, again the rodent eating foxes had higher values ($p = 0.007$; Svalbard: mean = 5.3, sd = 1.7, $N = 35$; Canada: mean = 7.6, sd = 3.5, $N = 9$). These results were further supported by the comparisons between populations (Table 3).

In conclusion, the results from placental scar counts partly support the density variation hypothesis, whereas litter sizes are best explained by the energy limitation hypothesis. Neither the hormone turbo hypothesis nor the resource allocation hypothesis explained the arctic fox data. The more complex view adopted in the jackpot hypothesis gained most support.

Discussion

We have found significant differences in reproductive rates between arctic foxes whose main food source is fluctuating rodents and foxes for which rodents are unimportant in the diet. This difference is manifested in both pre- and post-natal litter sizes, measured as placental scar counts and the number of cubs at weaning, respectively. Arctic foxes with fluctuating, unpredictable food resources have larger mean and maximum litter sizes. There is no information on the relation between litter size and total litter weight in wild arctic foxes. In fluctuating populations, large litters are associated with good food availability and we do therefore not expect a negative relation. The trade-off should be more evident in stable populations and when food availability changes during the reproductive season.

The arctic fox occurs in two distinct colour morphs, blue and white. Bræstrup (1941) suggested that these live in different habitats, with different genetics, diets and life histories. However, the proportion of the colour morphs in a population seems rather to be influenced by the extent of snow-cover and camouflage properties (Hersteinsson 1989, Birks and Penford 1990). The details of colour morph inheritance in the arctic fox are still unclear (Adalsteinsson et al. 1987, Filistowicz et al. 1997).

Inter-year differences in litter size means within populations can be explained by the fact that weaned litter size is strongly correlated with food abundance (Macpherson 1969, Hersteinsson 1984, Hall 1989). When arctic foxes in rodent areas reproduce, they mostly do so in years of high or very high rodent abundance. Thus, it is possible that average food availability for breeding foxes in areas without rodents is lower than it is for breeders in rodent areas. The difficulty arises when we look at the very large litters. Bird-cliffs and tidal zones can be extremely rich in food resources (e.g. Hersteinsson 1984, Prestrud 1992b). For example, a coastal dwelling fox who has access to a walrus (*Odobenus rosmarus*) carcass or a dense colony of breeding eider ducks (*Somateria mollissima*) would be expected to raise a large litter if food abundance was the only determinant of litter size. We would therefore expect at least a few of the several hundred 'non-rodent' litters to have more than 12 cubs. This is not the case (Table 1). Even in a population where there were individuals with a body fat content of 40%, no female had more than 11 placental scars ($N = 102$; Prestrud 1992a, Prestrud and Nilssen 1992), a number only half that of maximum scar counts in rodent areas (Macpherson 1969, Hammill 1983, Fay and Rausch 1992). It thus appears that energetic limitations can explain intrapopulation differences in litter size means, but not differences between cyclic and non-cyclic populations.

Hersteinsson (1990) showed that for arctic foxes in the stable Icelandic population, relative pre-weaning mortality increased with litter size. This suggests that there is selection against larger litter sizes in stable populations. Hersteinsson (1990) also found that the number of teats in Icelandic arctic fox females was

much higher than expected from litter sizes. The median number of teats was 13 and the range 11–17 ($N = 84$), which can be compared to the small litter sizes in that population (median 4, maximum 10, $N = 309$, Hersteinsson 1984). The closest relative to arctic foxes, the swift or kit fox (*Vulpes velox*), Geffen et al. 1992, 1996), has 8 teats and up to six young. The red fox normally has 8 teats and a maximum litter size of 9 (Ewer 1973, Sheldon 1992). It can thus be concluded that relatively isolated arctic fox populations without rodents in the diet, living in stable populations, have lost the capacity for having very large litters, but have retained a large number of teats.

Migrations of more than 1000 km have been registered for arctic foxes in several populations, both southward into the taiga as well as latitudinally and even north, far out on the pack ice (e.g. Pulliainen 1965, Cheseomore 1968, Bannikov 1970, Eberhardt and Hanson 1978). Yet, all non-rodent eating populations in this study are island populations. Non-rodent areas, such as West Greenland, are occasionally invaded by large numbers of 'lemming foxes' that seemingly have emigrated from North America in rodent crash years (Bræstrup 1941, Elton 1949). However, there is no evidence that these immigrants enter the population and start breeding (P. Hersteinsson pers. comm.). Although there is opportunity for migrations and gene flow between widely separated arctic fox populations, it does not seem to occur in substantial numbers. Circumpolar genetic studies on the arctic fox have started only recently and data on arctic fox population genetics are still largely lacking.

If lower maxima in stable populations is the result of selection for reduced variance in the reaction norm, the coefficients of litter size variation (CV) should be larger in fluctuating than in stable populations, whereas litter size means should be equal. However, there were no differences in CV, neither for placental scar counts nor for litter size. On the other hand, both scar count and litter size means were significantly different. Thus, the stable populations have been selected for having smaller litters than populations with unpredictable resource levels. The density variation hypothesis (Stenseth et al. 1985) assumes that all things except density variation are equal. This is not the case for arctic foxes, since differences in population density are correlated with differences in food availability (Kaikusalo and Angerbjörn 1995). The hypothesis does not fully agree with placental scar counts, since Hall (1989) in a rodent area found the mean number of placental scars to be low during two out of four years. These were years of rodent population lows. The results of England's (1970) comprehensive red fox studies can explain this. England found that ovulation rates and pre-implantation losses were related to food availability. Energetic limitations thus act also before implantation and affect scar counts. For arctic foxes, it seems that energy limitation

acts in concert with density variation to produce two genetic strategies. In areas with a relatively stable food supply, the ability to produce very large litters is lost and mean numbers of both placental scars and litter sizes are lower than in fluctuating populations. Within each genetic strategy, litter size is adjusted by food availability through ovulation rates and pre-natal losses caused by energetic stress. The effect of energy limitation will continue also after birth, with a reduction in litter sizes during lactation. The arctic fox's diet is almost exclusively carnivorous, so we have here only discussed the energy component of food as limiting. When generalising our conclusions to other species, we are probably more correct in referring to nutritional rather than energetic limitations.

The complete scenario outlined above can be illustrated as an adaptive difference in reaction norms between stable and fluctuating populations according to the jackpot hypothesis. If litter sizes are determined solely by energetic limitations, the reaction norm will be the same in stable and fluctuating populations, as illustrated in Fig. 4a. On the other hand, if litter sizes are completely determined by genetics, litter sizes will be constant over a wide range of resource levels but stable populations will have lower means (Fig. 4b). Neither of these illustrations correspond with data on arctic fox litter sizes. Instead, we suggest that determination of litter sizes is best explained by the jackpot hypothesis which combines the effects from nutritional (energetic) and genetic (density variation) factors. The reaction norm of arctic fox litter sizes can then be illustrated as in Fig. 4c. This hypothesis implies that the shape of the reaction norm is determined by the degree of cyclicity (*sensu* Stenseth et al. 1985). In populations with moderate fluctuations, we would thus expect a norm of reaction which is intermediate between "stable" and "unpredictable" in Fig. 4c.

The jackpot hypothesis could be further tested on other species with intraspecific differences in population stability. In the red fox, for example, we would predict a similar litter size difference, albeit not as pronounced, between stable and fluctuating populations that have little genetic exchange. In non-mammalian species, we would expect energy-dependent litter size reductions to occur mainly after birth or hatching. Egg clutch sizes in a bird species could provide a good measure to investigate the genetic component. However, we would need to find a species that occurs in both stable and fluctuating populations that are relatively isolated from one another.

From the hormone turbo hypothesis, population differences in reproductive rates could be explained if foxes feeding on rodents sometimes are being 'lured' into giving birth to a larger litter (Lindström 1988). Since this would happen only in years of increasing and high rodent abundance, however, the cost to the parents in terms of lost future reproductive success might

be low or even nil. We would therefore not expect a strong selection pressure against this 'mistake'. In species that feed on prey with less pronounced fluctuations, the situation with an extremely high proportion of reproductive females in the diet might never arise. Prediction 7 from the hormone turbo hypothesis was not supported by data on the arctic fox. The prediction is based on the assumption that energetic and genetic constraints are absent. However, the mechanism could also be an additional effect, boosting litter sizes in certain years when food resources are not limiting. This would best be tested in a feeding experiment, since the proportion of reproductive rodent females and rodent numbers are not independent in natural populations.

The reproductive allocation hypothesis suggests that animals experiencing a year of high food abundance spend very large amounts of energy in raising a large

litter, which renders them unable to breed the next year. Animals in stable environments, on the other hand, allocate a given total lifetime reproductive success to several years of breeding (Frafjord 1993). We have not found a negative effect of litter size on subsequent breeding. Breeding, at least in a stable population, results in lowered female fat reserves the following winter (Prestrud and Nilssen 1992), but the effect on subsequent reproduction remains to be shown. Without a substantial cost of reproduction, the hypothesis cannot explain population differences in litter size. Moreover, although animals with stable food resources may have a larger expected future reproductive output than animals in unstable populations, their chances of future reproduction are certainly not 100%. For an animal to 'willingly' reduce its reproductive output in this situation, the expected future number of offspring must be quite large. This does not seem to be the case for the arctic fox. Even in relatively stable and productive habitats most animals only have one or two reproductive seasons. Adult mortality has in several studies been around 50% in both rodent and non-rodent areas, regardless of whether mortality chiefly was caused by human hunting or starvation, disease and predators (Hersteinsson 1984, Hiruki and Stirling 1989, Prestrud 1992a, Tannerfeldt and Angerbjörn 1996). Thus, contrary to the reproductive allocation hypothesis, also animals in stable populations should produce the litter size that yields close to optimum reproductive output within each season. Furthermore, this hypothesis does not take into account that the cost of trying to produce large litters depends on the stage to which foetuses are brought. Actually, the cost of producing embryos that are lost early might be negligible in comparison with the cost of lactation (Bronson 1989).

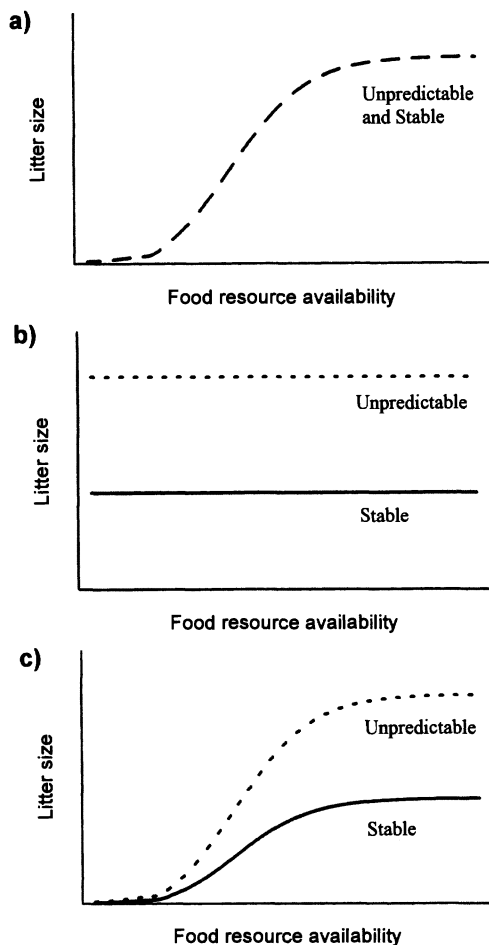


Fig. 4. Tentative reaction norms of arctic fox litter size in relation to food resource availability. According to a) the energy limitation hypothesis, b) the density variation hypothesis, and c) the jackpot hypothesis. Available data are best explained by the reaction norms presented in c), where litter size in the arctic fox is determined by the combined effect of immediate resource levels and the degree of resource predictability.

Conclusions

Arctic fox litter size is extremely variable and the maximum number of cubs is among the highest within the Carnivora. We have discussed five hypotheses on the determination of variation in litter size: one energetic, one genetic, one diet-determined, one that considers reproductive allocation and one based on adaptive plasticity and selection on reaction norms. Our findings suggest that litter size in the arctic fox is determined by the combined effect of immediate resource levels and the degree of resource predictability. A similar conclusion was drawn for voles by Stenseth et al. (1985). We describe reaction norms that suggest how litter size results from adaptive plasticity within each of two genetic strategies, where stable populations generally have smaller litter sizes. The differences in placental scar counts and maximum litter size between arctic foxes in rodent versus non-rodent areas, are thus due to differences in predictability. Due to a non-selective

situation during population crashes, and possibly also a relatively long increase phase, selection favours maturation of a large number of eggs in fluctuating populations. In stable populations, the ability to produce very large litters is lost, reducing both the number of implanted eggs and litter size. Within each genetic strategy, or reaction norm, and thus also within populations, litter sizes are adjusted through a number of plastic traits. These traits are influenced by nutritional limitations and include reduced ovulation rates, pre-implantation losses, resorption and abortion. After birth, litters are reduced further during the lactation period if food resources are scarce.

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