Free love in the far north: plural breeding and polyandry of arctic foxes (*Alopex lagopus*) on Bylot Island, Nunavut

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Abstract: Molecular studies show that canid breeding systems are more complex than field data have sometimes suggested. For example, microsatellite DNA fingerprints of offspring and adults within their social group indicate that many canid species thought to form monogamous pairs engage in polygyny, polyandry, and plural breeding. In many areas, arctic foxes (*Alopex lagopus* (L., 1758)) are considered monogamous, with the complexity of their social systems increasing as population isolation increases. We combined a genetic approach with spatial data of arctic foxes on Bylot Island, Nunavut, Canada, to investigate breeding patterns in a population less isolated than many previously studied. As in previous field studies, single breeding pairs were most common, but one case of plural breeding and one case of polyandry with multiple paternity were also observed. Reproductive output in arctic foxes is closely tied to the productivity of their habitat in a given year; we support the hypothesis that abundant resources at our study site have also contributed to complex breeding patterns among resident foxes. We also suggest that increased genetic variation among offspring of multiply mated females may provide an additional adaptive advantage to species in uncertain environments.

Résumé : Les analyses moléculaires montrent que les systèmes de reproduction des canidés sont plus complexes que ne le laissent quelquefois croire les données de terrain. Par exemple, les signatures des microsatellites d'ADN des rejetons et des adultes à l'intérieur de leur groupe social indiquent que plusieurs espèces de canidés qu'on croit généralement former des couples monogames s'adonnent à la polygynie, à la polyandrie et aux accouplements avec plusieurs partenaires. Dans beaucoup de régions, les renards arctiques (*Alopex lagopus* (L., 1758)) passent pour monogames, bien que la complexité de leurs systèmes sociaux augmente en fonction de l'isolement de la population. Nous combinons une méthodologie génétique à des données spatiales sur les renards arctiques de l'île Bylot, Nunavut, Canada, afin d'étudier les patrons de reproduction dans une population qui est moins isolée que beaucoup de celles étudiées précédemment. Comme dans les études antérieures, il y a prédominance de couples reproducteurs exclusifs; on observe cependant un cas de reproduction avec plusieurs partenaires et un cas de polyandrie avec paternités multiples. Pour une année donnée, le rendement reproductif des renards arctiques est fortement relié à la productivité de leur habitat; nous sommes d'accord avec l'hypothèse qui veut que des ressources abondantes dans notre site d'étude contribuent aussi au développement de patrons de reproduction complexes chez les renards résidents. Nous croyons de plus que la variation génétique accrue chez les rejetons des femelles accouplées à plusieurs partenaires apporte un avantage adaptatif supplémentaire chez les espèces qui vivent dans des milieux imprévisibles.

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Introduction

Molecular genetic techniques have begun to reveal complexities in mammalian mating systems that were not apparent from observational studies of social behavior. For example, many canid species were thought to form territorial groups consisting of a dominant mated pair and a collection of subordinates, often presumed to be offspring or relatives (Geffen et al. 1996). However, recent comparisons of microsatellite DNA fingerprints between juveniles and adults of their social group have challenged such simple structures in a number of species (e.g., Sillero-Zubiri et al. 1996; Baker et al. 2004; Kitchen et al. 2006).

In wolf-like canids, multiple paternity of single litters (African wild dog, *Lycaon pictus* (Temminck, 1820), Girman et al. 1997; Ethiopian wolf, *Canis simensis* Rüppell, 1840, Gottelli et al. 1994; Sillero-Zubiri et al. 1996) and plural breeding within social groups (African wild dog, Girman et al. 1997; grey wolf, *Canis lupus* Linnaeus, 1758, Meier et al. 1995) have been documented using genetic methods. More recently, polygyny (males breeding with multiple females), polyandry (females breeding with multiple males), multiple paternity (single litters with multiple sires), and plural breeding (multiple breeding females in a social group) have been demonstrated in fox-like canids such as red foxes (*Vulpes vulpes* Linnaeus, 1758, Baker et

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al. 2004), island foxes (*Urocyon littoralis* (Baird, 1857), Roemer et al. 2001), and swift foxes (*Vulpes velox* (Say, 1823), Kitchen et al. 2006), confirming the existence of complex mating patterns throughout the canid lineage.

The arctic fox (*Alopex lagopus* (Linnaeus, 1758)) is a small canid adapted to Arctic and alpine climates that are often characterized by spatiotemporal resource variability (Prestrud 1991; Angerbjörn et al. 1999; Eide et al. 2004, 2005). Especially in continuous, continental portions of their range, arctic foxes are territorial primarily during the breeding season and tend to form smaller social groups than other canids (Garrott et al. 1984; Audet et al. 2002; Baker et al. 2004). However, field studies demonstrate increasing social complexity with increasing population isolation (Kruuk and Macdonald 1985; White 1993; Kruchenkova and Goltsman 1994; Goltsman et al. 2003, 2005*a*, 2005*b*; Tannerfeldt et al. 2003; Angerbjörn et al. 2004*a*): Mednyi Island foxes, which have been completely isolated since the Pleistocene, occur in permanent families ranging from 2 to 6 adults and yearlings (Angerbjörn et al. 2004*b*; Goltsman et al. 2005*a*). On Mednyi and in similarly isolated populations, single breeding pairs remain most typical (White 1993; Goltsman et al. 2003; Angerbjörn et al. 2004*a*), but groups commonly contain multiple females and occasionally multiple males (Kruuk and Macdonald 1985; White 1993; Angerbjörn et al. 2004*a*; Goltsman et al. 2005*a*, 2005*b*). Plural breeding is suggested by cohabitation of cubs of different sizes (White 1993; Tannerfeldt et al. 2003), and two or more lactating females may share a single den (White 1993; Strand et al. 2000; Angerbjörn et al. 2004*a*; Goltsman et al. 2005*a*). However, island populations of many species show greater social, if not necessarily breeding, complexity (Goltsman et al. 2005*a*) and because lactation may occur in arctic foxes without reproduction (White 1993; Goltsman et al. 2005*a*), the precise nature and variety of their breeding patterns, particularly in more continuous populations, could be clarified using molecular methodology.

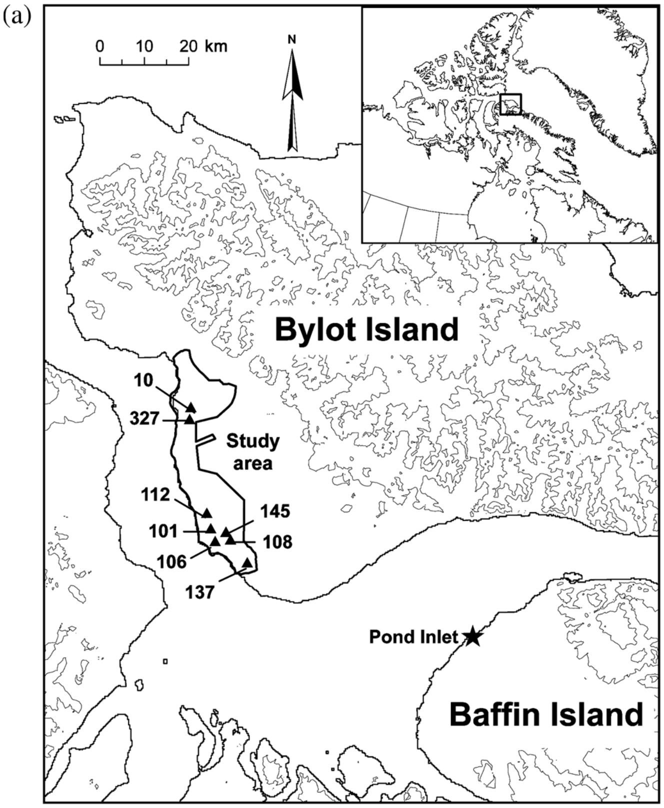
For the present study, we collected DNA samples from arctic foxes trapped at dens on Bylot Island, Nunavut (Fig. 1*a*). The combination of social group data and microsatellite fingerprinting techniques allowed us to explore mating patterns in an island fox population that is connected by annual sea ice to the larger distribution of the species in Canada.

Materials and methods

Study area

Our study was conducted on the south plain of Bylot Island (73°00′N, 80°00′W) in Sirmilik National Park, Nunavut, Canada (Fig. 1*a*). The area is characterized by large upland mesic plateaus covering 90% of the landscape (Massé et al. 2001) and intersected by several valleys filled with moist lowland habitats. More than 20 000 greater snow geese (*Chen caerulescens atlantica* Linnaeus, 1758) pairs breed in this area annually (Reed et al. 2002), and many other migratory bird species are present during the arctic fox denning season (Lepage et al. 1998). The brown lemming (*Lemmus sibiricus* (Kerr, 1792)) and the collared lemming (*Dicrostonyx groenlandicus* (Traill, 1823)) are the primary prey of foxes on Bylot Island; foxes also use goose

Fig. 1. (*a*) Study area on Bylot Island (73°00′N, 80°00′W), Nunavut, Canada. Triangles represent occupied fox dens (2004) and den numbers are given. (*b*) Summary of inclusion/exclusion analysis. Each den is represented by a horizontal box. Sampled individuals are labeled with the letters BY; unsampled individuals predicted by exclusion analysis are indicated by ?'s and coded with den numbers and letters. Horizontal lines within den boxes indicate the presence of multiple same-sex parents at a den. For example, in den 145, male BY04 was included as the father of BY06 and BY12, but putative father 145A would be required to explain the remaining offspring; two unsampled females are also inferred at this den. Mean and standard deviation of cub mass (g) at time of capture are given.



(b)

Den	Male	Female	Offspring	Mass
010	BY15	? 010A	All	1965 ± 80
101 - Polyandry - Multiple Paternity	? 101A ? 101B (cubs cannot be divided among these males)	BY07	BY10 BY16 BY19 BY28 BY44 BY22 BY43 BY14 BY49	950 ± 97
106	BY01	BY21	All	1468 ± 67
108	? 108A	? 108B	All	1346 ± 117
112	? 112A	? 112B	All	1236 ± 24
137	BY34	? 137A	BY03	2900
145 - Plural breeding	BY04	? 145B ? 145C (cubs cannot be divided)	BY06 BY12	1324 ± 177
	? 145A		BY05 BY13 BY17 BY26	
327	? 327A	? 327B	All	1900 ± 71

eggs and chicks, especially when rodent populations decline (Bêty et al. 2001).

Field methods and sample collection

In the summer of 2003 we performed an extensive den survey by foot and snowmobile over approximately 425 km^2 (Fig. 1*a*). The study site was delimited to the west by Navy Board Inlet and to the north and east by semideserts where arctic fox dens appeared to be rare or absent. More dens are present to the south but logistical limitations prevented us from surveying this area.

The position of every fox den discovered was recorded using a global positioning system. In 2004, each den was visited 2 or 3 times to identify those inhabited by reproductive foxes. Arctic foxes were observed at 18 dens, but adults moved cubs to new dens on at least 3 occasions; therefore, no more than 15 litters existed in the study area. Between 19 June and 28 July, foxes were trapped at 8 occupied dens using collapsible live traps (Model 205, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) placed directly on the den or padded leghold traps (Softcatch No. 1, Oneida Victor Inc. Ltd., Cleveland, Ohio, USA) positioned within 100 m. Traps were kept under continuous surveillance or visited at least every 12 h, depending on the site. We anesthetized captured adults by injecting 15 mg of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) into the upper rear leg muscle; juveniles were manipulated without chemical immobilization using a large fabric bag. Each individual was measured, weighed, sexed, and tagged on both ears using a unique set of colored and numbered plastic tags (Dalton Rototags). Twenty to 40 summer hairs were collected from the back or flank of each animal and stored dry for genetic analysis; ear plugs from tagging were also retained.

Capture techniques and immobilization procedures were approved by the Université du Québec à Rimouski Animal Care Committee (permit No. CPA15-02-01) and field research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada (permit No. SNP-2004-003).

Microsatellite DNA fingerprinting

DNA was extracted using a QIAGEN tissue protocol (QIAGEN, Hilden, Germany). Twelve independently assorting (L.E. Carmichael et al., unpublished data), biparentally inherited microsatellite loci were PCR-amplified from each individual using primers designed from domestic dogs (CPH5, CPH9, and CPH15, Fredholm and Wintero 1995; CXX671, CXX733, CXX745, CXX758, and CXX771, Mellersh et al. 1997; CXX140, CXX147, CXX173, and CXX250, Ostrander et al. 1993) and labeled with fluorescent tags (FAM, TET, or HEX, Applied Biosystems, Foster City, California). Single-locus amplifications of CPH5, CPH9, CXX140, CXX147, CXX250, or CXX745 contained 0.16 μmol/L each primer, 0.12 mmol/L dNTPs, 2.5 mmol/L $MgCl_2$, 1× PCR buffer (50 mmol/L KCl, 10 mmol/L Tris-HCl, pH 8.8, 0.1% Triton X-100), 1 U of Taq polymerase, and approximately 40 ng of template in a total volume of 15 μL. For multiplex reactions of CXX173/CXX671, CPH15/CXX758, or CXX733/CXX771, we increased the dNTP concentration to 0.16 mmol/L and $MgCl_2$ to 2.7 mmol/L. All amplifications were conducted in Eppendorf Mastercycler ep thermocyclers (Eppendorf AG, Hamburg, Germany) using the following temperature profile: 2 min at 94 °C; 3 cycles of 45 s at 94 °C, 30 s at 50 °C, and 10 s at 72 °C; 30 cycles of 35 s at 94 °C, 35 s at 50 °C, and 5 s at 72 °C; and 30 min at 72 °C. Reaction products were pooled and separated on an ABI PRISM 377 DNA Sequencer (Applied Biosystems) and genotypes assigned using GeneScan Version 3.1 and Genotyper Version 2.0 software (Applied Biosystems). Genotypes for each individual were replicated from ear plugs, in a separate laboratory, and data from both sources were compared for accuracy.

We used GENEPOP Version 3.4 (Guo and Thompson 1992; Raymond and Rousset 1995) to test conformance to Hardy–Weinberg equilibrium among adult foxes in our sample prior to parentage analysis.

Assignment of parentage and calculation of relatedness

Our sample of 49 individuals contained only 7 adult foxes, a small proportion of the total population. Owing to low adult sample size, population allele frequency estimations are likely inaccurate. Therefore, probabilistic or likelihood-based assignments of parentage could not be performed with confidence. We used instead an inclusion/exclusion test based on simple Mendelian heredity of codominant microsatellite markers, whereby offspring inherit one allele at each locus from each parent.

Each adult fox was assumed to belong to the social group associated with its den of capture. Genotypes of resident adults were tested against the genotypes of cubs found at their den; adults who shared at least one allele at every locus with a cub were included as potential parents of that cub. At den 106, one adult male and one adult female were captured; paternal alleles were checked against offspring after maternal alleles had been identified (i.e., adults were treated as a parental set). Although Baker et al. (2004) and Roemer et al. (2001) considered single-locus mismatches adequate for full parental exclusion, we interpreted them as indicating ‘‘potential exclusion’’ to allow for the possibility of germ-line mutation. Mismatches at two or more loci were considered sufficient for full exclusion (Kitchen et al. 2006).

Female foxes are likely to be spatially associated with their own cubs or cubs of their social group only (Strand et al. 2000). However, as in other canids, male foxes may fertilize females of other social groups and may therefore sire offspring found at other dens (Baker et al. 2004; Kitchen et al. 2006). For cubs in dens where the resident male had been excluded as a father or where no adults were sampled, all other sampled males were tested as potential fathers. For dens with no sampled adults, the number of unique alleles observed at a single locus was used to estimate the minimum number of parents required to produce the observed offspring.

Relatedness coefficients (*r*, Queller and Goodnight 1989) are indices of the proportion of alleles identical by descent between two individuals, accounting for the frequencies of those alleles in the population. A pair of individuals with *r* between –1 and 0 are less related, on average, than two randomly chosen individuals, while those with *r* between 0 and +1 are more related; $r \approx 0.5$ is expected for first-degree relationships (parent–offspring or full sibling), while $r \approx 0.25$ is predicted for half-siblings or other similarly related pairs. The midpoint 0.375 can be used as a cutoff to distinguish between first- and second-degree relatives (Blouin et al. 1996; Kitchen et al. 2006). Pairwise r was calculated between all foxes using SPAGeDi Version 1.2 (Hardy and Vekemans 2002). Average values and standard deviations were also calculated among foxes at each den. Again, owing to small sample size, allele frequencies could not be estimated with confidence. Therefore, r values should be considered approximate and were not used to draw conclusions but to provide additional support for conclusions based on inclusion/exclusion analysis.

Results

Sampling and genotyping

Two adult females, 4 adult males, and 42 juvenile foxes were sampled from a total of 8 dens. An additional male, BY08, was sampled near the greater snow goose nesting colony near the den sites but was genetically excluded as a potential father for all juveniles in the study.

Genotyping of the 49 foxes was 99.8% complete, and no fox was typed for fewer than 11 loci. Among adult foxes, no microsatellite deviated significantly from Hardy–Weinberg equilibrium. Taken together, these results suggest that null alleles were rare or absent in our sample. High levels of heterozygosity and gene flow inferred among all Canadian populations of arctic foxes (L.E. Carmichael et al., unpublished data) also suggest inbreeding is not a concern.

On three occasions, we observed adult foxes moving cubs between dens. This behavior is common, as home ranges generally include a number of potential dens (e.g., White 1993; Tannerfeldt et al. 2003). On Bylot Island, the translocations occurred late in the denning season, when cubs were older and thus heavier. However, there was no correlation between average cub mass and genetic inference of complex breeding patterns (Fig. 1*b*). Moreover, during a trapping session at a given den, we never observed a juvenile previously marked at another den. Therefore, pups sampled at each den most likely represent offspring of single social groups. The genetic data presented here could still support a number of possible mating configurations, but we present the most parsimonious solutions, involving the smallest number of possible parents for each litter.

A visual summary of our results is presented in Fig. 1*b*. Genotypes of all 48 foxes are given in Table S1[2].

Single breeding pairs

Adult foxes were not sampled at dens 108, 112, or 327. However, although 9 of 12 loci had more than 5 alleles in the adult sample, the cubs from each den contained no more than 4 unique alleles at any locus; therefore, a single male–female pair would be adequate to explain offspring at each den. Relatedness among cubs averaged 0.53 ± 0.14 at den 108, 0.54 ± 0.14 at den 112, and 0.4 at den 327, supporting the conclusion that each litter consisted of full siblings. However, no male in our sample shared one or more alleles per locus with any of these cubs, and therefore their paternity is unknown.

One adult male and one cub were sampled from den 137; the male was included as a possible father of the cub. At den 010, a single male (BY15) was captured and included as a father for all 6 cubs in the litter. Although adult females were not sampled at this den, no more than two putative maternal alleles were observed at any locus, and therefore one mother could explain all cubs in this litter. One adult female and one unrelated adult male (r = –0.13) were sampled at den 106, which contained 4 juvenile foxes. This pair of adults was included as a parental set for all cubs at this den. Therefore, single breeding pairs of adult foxes existed at 6 of 8 dens (75%).

Plural breeding

Adult male BY04 was included as a father for 2 of the 6 pups found at den 145 ($r = 0.45 \pm 0.03$) but excluded at 8 or more loci for the remaining 4; a second male would thus be required to explain these juveniles. This social group may also have included 2 adult females: at locus 173, offspring attributed to male BY04 contained putative maternal alleles 124 and 130, while one cub attributed to the second, unknown male was homozygous for allele 128 (see Table S1[2]). Polyandry and multiple paternity with a maternal germ-line mutation is possible, but plural breeding of two mated pairs seems more likely.

Polyandry with multiple paternity

Adult female BY07 was sampled at den 101 and included as a mother for the 9 cubs found there. However, a second, unidentified female was observed suckling cubs at this den (M.-A. Giroux, personal observation). This female may have lost her litter but remained with the family group (White 1993) or may have been a yearling helper female experiencing induced lactation (Goltsman et al. 2005*a*).

No sampled male was included as the father of any cub at den 101; however, the cubs attributed to female BY07 possessed three putative paternal alleles at loci CXX250, CXX733, CXX745, and CXX758. Relatedness between cubs ranged from –0.14 to 0.75 ($r = 0.31 \pm 0.22$). Therefore, polyandry with multiple paternity is the most parsimonious explanation for the 9 cubs found at this den.

Discussion

Field studies indicate that social structure in arctic foxes is variable and can be complex (Hersteinsson and Macdonald 1982; Korhonen and Alasuutari 1994; Strand et al. 2000; Audet et al. 2002). In many areas, reproduction is restricted to the dominant pair (e.g., Garrott et al. 1984; Kullberg and Angerbjörn 1992; Korhonen and Alasuutari 1994; Eide et al. 2004), while in others, particularly on isolated islands, complex social groups form and may result in polygyny and plural breeding (White 1993; Tannerfeldt et al. 2003; Goltsman et al. 2005*a*). Though our sample size is small, the 25% frequency of complex breeding patterns in

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[2] Supplementary data for this article are available on the journal Web site (http://cjz.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5141. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

the Bylot Island population — which likely endures little physical or reproductive isolation (L.E. Carmichael et al., unpublished data) — is comparable to the frequency observed in studies of truly isolated island populations (35%, White 1993; Goltsman et al. 2003). Our results also provide the first genetic evidence of polyandry with multiple paternity. Further molecular studies of arctic fox breeding patterns, in other areas and with larger sample sizes, will be most interesting.

Group size and breeding season territoriality of arctic foxes have been linked to spatiotemporal resource abundance in a social group's home range (Angerbjörn et al. 2004*a*; Eide et al. 2004). Arctic foxes are known to cache lemmings and bird eggs for winter consumption (Samelius and Alisauskas 2000; Eide et al. 2004; Careau et al. 2006), and subordinate animals of social groups, which may or may not provision cubs directly (White 1993; Strand et al. 2000; Goltsman et al. 2005*a*), have been observed caching food within the territory of the breeding pair (Eide et al. 2004). This behavior suggests a possible energetic advantage to the dominant pair, beyond direct helping, that may permit formation of larger social groups (Angerbjörn et al. 2004*a*; Eide et al. 2004). Plural breeding may thus be elevated in resource-rich habitats. Our study was conducted in an area of Bylot Island that includes both lemmings and avian nesting grounds, and it is worth noting that den 145, representing plural breeding, was located near the snow goose nesting colony.

Explanations for polyandry and its associated multiple paternity are varied, including both material benefits and genetic advantages such as assurance of compatibility between maternal and paternal genomes (Zeh and Zeh 2001). Multiple paternity also allows a female to increase the genetic variation contained in a single season's reproductive output. This increase in variation might result in an increased probability that at least one cub in a litter will be optimally adapted to its current environment or better equipped to deal with changes in its environment over time. The reproductive output of arctic foxes is closely tied to the productivity of their habitat in any given year (Angerbjörn et al. 1995), and multiple paternity may provide an additional adaptive advantage with respect to both recurrent ecological fluctuations and incipient climate-induced changes in the polar habitat of the arctic fox.

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