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Original Article

Spatial variation in food availability predicts extrapair paternity in the arctic fox

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Extrapair paternity (EPP) is described in many socially monogamous species, but within-population variability in its frequency is poorly documented. Availability and distribution of food may influence polyandrous behaviors, either directly by affecting the need for paternal care or indirectly via their effect on population density. We quantified the frequency of EPP in a population of arctic foxes (*Vulpes lagopus*), a predominantly socially monogamous species with high paternal investment. We then tested whether spatial (presence of a goose colony) and temporal (cycles of lemmings) variations in food availability were linked to variations in mating systems within the population. From 2003 to 2008, we studied the mating systems of arctic foxes on Bylot Island (Nunavut, Canada) by combining molecular analyses with behavioral observations during cub rearing. Although the dominant social mating system was monogamy, at least 31% of cubs with known social father were born from extrapair matings (in 10 of 38 litters sampled). Likelihood of EPP was associated with food availability. It was greatest (86%) at the center of the goose colony and decreased sharply with increasing distance from it. EPP can thus be frequent in the socially monogamous arctic fox, and intraspecific variability in extrapair matings is strongly correlated with food availability during cub rearing.
Key words: arctic fox, extrapair paternity, mating system, resource availability, *Vulpes lagopus.* *[Behav Ecol 22:1364–1373 (2011)]*

INTRODUCTION

Until the advent of molecular markers in ecology, birds were thought to be predominantly monogamous, whereas mammals were thought to be mostly polygamous (Lack 1968). Fewer than 3% of mammal species are socially monogamous. These species are mostly primates, rodents, and canids (Kleiman 1977), with evidence coming from long-term pair bonds, high territoriality, cooperative care of young, and intrasexual hostility (Kleiman 1977; Moehlman 1986). However, socially monogamous pairing and high levels of paternal investment do not necessarily reflect mating exclusivity. Genetic evidence of extrapair paternity (EPP) is accumulating in many socially monogamous birds (reviewed in Griffith et al. 2002) and mammals (e.g., mountain brushtail possums, *Trichosurus cunninghami*, Martin et al. 2007; alpine marmots, *Marmota marmota*, Cohas et al. 2006; prairie voles, *Microtus ochrogaster*, Solomon et al. 2004). In mammals, however, reliable studies on EPP frequency and its ecological correlates are still rare, making it difficult to test hypotheses about the evolutionary forces leading to extrapair copulations.

For socially monogamous females, potential benefits of extrapair fertilizations include more optimal offspring heterozygosity or greater within-brood genetic diversity (Zeh and Zeh 1996; Jennions and Petrie 2000; Neff and Pitcher 2005), higher quality of genes transmitted to offspring (Orians 1969; Neff and Pitcher 2005), and fertility insurance (Hoogland 1998). Extrapair fertilization can also be costly for females; they should solicit or refuse extrapair copulations depending on the net benefits they receive (Westneat 1990). In addition to the increased risk of disease transmission during copulations (Poiani and Wilks 2000), extrapair copulations could lead to reduced paternal care by the cuckolded male. These costs could overwhelm potential genetic benefits of EPP, reducing the likelihood of extrapair copulations in species in which paternal investment is important (Griffith et al. 2002).

The abundance and distribution of resources are likely to influence female mating behavior for 2 reasons. First, environmental quality could influence how much females gain from paternal care to their offspring and therefore the likelihood of EPP (Gowaty 1996). Indeed, paternal care may be beneficial to offspring survival when resources are scarce. In such conditions, selection should eliminate those female behaviors potentially leading to reduced paternal care, such as seeking extrapair copulations. In contrast, when resources are abundant, paternal care may influence less offspring survival, and its benefits to the female may be overwhelmed by potential benefits of EPP. The amount of male care that females risk to lose can influence the shape of this relation between resource abundance and EPP. For instance, Forstmeier (2003) found no link between EPP and territory quality in polygynous dusky warblers (*Phylloscopus fuscatus*), presumably because second-status females had little male care at risk. In the cooperatively breeding superb starling (*Lamprotornis superbus*, Rubenstein 2007), EPP was even negatively correlated to territory quality as polyandrous females benefited from additional care by male helpers in low-quality territories. However, in socially monogamous species with biparental care, EPP frequency should increase with increased territory quality.

Second, resource distribution can also affect the distribution of individuals, potentially indirectly affecting mating behaviors. When food is limiting in a population, greater food

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abundance should increase density of breeding animals, thus increasing the probability of encounters between males and females seeking extrapair copulations. In serins (*Serinus serinus*), EPP was more frequent when food was experimentally increased (Hoi-Leitner et al. 1999). Spatial and temporal variability in food abundance may therefore predict the occurrence of EPP, although few studies link these 2 parameters (but see Vaclav et al. 2003; Humbird and Neudorf 2008).

The arctic fox (*Vulpes lagopus*) is a solitary forager in which the social group consists of the breeding pair and their young, with occasionally an additional nonbreeding female. Arctic foxes were considered strictly monogamous (Hersteinsson et al. 1989; Audet et al. 2002) until a recent genetic study based on a small sample size revealed 2 instances of EPP (Carmichael, Szor, et al. 2007). Because paternal investment may be a determinant of survival in some fox species (Wright 2006), it is unclear whether EPP is common in arctic foxes. Most arctic fox populations face spatial and temporal variations in resource abundance, with effects on reproductive output and demography (Frafjord 1993; Tannerfeldt and Angerbjörn 1998; Angerbjörn et al. 1999; Angerbjörn et al. 2004). This species is therefore well suited to investigate the links between variation in resource availability and EPP.

Our study population inhabits Bylot Island, Nunavut, Canada, where arctic foxes feed primarily on collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus sibiricus*) lemmings that show strong multiannual fluctuations in abundance (Gruyer et al. 2008). Part of the population also feeds on eggs and adult birds at a large greater snow goose (*Anser caerulescens*) colony, especially when lemming abundance is low (Bêty et al. 2001; Gauthier et al. 2004). However, goose availability is spatially limited, and foxes feed on goose mostly when their dens are within 4 km of the colony's edge (Giroux 2007).

Our first objective was to determine whether recent finding of EPP in arctic foxes (Carmichael, Szor, et al. 2007) represents a common occurrence in the species. Our second objective was to test the hypothesis that higher food abundance leads to more occurrences of EPP. We tested 2 predictions: 1) EPP is more frequent when dens are located near a concentered food source (the goose colony), and 2) EPP is more frequent in years of high lemming abundance.

MATERIALS AND METHODS

Captures and sampling

We monitored arctic foxes on the south plain of Bylot Island (lat 73°N, long 80°W), located in Sirmilik National Park, Canada, during summers 2003–2008. In the summers 2003 and 2004, an area of 650 km^2 was systematically searched for arctic fox dens (62 dens had been found before 2003). From 2003 to 2008, all recorded den sites ($n = 96$) were visited at least twice annually (early June and early July) to look for signs of reproduction. We trapped adults using collapsible live traps (Tomahawk cage traps #205, Tomahawk Live Trap Company, Tomakawk, WI) or padded leghold traps (Softcatch #1, Oneida Victor Inc. Ltd. Cleveland, OH) visited every 6–12 h. We trapped cubs with collapsible live traps placed directly on the den and kept under continuous surveillance. Each individual was sexed, and both ears were tagged using a unique set of colored numbered plastic tags (Rototags; Dalton Supplies, Henley-on-Thames, UK). Tissue samples from the resulting ear plugs were collected and stored in 70% ethanol for genetic analyses.

Behavioral observations

We kept dens under continuous surveillance during cub trapping (trapping surveillance periods) and could therefore assess number and identity of adults attending the den as well as minimum litter size. Surveillance duration varied between dens but lasted on average 32.0 ± 14.9 h (±standard deviation [SD]; Tables 1 and 2). We considered a tagged adult as social parent of a litter if it attended the den during the cub-rearing period. We also noted the minimum number of untagged adults attending the den based on their color patterns and physical characteristics. Trapping surveillance periods were spread from mid-June to mid-August after cubs had emerged from the den.

In 2007 and 2008, during trapping surveillance periods, we also performed detailed observations of fox behavior during some subperiods that we called "focal observation periods." We used 2 techniques. First, we performed focal observations from blinds located 350–700 m from the dens, using 10 × 60

Table 1

Summary of sampling effort (trapping surveillance periods, focal observation periods, and photographs from automatically triggered cameras) at arctic fox reproductive dens on Bylot Island, Nunavut, Canada, 2003–2008

	2003	2004	2005	2006	2007	2008	Total
Number of monitored dens	99	100	101	111	99	103	613[a]
Minimum number of litters within the study area	3	17	7	2	10	22	61
Number of litters observed during ≥1 trapping surveillance periods	3	8	5	2	9	9	36
Duration (h) of trapping surveillance periods (mean ± SD)	49.4 ± 7.8	35.4 ± 14.8	31.1 ± 16.2	40.1 ± 19.2	28.7 ± 16.4	25.2 ± 10.6	1152.6
Number of focal observation periods at dens used by ≥1 tagged adults	0	0	0	0	8	6	14
Duration (h) of focal observation periods per litter (mean ± SD)	—	—	—	—	19.7 ± 16.4	28.5 ± 10.7	329
Number of litters with automatic cameras placed at den	0	0	0	0	9	11	20
Number of hours with a camera (mean ± SD)	—	—	—	—	94.4 ± 49.6	232.7 ± 193.5	3410
Number of pictures recorded (mean ± SD)	—	—	—	—	1344 ± 1077	6159 ± 5563	79 846

[a] Sample sizes correspond to "den years" because most dens were monitored every year.

Table 2

Social and genetic parentage of tagged cubs from arctic fox litters on Bylot Island, Nunavut, Canada from 2003 to 2008

						Social parents			Genetic parents		
Year	Den ID	Duration of trapping surveillance (h)	Minimum litter size	Tagged cubs (♂,♀)	Cubs "*r*"	Father	Mother(s)	Parents "*r*"	Father(s)	Mother	Paternity (*n*)—Outcome
2003	113	52.5	4	2 (2,0)	0.39	Ukn	F33	NA	Una	F33	Single—3
2003	115	55.1	7	6 (4,2)	0.44	Ukn	Ukn	NA	Una	Una	Single—3
2003	137	40.5	6	4 (2,2)	0.41	M20	Ukn	NA	M20	Una	IPP—1
2004	010	36.4	8	6 (6,0)	0.39	M67	F75	0.11	M67	F75	IPP—1
2004	101	34.7	10	9 (4,5)	0.44 (0.22)	Ukn	F56, Ukn	NA	Una1, **Una2**	F56	Multiple—5
2004	106	48.1	7	4 (3,1)	0.60	M44	F43	−0.06	M44	F43	IPP—1
2004	108	4.3	10	7 (2,5)	0.40	Ukn	F33	NA	Una	F33	Single – 3
2004	112	27.2	9	6 (2,4)	0.70	Ukn	F91	NA	Una	F91	Single—3
2004	137	44.8	2	1 (1,0)	NA	M20	Ukn	NA	M20	Una	IPP—1
2004	145	35.5	6	6 (3,3)	0.28 (0.19)	M13	Ukn	NA	M13, **Una**	Una	IPP (2), EPP (4)—4
2004	327	51.0	7	2 (1,1)	0.21	Ukn	Ukn	NA	Una	Una	Single—3
2005	001	39.3	9	6 (2,4)	0.37	M67	F75	0.11	M67	F75	IPP—1
2005	106	21.9	7	6 (4,2)	0.35	Ukn	F33	NA	Una	F33	Single—3
2005	115	14.9	7	1 (1,0)	NA	M94	F93	0.11	M94	F93	IPP—1
2005	134	55.3	5	2 (2,0)	0.43	Ukn	Ukn	NA	Una	Una	Single—3
2005	137	24.3	3	2 (0,2)	0.51	M20	Ukn	NA	M20	Una	IPP—1
2006	201	26.5	1	1 (1,0)	NA	M99	Ukn	NA	M99	Una	IPP—1
2006	204	53.7	5	5 (2,3)	0.56	M111	F123	−0.21	**Una**	F123	EPP—2
2007	105	25.1	7	6 (4,2)	0.37 (0.16)	M64	F77	−0.08	M64, **Una**	F77	IPP (3), EPP (3)—4
2007	106	39.9	7	7 (3,4)	0.54	M190	F33	0.06	**Una**	F33	EPP—2
2007	111	23.7	4	4 (2,2)	0.50	M20	F150, Ukn	0.03	M20	Una	IPP—1
2007	114	13.9	4	1 (0,1)	NA	M173	F154	−0.05	M173	F154	IPP—1
2007	115	25.5	11	7 (5,2)	0.54	M116	Ukn	NA	M116	Una	IPP—1
2007	123	22.6	12	11 (8,3)	0.42	M125	Ukn	NA	**Una**	Una	EPP—2
2007	131	38.3	9	7 (2,5)	0.43	M179	F181	0.12	M179	F181	IPP—1
2007	137	13.5	6	4 (2,2)	0.23 (0.17)	Ukn	F185	NA	Una1, **Una2**	F185	Multiple—5
2007	204	27.0	4	3 (1,2)	0.50	M49	F123	0.15	M49	F123	IPP—1
2008	001	Cameras only	4	4 (1,3)	0.35	Ukn	F249	NA	Una	F249	Single—3
2008	003	Cameras only	5	3 (1,2)	0.29	Ukn	Ukn	NA	Una	Una	Single—3
2008	106	25.9	8	6 (1,5)	0.40 (0.12)	M190	F33	0.06	M190, **M64**	F33	IPP (5), EPP (1)—4
2008	111	27.6	11	9 (4,5)	0.42	M237	F238	−0.18	M237	F238	IPP—1
2008	113	28.7	8	6 (3,3)	0.48 (0.16)	M197	Ukn	NA	M197, **Una1, Una2**	Una	IPP (2), EPP (4)—4
2008	115	40.8	4	2 (0,2)	0.54	M116	Ukn	NA	M116	Una	IPP—1
2008	131	10.5	4	1 (0,1)	NA	M179	F181	0.12	M179	F181	IPP—1
2008	145	27.2	12	11 (5,6)	0.50 (0.29)	M64	F201	−0.12	M64, **Una**	F201	IPP (8), EPP (3)—4
2008	204	11.6	4	1 (1,0)	NA	Ukn	Ukn	NA	Una	Una	Single—3
2008	207	16.8	5	1 (0,1)	NA	M212	F213	0.20	M212	F213	IPP—1
2008	327	37.8	9	6 (3,3)	0.50	M245	Ukn	NA	M245	Una	IPP—1

NA = not applicable, Ukn = unknown, Una = unassigned, cubs "*r*" = relatedness coefficient between presumed full-sibs (half-sibs) cubs, parents "*r*" = relatedness coefficient between parents of a social pair. Extrapair fathers are in bold. The 8 litters from 2004 are those reported in Carmichael, Szor, et al. (2007). Outcome numbers refers to outcomes of Figure 2.

spotting scopes. We kept dens under continuous surveillance and recorded frequency of visits (den attendance; number of visits per day) and frequency of visits with food (food provisioning; number of provisioning events per day) by adults. Weaning occurs only within a few weeks after cubs' emergence, so that lactating behavior was scarcely observed in those observation periods. Second, we used infrared automatic color cameras to record behavior at dens (Silent Image PM35C31 and RapidFire Professional PC85; Reconyx, Holmen, WI). Cameras were programmed to take 5 photographs per second when movement was detected. We set cameras alone or in pairs, depending on size and configuration of dens, trying to obtain a full view of the den. We analyzed photographs to determine the number of young present and adult identity, attendance, and food provisioning. We performed focal observations at 14 dens with at least one tagged adult and installed cameras at 12 dens with at least one tagged adult (Table 1). This enabled us to assess den attendance and food provisioning by both tagged social parents in 8 litters (Supplementary Appendix 3).

DNA extraction and paternity analyses

DNA was extracted from ear plug samples using Qiagen tissue protocol (QIAGEN, Hilden, Germany). Ten microsatellite markers designed for domestic dogs (CPH5, CPH9, CPH15, Fredholm and Wintero 1995; CXX733, CXX745, CXX758, Mellersh et al. 1997; CXX140, CXX147, CXX173, CXX250, Ostrander et al. 1993) and tested in arctic fox by Carmichael, Szor, et al. (2007) were labeled with fluorescent tags (FAM, TET, or HEX; Applied Biosystems, Foster City, CA). Amplification solutions contained 0.2 μM of each primer, 0.50 mM deoxynucleoside triphosphates, 1 mg/ml bovine serum albumin, 2.5 mM $MgCl_2$, 1 × polymerase chain reaction (PCR) buffer (50 mM KCl, 10 mM Tris–HCl, pH 8.8, 0.1% Triton ×100), 1 U of Taq polymerase, and approximately 40 ng of template in a total volume of 15 μl. All amplifications were conducted in a Biometra T1 thermocycler (Biotechnica, Hannover, Germany). The PCR program was as follows: 3 min at 94 °C; 35 cycles of 45 s at 94 °C, 30 s at Tm (50 °C–59 °C), 30 s at 72 °C, and 30 min at 72 °C. Reaction products were loaded and migrated on 6% polyacrylamide gels. All individuals from the same den per year were migrated alongside so that their genotypes could be directly compared. Gels were visualized with FMBio scanner (Hitachi Software Engineering) and manually genotyped with the software Image Analysis 3.0.0.21 (MiraiBio).

We tested for deviations from Hardy–Weinberg equilibrium per locus and for linkage disequilibrium between pair of loci, using exact tests in Genepop 3.4 (Raymond and Rousset 1995; Supplementary Appendix 1). Parentage was determined through a likelihood-based approach using PASOS 1.0 (Duchesne et al. 2005). PASOS is especially designed for parental allocations when a proportion of the potential parents has not been genotyped. In contrast to exclusion methods, which may result in exclusion of the true parent if errors or mutations are present (Marshall et al. 1998), PASOS tolerates some degree of allele mistyping. We thus estimated the proportion of loci typed incorrectly by regenotyping 10% of the population and used PASOS to calculate parental allocations. Of the 520 single-locus genotypes compared, we observed 1 allelic dropout and 10 false alleles, giving a mean genotyping error rate per locus of 2%. The software also computes a correctness rate for allocations, that is, the probability that allocations are correct. To prevent rejection of a true parent due to genotyping error, we performed again genotyping at all loci for all cubs presenting mismatches with their social parent at less than 4 loci (5 cubs). This allowed us to correct 3 genotyping errors at one locus.

Siblings from different cohorts were present in the population. To have sufficient resolution power, we restricted candidate parents to adult males and females observed or captured either the year the cubs were born or the year before. Genotypes were first analyzed with PASOS to assign a parent pair. If a pair could not be assigned, we assigned either maternity or paternity alone. When no adult was assigned as a potential parent of the litter, the minimum number of parents was estimated from the number of unique alleles in the cubs' genotypes. This approach allowed us to determine the identity and minimum number of sexual partners of each sex for most litters. Relatedness coefficients (r; Queller and Goodnight 1989) are indices of the proportion of alleles identical by descent between 2 individuals, accounting for the frequencies of those alleles in the population. $r \approx 0.5$ is expected for first-degree relationships (parent–offspring or full sibling), and $r \approx 0.25$ is predicted for half-siblings. Pairwise r was calculated between all foxes using SPAGeDi version 1.2 (Hardy and Vekemans 2002). Average values were also calculated among cubs at each den (mean relatedness between cubs) and among adults of the same pair when both were tagged (mean relatedness between pair members).

Effect of food availability

We classified variability in food availability for each litter based on spatial and temporal availability of geese and lemmings, respectively. We defined goose availability as the distance between the den and the goose colony's center point (Figure 1). This center point was estimated from a mean contour polygon created using goose nesting density estimates from helicopter surveys in 2007 and 2008. When more than one den was occupied by the same foxes in a given year, the mean point between dens was used as den location for analyses (in such a case, dens were always <4 km from each other, mean = 1.5 km ± 1.1). We used 2 categories of lemming abundance (low: 0.55 ± 0.33 lemmings/ha, $n = 4$ years and 14 samples; high: 3.08 ± 0.30 lemmings/ha, $n = 2$ years and 14 samples) as estimated from ecosystem monitoring performed on Bylot Island (Gruyer et al. 2008).

Statistical analyses

We used paired t-tests to compare intensity of parental care (den attendance and food provisioning) among partners. Mean values of relatedness were compared between unique pairs with and without mating infidelity using Wilcoxon tests. We used the distance of the reproductive den to the center of the goose colony and annual lemming abundance (high or low) as the predictor variables of EPP, using a mixed model for categorical dependent variables (GLIMMIX) with year and mother ID as random variables. This procedure is similar to general linear models but fits a binary response. The best model was retained using a stepwise backward procedure, starting with both covariates and their interaction, then removing nonsignificant terms ($P > 0.05$) until only significant terms were left. We then performed a logistic regression using distance from the goose colony center as the predictor variable to estimate the parameters of the relationship between goose availability and EPP.

All means are reported ±1 SD. We conducted statistical analyses using SAS software 9.1.3 (SAS Institute 2005).

RESULTS

Description of arctic fox mating system

Capture and sampling success

We captured and sampled tissue from 62 adults (28 females and 34 males) and 176 cubs (88 females and 88 males) from

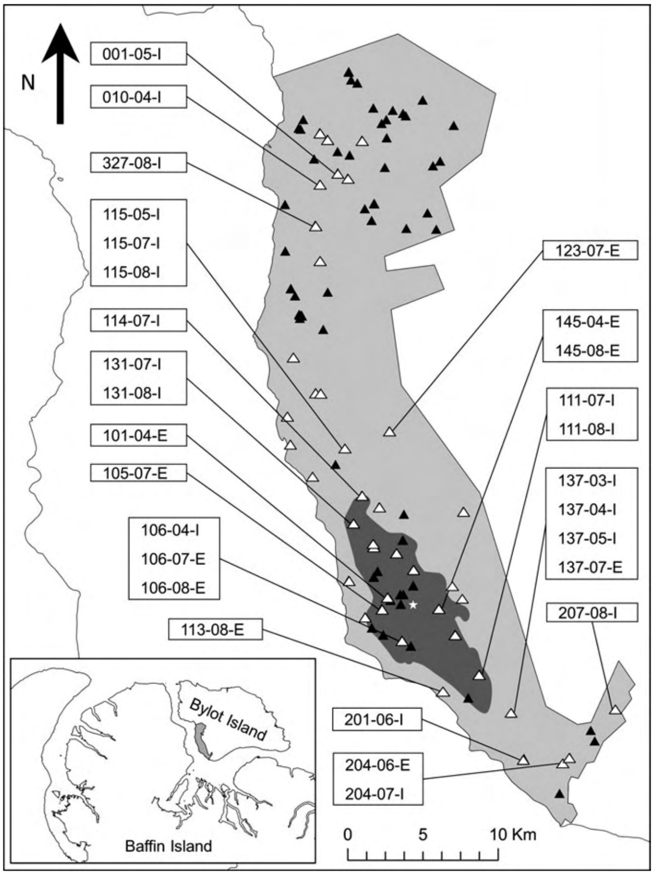

Figure 1
Arctic fox study area (light shaded polygon) and goose colony (dark shaded polygon) on Bylot Island, Nunavut, Canada. Dens that were active during the study are represented with an open triangle, whereas inactive dens are represented with a black triangle. Numbered dens indicate litters with resolved mating strategy. Identification of numbered dens is as follows: den ID—last 2 digits of year—mating strategy (E = EPP, I = IPP). The star indicates the center of the goose colony.

38 litters (Table 2). Sampling effort corresponded to 70% of cubs observed at dens. The minimum litter size ranged from 1 to 12 (mean = 6.6 ± 2.8, n = 38). The annual minimum number of litters in the study area varied from 2 to 22 (mean = 10.3 ± 8.2, n = 6 years).

Social parentage

From 2003 to 2008, visual observations and automatic camera photographs of tagged adults at dens allowed us to assign a social father to 26 litters and a social mother to 21 litters. Some of these social fathers and mothers were parents of more than 1 litter across the study years: 5 males were fathers of 2 litters, 1 male was father of 4 litters, 3 females were mothers of 2 litters, and 1 female was mother of 4 litters. The breeding pair and its cubs of the year formed the dominant social unit, but we observed 2 cases (den 101 in 2004 and den 111 in 2007) in which 2 females were present at the same den and nursed the cubs. In both cases, one female was tagged and the other was not, so we could not assess the relatedness between females. We never observed more than one male at a reproductive den.

Genetic parentage

The genotyping of 238 sampled foxes was 99.8% complete, and no individual was typed for fewer than 9 loci. This includes all sampled foxes used by Carmichael, Szor, et al. (2007). No microsatellite loci deviated significantly from Hardy–Weinberg equilibrium among adult foxes, suggesting that null alleles were rare or absent in our sample. We assigned both parents to 56 cubs from 13 litters (32% of sampled cubs). We assigned paternity alone to 31 cubs from 10 litters (18% of sampled cubs) and maternity alone to 56 cubs from 9 litters (32% of sample cubs). This resulted in 87 cubs from 23 litters (49% of sampled cubs) with assigned father and 112 cubs from 22 litters (64% of sampled cubs) with assigned mother (Figure 2). Correctness rate of allocations was 96.5% for sampled males and 97.9% for sampled females.

In all cases, no mismatch was observed between assigned parent and offspring. When the social father was rejected as genetic father, mismatches between genotypes were present at least at 2 loci (mean = 5.5 ± 1.7 loci; Supplementary Appendix 2). The males who gave care to offspring without being their genetic father are discussed below as cuckolded males.

Mating system

Some parents were untagged at the time of cub trapping, and we were not able to genotype all parents. Therefore, there may be some unreported social parents, and genetic patterns may sometimes support several mating configurations. We present here the most parsimonious solutions, that is, those involving the smallest possible number of parents in each litter.

In 31 of the 38 litters sampled (128 cubs), all offspring could have been sired by a single male–female pair, and relatedness between cubs of the same litter (Table 2) suggests that they were all full-siblings. In addition, in 20 of those 31 litters, the

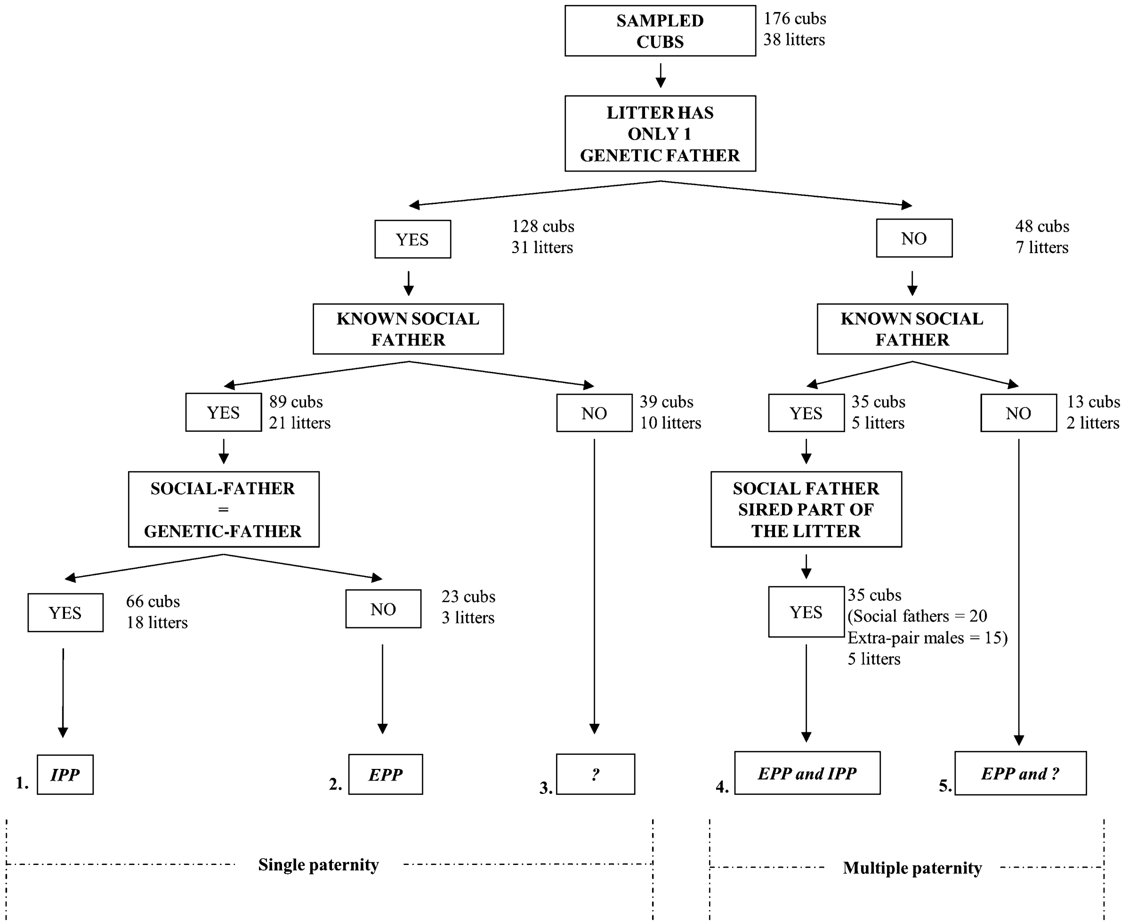

Figure 2
Flow chart used to assess mating system in female arctic foxes on Bylot Island, Nunavut, Canada, 2003–2008. Five outcomes emerged from the flow chart depending on the corroboration of available information.

social mother was known and assigned as genetic mother, and cubs could have been sired by a single male. We therefore classified those 31 litters as "single paternity" (Figure 2, outcomes 1, 2, and 3).

However, single paternity in a litter reflected different mating systems. Twenty-one of the 31 litters with single paternity had a known social father of which 18 litters were fathered by the social male (mating fidelity and intrapair paternity [IPP], Figure 2, outcome 1) and 3 litters were fathered entirely by an extrapair male (mating infidelity and EPP, Figure 2, outcome 2). There were also 10 litters with single paternity and an unknown social father in which we could not assess the fidelity of the female to her social partner (Figure 2, outcome 3).

In the 7 remaining litters, at least 3 (6 litters) or 4 (1 litter) parents were required to explain the genetic combination of offspring. In 5 of those 7 litters (all with 3 genetic parents), the social mother was assigned as genetic mother of all cubs, and cubs were divided into 2 groups of half-siblings (Table 2). The third parent must therefore have been a male. In the last 2 litters (with 3 and 4 parents), the social mother was unknown, but the social father was known and sired only part of the litter. In addition, cubs were divided, respectively, in 2 and 3 groups of half-siblings (Table 2), so that they must have shared a common parent. We therefore considered that in these last 2 litters, a single female sired all the cubs and remaining parents were males. We conclude that in all 7 litters with more than 2 genetic parents, the supplementary adult(s) were always males (multiple paternity, Figure 2, outcomes 4 and 5).

We only observed one social father in each den and therefore presumed that all cases of multiple paternity represent EPP (Figure 2, outcome 4 and 5). In 5 of the 7 litters with multiple paternity, the social father was assigned and had sired a portion of the litter (mating infidelity with both EPP and IPP, Figure 2, outcome 4). In the 2 remaining litters with multiple paternity, the social father was unknown, but we considered that at least part of the litter was sired by an extrapair male (mating infidelity and EPP, Figure 2, outcome 5). We used the smallest group of half-siblings of those litters in the calculation of minimum number of cubs born from EPP.

We thus estimate that 38 cubs with known social father (cuckoldry, $n = 23$, Figure 2, outcome 2; partial cuckoldry, $n = 15$, Figure 2, outcome 4) and 4 cubs with unknown social father (cuckoldry, Figure 2, outcome 5) were born from EPP, representing 24% of tagged cubs and 31% of cubs with resolved paternity.

In the 2 litters in which 2 females were observed attending cubs, the tagged female was rejected as a parent of the offspring and only one female (presumably the untagged female) was required to explain the genotypes of cubs. We have therefore no evidence of genetic polygyny (2 females mating with the same male), plural breeding (2 pairs mating together), or litter mixing in the same den.

We identified the father of only one of the extrapair offspring. In 2008, the extrapair cub of den 106 was born from female 33 (the social mother of litter 106) and male 64 (the social male of litter 145) located approximately 3 km from den 106. Interestingly, male 64 was also the 4-year-old son of female 33. The social partner of female 33 in 2008 was not the father of male 64; he died during the winter 2006–2007. Misassignment due to close relatedness is therefore excluded, and this represents a case of incest between 2 foxes otherwise socially paired with unrelated partners.

Mean relatedness (r) between members of a parental pair was 0.01 ($n = 13$), and relatedness was not statistically different between pairs showing cuckoldry (mean = −0.09, $n = 4$) and pairs showing exclusive mating fidelity (mean = 0.05, $n = 9$; Table 2; Wilcoxon 2-sample test, $Z = -1.78$, $P = 0.08$).

Parental care

Both parents attended the den and fed the young during the rearing period (Figure 3). Den attendance was 56% lower for cuckolded males than for other males (22% ± 22 for cuckolded males, $n = 4$, 50% ± 36 for other males, $n = 4$, Figure 3), and this difference was statistically significant (Wilcoxon Exact test, $P = 0.05$, $n = 8$). Food provisioning was 52% lower for cuckolded males than for other males (30% ± 30 for cuckolded males, 63% ± 27 for other males, Figure 3), but this difference was not statistically different (Wilcoxon Exact test, $P = 0.10$). In addition, cuckolded males attended their litter significantly less (number of visits per day; Supplementary Appendix 3) than their partner (paired t-test, $t = 3.35$, $P = 0.02$), whereas den attendance was similar between parents in litters without cuckoldry (paired t-test, $t = -0.12$, $P = 0.45$, Figure 3). Food provisioning (number of provisioning events per day; Supplementary Appendix 3) was not statistically different between male and female parents for both litters with (paired t-test, $t = 1.29$, $P = 0.14$) and without cuckoldry (paired t-test, $t = -1.15$, $P = 0.17$) (Figure 3).

It is important to note that, in the above analysis, we used as independent data points 2 pairs that had been sampled more than 2 years each. This is because one female switched during the study from genetic monogamy to genetic polyandry, and variation within individuals (between years, 31.5% ± 24.9) in paternal den attendance and food provisioning was similar to variation between individuals (within years, 37.54% ± 29.52).

Effects of food resources on the arctic fox mating system

Distance from the center of the goose colony was the only significant variable in the full GLIMMIX model (distance to colony: $P = 0.05$; lemming abundance: $P = 0.25$, interaction: $P = 0.15$). After removing the interaction term, effect of lemming abundance was still nonsignificant ($P = 0.47$) so that the best model contained only distance to colony as predictor of EPP ($F = 4.48$, degrees of freedom = 24, $P = 0.04$). The logistic regression between distance from center of the goose colony and frequency of EPP was significant (chi square = 4.48, $P = 0.03$, $n = 28$, max-rescaled $R^2 = 32\%$). The probability of female EPP decreased by 19% for each 1 km increase in distance between the den and the center of the goose colony (odds ratio = 0.81, IC^{95}: 0.66–0.99). The logistic regression curve shows that the probability of EPP was high in the goose colony but low outside the polygon of high goose density (Figure 4). EPP was almost absent 10 km away from the nearest edge of the goose colony. However, caution must be used when interpreting data points located far from the colony as sample size is small at >25 km.

DISCUSSION

We showed that the dominant social mating system in the Bylot population of arctic foxes is monogamy with biparental care. This is similar to findings from other arctic fox populations (Macpherson 1969; Garrott et al. 1984; Strand et al. 2000). Only 2 dens had an extra adult, in each case, a nonreproductive female. However, despite a predominantly socially monogamous mating system and an important contribution of males to den attendance and food provisioning of cubs (Figure 3), arctic foxes showed high levels of EPP; almost one third of cubs (31%) with known social father were born from a male from outside the social unit, and 31% of litters with known social father revealed EPP (Figure 2 and Table 2). Extrapair or extragroup copulations/paternity have also been reported in other canid species (Ethiopian wolf, *Canis simensis*, Sillero-Zubiri et al. 1996; African wild dog, *Lycaon pictus*, Girman et al. 1997; swift fox, *V. velox*, Kitchen et al. 2006; red fox, *V. vulpes*, Baker et al. 2004; island fox, *Urocyon littoralis*, Roemer et al. 2001). Level of EPP observed in arctic foxes from Bylot Island (31%) was rather high for a socially monogamous mammal (range = 0–43.8%, Clutton-Brock and Isvaran 2006; mean = 25%, range = 0–56%, Soulsbury 2010). It is much lower than in the closely related socially polygynous red fox (80%; Baker et al. 2004) but well within the range observed in other socially monogamous canids (island fox: 25%; Roemer et al. 2001; swift fox: 52%, Kitchen et al. 2006;

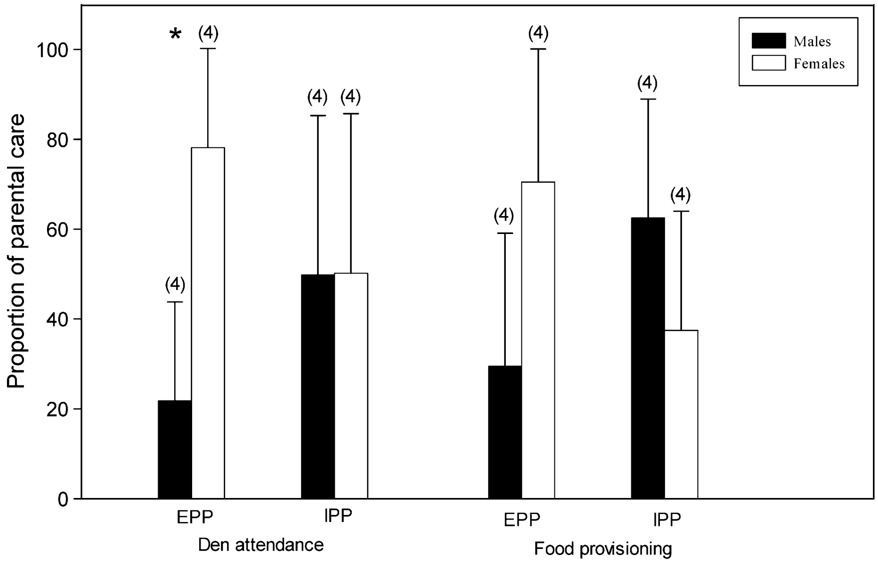

Figure 3
Comparison of the proportion of parental care provided to cubs by males and females in genetically polyandrous (EPP) and monogamous (IPP) pairs for arctic foxes studied on Bylot Island, Nunavut, Canada, 2007–2008. Parental care was quantified as frequency of visits to the den (den attendance) or frequency of food return to the den (food provisioning).

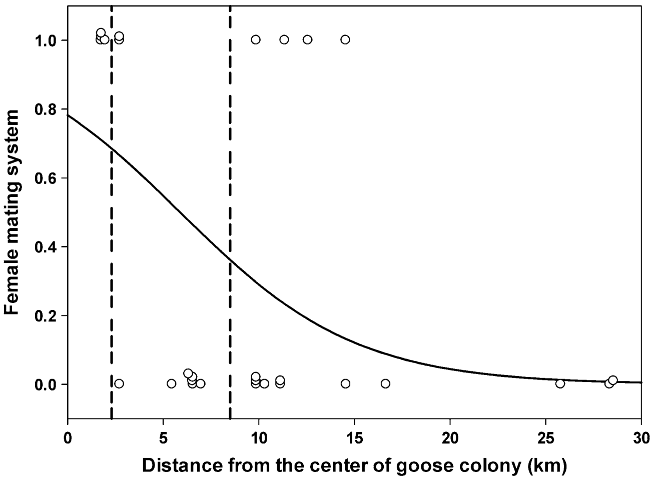

Figure 4
Mating system of female arctic foxes as a function of the distance between their den(s) and the center of the goose colony on Bylot Island, Nunavut, Canada, 2003–2008 (0 = IPP [monogamy], 1 = EPP). White circles represent litters. Vertical lines show the smallest and largest distances from the center to the edge of the goose colony.

bat-eared fox (*Otocyon megalotis*): 10%, Wright et al. 2010). Multiple paternity in Bylot arctic foxes (18% of litters) was also similar to figures found in other socially monogamous mammals (mean = 20%, range = 0–57%, Soulsbury 2010).

Females may have extrapair copulations to avoid inbreeding and to increase their offspring's heterozygosity (Tregenza and Wedell 2002; Foerster et al. 2003). However, in a meta-analysis of 55 bird species, Akçay and Roughgarden (2007) found no correlation between pair genetic similarity and EPP. In the Bylot population of arctic foxes, pair members were unrelated (mean relatedness between pair members [r] = 0.01), and relatedness between pair members was not statistically different between pairs with and without mating infidelity. This is similar to reports from other canids (swift fox: r = 0.04, Kitchen et al. 2006; red fox: r = −0.14, Iossa et al. 2009). However, our results suggest that females may be even less likely to cuckold more related males. Furthermore, at least one case of EPP involved incest, which reinforces this hypothesis of mate choice toward genetically similar partners. Incest is thought to occur when individuals have incomplete knowledge of relatedness and the costs of avoiding inbreeding are high (Wheelwright et al. 2006). None of these conditions were probably met here; the male was raised by the female; they were both otherwise socially paired with an unrelated partner and were holding territories located in an area of high resource abundance. One hypothesis is that this female improved her inclusive fitness through kin selection by increasing the reproductive success of her son.

Enhanced within-brood genetic diversity rather than offspring heterozygosity seems more likely to have influenced the evolution of polyandrous behaviors in arctic foxes. Yasui (1998) proposed that the fittest genes for the next generation are predictable if offspring develop under stable environmental conditions. In those cases, female's mate choice is expected to favor males of higher quality (genetic quality or heterozygosity, Orians 1969; Kempenaers 2007). Conversely, in fluctuating environments, the fittest genes for the next generation are not predictable. In these situations, increased within-brood genetic diversity of polyandrous females may enhance the probability that at least one young survives and reproduces successfully in the changing environment (Jennions and Petrie 2000). Polyandry may be particularly adaptive in environments, such as high arctic ecosystems, where harsh seasonal conditions prevail. However, 30% of litters with EPP were sired by only one male and thus did not increase genetic diversity in the litter.

Some circumstances may limit EPP in arctic foxes. Our study is the first to show a correlation between the frequency of EPP and spatial variation in food availability in canids (Figure 4). This may be explained either by variations in need for paternal care or in opportunities for extrapair copulations. At the species level, the rate of EPP is negatively associated with the importance of paternal care on reproductive success (reviewed in Griffith et al. 2002). Because EPP may be linked to reduced paternal care, females who cannot afford this cost are assumed to avoid extrapair copulations (Petrie and Kempenaers 1998). Our behavioral observations suggest some support to this assumption of a link between EPP and paternal care (Figure 3), but larger sample sizes and longer periods of observation would be needed to quantify reliably this correlation. Gowaty (1996) proposed that females who have the most to lose from a reduction in male investment are both of poor quality themselves and in poor quality environments. Within the Bylot Island population of arctic foxes, proximity to the goose colony corresponded to more occurrences of EPP (Figure 4). In addition, EPP was more frequent at the center than at the edges of the colony. This may be due to the predictably higher resource availability in the center of the goose colony because the extent of the goose colony may change slightly annually (Bêty et al. 2001). Variations in lemming abundance may have a similar impact on the prevalence of EPP, but this was not supported by our results. In a study of Eurasian kestrel (*Falco tinnunculus*) facing strong variations in food abundance, Korpimäki et al. (1996) found that EPP was more likely to occur in years of increasing food abundance than in years of decreasing or low food abundance. They suggested that the importance of paternal care may limit EPP in this species. Humbird and Neudorf (2008) also found that female northern cardinals (*Cardinal cardinalis*) were more likely to perform extraterritorial movements when provided with a food supplement. However, food abundance is likely not the only proximal cause of variation in EPP in Bylot arctic foxes because there was a spatial but not temporal correlation between variations in EPP and food abundance.

Our study is not experimental, so the correlation between resource abundance and EPP may be due to confounding variables. One possibility is the effect of local density because both breeders and wanderers are more numerous near the goose colony (Szor et al. 2008), where food availability is extended throughout winter due to fox hoarding (Bantle and Alisauskas 1998; Careau et al. 2007; Samelius et al. 2007; Careau, Giroux, et al. 2008; Careau, Lecomte, et al. 2008). Higher local density may increase the opportunities for extrapair copulations for females holding food-rich territories (Griffith et al. 2002). This is consistent with our results showing more EPP in the center of the goose colony than at the edges. Note, however, that density of breeding individuals is also strongly linked to lemming abundance on Bylot. That EPP was not correlated with lemming abundance suggests that density of breeding females alone could not explain variations in EPP. Another possibility is that high-quality females were more likely to both engage in extrapair copulations (if they had less to lose from reduced paternal care) and hold dens close to the center of the goose colony. This would also have generated a spatial but not temporal link between food abundance and EPP. We lack data to test this hypothesis.

Variations in the extent of EPP observed between arctic foxes and other canids may be due to differential paternal care requirements. Harsh conditions and low food abundance associated with the Arctic environment may explain, at least in part, why arctic foxes may be more genetically monogamous than other closely related canids, like the socially monogamous swift fox and the socially polygynous red fox.

In our study, only one of the 11 extrapair fathers was a male we had sampled and genotyped, though our field observations suggested that we had sampled a high proportion of individuals in the population. A portion of extrapair fathers are likely males not present within our study area during summer or at least not holding a territory. This contrasts with what is usually found in mammals and birds for which a large proportion of extrapair fathers are neighboring territory holders (e.g., Yezerinac et al. 1995; Foerster et al. 2003). Satellite tracking shows that even foxes defending territories move regularly over the sea ice when this habitat is available (Berteaux D, unpublished data). Extraterritorial excursions during the spring may represent opportunities for genetic mixing among fox populations. EPP could thus strongly impact effective population size by introducing genes from males not holding territories in the local population. Effective population size is positively associated with population fitness (Reed 2005) because less genetic diversity reduces growth rate and increases extinction rate (Keller and Waller 2002). In a meta-analysis of 34 data sets, Reed and Frankham (2003) estimated that genetic diversity of a population could explain 15–20% of its fitness variation. In arctic foxes, behavioral strategies, such as extraterritorial movements and EPP, that increase gene flow are probably important for the genetic structure of populations. This is in good agreement with data on arctic fox population genetics (Dalén et al. 2005; Carmichael, Krizan, et al. 2007; Geffen et al. 2007). A better understanding of the behavioral ecology of arctic foxes on the sea ice, particularly during the copulation period, is strongly needed.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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SUPPORTING INFORMATION

Appendix 1 : Allelic diversity, proportion of exp./obs. heterozygotes, Fis estimates and Pvalues of Hardy-Weinberg exact tests calculated from genotypes of 62 adult arctic foxes captured on Bylot Island, Nunavut, Canada, from 2003-2008.

Loci	Nb. of alleles	Exp. hetero	Obs. hetero	Fis	P value
5	12	0.857	0.882	-0.029	0.845
9	6	0.622	0.678	-0.089	0.984
15	8	0.666	0.722	-0.085	0.991
140	10	0.781	0.824	-0.554	0.972
147	11	0.793	0.784	0.012	0.245
173	5	0.697	0.739	-0.060	0.918
250	10	0.832	0.829	0.004	0.150
745	10	0.798	0.829	-0.018	0.408
758	15	0.830	0.812	0.012	0.309
771	16	0.819	0.784	0.044	0.141

Appendix 2. Microsatellite DNA fingerprints of adult and young foxes from 38 litters sampled on Bylot Island, Nunavut, Canada, from 2003-2008. For each cub, presumed paternal alleles are given in **bold** and presumed maternal alleles are given in *italics*. Shaded alleles imply extra-pair paternity. In cases where the genotype of the social father is unknown, alleles in boxes imply multiple male parents. Data is presented by year, and den identification number.

Year	**Den ID**
2003	**113**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Female	33	129	151	155	146	177	121	130	275	237	100
			131	155	157	148	181	121	132	275	241	102
Juvenile	Male		*131*	*155*	*155*	*146*	*177*	*121*	124	*275*	219	*100*
			121	155	*157*	*148*	*181*	121	*130*	277	*241*	*102*
Juvenile	Male		121	*155*	*155*	*146*	*177*	*121*	124	*275*	219	*100*
			129	155	*157*	*148*	*181*	121	*130*	277	*241*	*102*

Year	**Den ID**
2003	**115**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Juvenile	Male	21	127	153	151	148	169	121	128	271	227	98
			131	157	155	154	175	123	132	271	233	100
Juvenile	Female	22	125	155	155	144	169	121	124	271	233	100
			127	155	163	148	175	123	134	271	237	100
Juvenile	Male	23	125	155	155	144	177	121	128	271	235	98
			127	155	163	146	177	125	134	271	237	104
Juvenile	Male	25	119	153	155	146	169	121	128	271	227	98
			125	155	163	154	177	125	132	279	235	104
Juvenile	Female	26	125	155	155	144	169	121	124	271	227	98
			127	157	163	148	177	125	132	271	233	104
Juvenile	Male	27	125	153	155	146	169	121	128	271	227	98
			127	155	163	154	175	125	132	271	235	100

Year	**Den ID**
2003	**137**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	20	113	151	155	142	175	125	124	265	219	96
			131	151	157	148	181	127	132	271	237	102
Juvenile		29	**113**	**151**	**155**	144	165	121	128	**271**	**237**	**96**
			133	151	159	**148**	**181**	**125**	**132**	275	241	108
Juvenile		31	**113**	**151**	**155**	**142**	**181**	121	**124**	**271**	227	**96**
			133	155	159	144	181	**125**	128	271	**237**	104
Juvenile		32	**131**	**151**	**155**	**142**	**175**	**125**	128	**271**	**219**	**96**
			133	155	**157**	144	181	**127**	**132**	271	241	104
Juvenile		34	**131**	**151**	**155**	144	**181**	121	**124**	**265**	**237**	**102**
			133	151	**157**	**148**	181	**125**	128	275	241	104

Year	**Den ID**
2004	**010**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	
Adult	Male	67	125	151	151	146	169	121	126	269	235	98
			133	157	155	148	177	123	128	275	241	104
Adult	Female	75	131	151	157	144	177	121	122	273	237	94
			133	155	159	148	181	125	126	275	241	104
Juvenile	Male	66	**125**	*151*	**155**	**146**	**169**	*121*	*122*	**269**	**241**	**98**
			131	**157**	*159*	*148*	*177*	**123**	**126**	*273*	*241*	*104*
Juvenile	Male	68	*131*	**151**	**155**	**148**	**177**	**123**	*122*	**269**	**241**	*94*
			133	*155*	*157*	*148*	*177*	*125*	**126**	*275*	*241*	**104**
Juvenile	Male	69	*131*	*151*	**155**	*144*	**169**	**121**	*122*	**275**	**235**	*94*
			133	**157**	*157*	**146**	*177*	*121*	**128**	*275*	*237*	**104**
Juvenile	Male	70	**125**	**151**	**155**	**146**	**177**	**121**	*126*	**269**	**235**	**104**
			133	*151*	*159*	*148*	*177*	*125*	**128**	*273*	*241*	*104*
Juvenile	Male	71	**125**	**151**	**155**	**148**	**177**	*121*	*122*	**269**	*237*	**104**
			131	*155*	*159*	*148*	*177*	**123**	**126**	*275*	**241**	*104*
Juvenile	Male	72	**125**	*151*	**151**	**148**	**177**	**121**	*122*	**275**	**235**	*94*
			131	**157**	*157*	*148*	*181*	*121*	**128**	*275*	*237*	**104**

Year	**Den ID**												
2004	**101**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Female	56	121	151	155	152	175	123	122	277	225	98
			129	155	155	154	177	125	132	281	237	106
Juvenile	Male	49	*121*	*155*	*155*	146	*175*	121	*122*	271	*225*	*98*
			127	155	157	*154*	179	*125*	*132*	*281*	*237*	*106*
Juvenile	Female	50	*121*	*151*	*155*	148	*175*	121	*122*	273	*237*	*98*
			127	*155*	157	*154*	181	*123*	122	*277*	237	98
Juvenile	Female	51	127	*151*	*155*	146	*177*	121	*122*	273	*237*	*98*
			129	155	157	*152*	181	*125*	122	*277*	237	*106*
Juvenile	Female	52	*121*	*151*	*155*	148	*175*	121	*132*	*277*	*225*	*106*
			129	*155*	155	*152*	*177*	*125*	132	*281*	231	106
Juvenile	Female	53	*121*	*155*	*155*	146	*175*	121	124	273	221	*98*
			127	155	157	*152*	185	*123*	*132*	*281*	*225*	98
Juvenile	Male	54	127	*151*	*155*	146	*175*	121	*122*	271	*237*	*98*
			129	155	157	*152*	185	*123*	122	*281*	237	98
Juvenile	Female	55	*121*	*155*	*155*	148	*177*	121	124	273	221	*98*
			127	155	157	*152*	181	*125*	*132*	*277*	*225*	98
Juvenile	Male	57	*121*	*155*	*155*	146	*177*	121	*122*	273	*225*	*106*
			127	155	157	*154*	181	*125*	*132*	*277*	*237*	106
Juvenile	Male	58	127	*151*	*155*	146	*177*	121	*122*	273	*237*	*106*
			129	155	157	*152*	181	*125*	122	*281*	237	106

Year	**Den ID**
2004	**106**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	44	113	155	155	146	175	123	124	271	219	106
			131	155	157	148	181	123	134	279	231	110
Adult	Female	43	121	151	155	148	175	121	132	265	231	102
			131	155	163	148	177	121	132	275	237	106
Juvenile	Male	45	**131**	**155**	**155**	**148**	*175*	*121*	*132*	**271**	**219**	*102*
			131	*155*	*163*	*148*	**181**	**123**	**134**	*275*	*237*	**106**
Juvenile	Female	46	**131**	**155**	**155**	**146**	**175**	*121*	*132*	*265*	**219**	*106*
			131	*155*	*163*	*148*	*175*	**123**	**134**	**279**	*231*	**110**
Juvenile	Male	47	**113**	*151*	**155**	**146**	**175**	*121*	*132*	*275*	**219**	*102*
			121	**155**	*163*	*148*	*175*	**123**	**134**	**279**	*231*	**110**
Juvenile	Male	48	*121*	*151*	**155**	**148**	**175**	*121*	*132*	**271**	**219**	*102*
			131	**155**	*163*	*148*	*177*	**123**	**134**	*275*	*237*	**110**

Year	**Den ID**
2004	**108**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Female	33	129	151	155	146	177	121	130	275	237	100
			131	155	157	148	181	121	132	275	241	102
Juvenile	Female	59	123	*151*	*155*	*148*	*181*	*121*	124	*275*	219	*102*
			131	*155*	*157*	148	181	121	*132*	277	*237*	102
Juvenile	Female	60	123	*155*	*157*	*146*	*177*	*121*	*132*	*275*	231	*102*
			129	155	163	*148*	*181*	121	132	277	*237*	106
Juvenile	Female	61	121	*155*	*155*	*146*	175	*121*	124	265	219	*102*
			129	155	163	*148*	*181*	121	*130*	*275*	*241*	102
Juvenile	Male	62	121	*155*	*155*	*146*	175	*121*	*132*	*275*	231	*102*
			131	155	*157*	*148*	*181*	121	132	277	*237*	106
Juvenile	Female	63	123	*151*	*155*	*146*	*177*	*121*	124	*275*	219	*100*
			131	*155*	*157*	146	*181*	121	*132*	277	*237*	*102*
Juvenile	Male	64	123	*151*	*155*	*148*	175	*121*	124	*275*	219	*100*
			131	*155*	163	148	*181*	121	*132*	277	*237*	*102*
Juvenile	Female	65	121	*151*	*155*	*146*	*177*	*121*	*130*	265	231	*102*
			131	*155*	155	*148*	*181*	121	*132*	*275*	*241*	106

Year	Den ID
2004	112

Age	Sex	ID	5	9	15	140	147	173	250	745	758	771
Adult	Female	91	119	151	155	136	169	125	124	265	235	98
			127	155	157	136	177	127	132	275	237	106
Juvenile	Female	36	*127*	*151*	*155*	*136*	*169*	*125*	126	*265*	*237*	102
			133	*155*	155	148	175	125	*132*	269	237	*106*
Juvenile	Female	37	*127*	*151*	*155*	*136*	175	*125*	*124*	269	*235*	94
			133	151	155	148	*177*	*127*	126	*275*	*237*	*98*
Juvenile	Female	38	*127*	*151*	*155*	*136*	*169*	*125*	126	269	*237*	102
			133	*155*	155	148	175	*127*	*132*	*275*	237	*106*
Juvenile	Female	39	*119*	*151*	*155*	*136*	175	*125*	*124*	269	*235*	94
			133	151	*157*	148	*177*	*127*	126	*275*	*237*	*98*
Juvenile	Male	40	*127*	*151*	*155*	*136*	*169*	*125*	126	269	*237*	*98*
			133	*155*	*157*	148	175	125	*132*	*275*	237	102
Juvenile	Male	42	*127*	*151*	*155*	*136*	175	*125*	*124*	*265*	*235*	94
			133	*155*	*157*	148	*177*	*127*	126	269	*237*	*106*

Year	Den ID
2004	137

Age	Sex	ID	5	9	15	140	147	173	250	745	758	771
Adult	Male	20	113	151	155	142	175	125	124	265	219	96
			131	151	157	148	181	127	132	271	237	102
Juvenile	Male	19	117	**151**	**155**	**142**	**175**	121	122	**265**	**219**	**96**
			131	155	155	144	**181**	**127**	**132**	275	227	104

Year	**Den ID**
2004	**145**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	13	121	151	157	142	175	125	124	265	225	98
			121	155	163	144	185	125	126	275	237	100
Juvenile	Female	10	**121**	**151**	151	140	177	**125**	122	**275**	233	**98**
			129	151	**163**	**142**	**185**	129	**126**	277	**237**	**100**
Juvenile	Male	11	131	**151**	151	140	177	123	122	269	221	102
			133	157	155	146	181	127	**124**	277	239	102
Juvenile	Male	12	**121**	**155**	**157**	140	165	123	**124**	**275**	**225**	**98**
			129	155	159	**144**	**175**	**125**	124	277	239	98
Juvenile	Female	14	131	**155**	151	146	169	127	122	269	233	102
			133	157	155	150	177	129	132	277	233	102
Juvenile	Male	15	131	**155**	151	140	169	127	122	269	233	**98**
			133	155	155	148	177	129	132	271	233	102
Juvenile	Female	16	131	**151**	155	148	165	127	**124**	269	233	96
			133	**155**	159	150	169	129	132	277	239	102

Year	**Den ID**
2004	**327**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Juvenile	Female	17	113	151	153	148	173	121	122	269	235	100
			131	155	155	148	177	127	126	275	241	102
Juvenile	Male	73	117	151	151	146	173	121	122	269	235	98
			133	155	155	146	181	127	126	275	241	100

Year	**Den ID**											
2005	**001**											
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	67	125	151	151	146	169	121	126	269	235	98
			133	157	155	148	177	123	128	275	241	104
Adult	Female	75	131	151	157	144	177	121	122	273	237	94
			133	155	159	148	181	125	126	275	241	104
Juvenile	Female	79	**133**	*155*	**151**	*144*	**169**	**121**	*126*	**269**	**235**	*94*
			133	**157**	*159*	**146**	*177*	*125*	**128**	*273*	*237*	**98**
Juvenile	Female	80	**125**	*155*	**151**	*144*	**177**	*121*	**126**	**269**	*237*	*94*
			133	**157**	*157*	**146**	*177*	**123**	*126*	*275*	**241**	**98**
Juvenile	Male	81	**125**	*151*	**151**	*144*	**177**	**123**	*122*	**275**	**241**	**98**
			131	**157**	*159*	**148**	*181*	*125*	**126**	*275*	*241*	*104*
Juvenile	Female	82	*131*	*151*	**155**	**148**	**177**	**121**	*122*	*273*	**235**	**104**
			133	**157**	*157*	*148*	*181*	*121*	**128**	**275**	*241*	*104*
Juvenile	Female	83	**125**	*155*	**155**	*144*	**169**	**121**	*122*	**269**	**235**	**104**
			131	**157**	*159*	**146**	*181*	*121*	**128**	*275*	*237*	*104*
Juvenile	Male	84	**133**	**151**	**151**	**148**	**169**	*121*	*122*	*273*	*237*	**98**
			133	*151*	*159*	*148*	*177*	**123**	**126**	**275**	**241**	*104*

Year **Den ID**
2005 **106**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Female	33	129	151	155	146	177	121	130	275	237	100
			131	155	157	148	181	121	132	275	241	102
Juvenile	Female	85	123	*151*	*155*	*148*	175	*121*	124	265	219	*102*
			131	*155*	*157*	148	*181*	121	*130*	*275*	*241*	102
Juvenile	Male	86	123	*151*	*155*	*146*	*177*	*121*	124	*275*	219	*100*
			131	*155*	*157*	*148*	177	121	*130*	275	*241*	106
Juvenile	Male	87	123	*155*	*155*	*148*	175	*121*	*132*	265	231	*102*
			129	155	155	148	*177*	121	132	*275*	*237*	106
Juvenile	Female	88	121	*155*	*157*	*148*	*181*	*121*	*132*	265	231	*100*
			131	155	163	148	181	121	132	*275*	*237*	*102*
Juvenile	Male	89	123	*155*	*155*	*146*	175	*121*	*132*	265	231	*100*
			131	155	*157*	*148*	*177*	121	132	*275*	*237*	106
Juvenile	Male	90	121	*151*	*155*	*146*	175	*121*	124	*275*	219	*102*
			129	*155*	163	*148*	*177*	121	*132*	275	*237*	102

Year **Den ID**
2005 **115**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	94	121	155	155	146	181	121	130	275	231	100
			131	155	155	148	181	121	132	277	241	102
Adult	Female	93	125	155	155	146	169	123	132	271	227	98
			131	157	155	148	177	125	134	271	237	100
Juvenile	Female	92	*125*	**155**	**155**	**148**	*177*	**121**	**132**	*271*	*227*	*98*
			131	*155*	*155*	*148*	**181**	*125*	*132*	**275**	**231**	**102**

Year **Den ID**
2005 **134**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Juvenile	Male	95	133	155	151	144	171	123	122	269	227	94
			133	157	155	146	177	127	128	273	239	98
Juvenile	Male	96	133	151	151	148	177	123	122	269	227	100
			133	151	155	150	181	127	128	273	237	106

Year	**Den ID**
2005	**137**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	20	113	151	155	142	175	125	124	265	219	96
			131	151	157	148	181	127	132	271	237	102
Juvenile	Female	97	117	**151**	**155**	144	**175**	**125**	122	**271**	227	**96**
			131	151	155	**148**	**181**	125	**124**	275	**237**	108
Juvenile	Female	98	**131**	**151**	**155**	144	**175**	121	122	**271**	227	**102**
			133	155	155	**148**	**181**	**125**	**124**	275	**237**	104

Year	**Den ID**
2006	**201**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	99	117	155	155	144	173	121	126	269	235	96
			131	157	161	148	181	125	132	275	239	102
Juvenile	Male	117	**117**	151	157	**144**	**173**	**121**	**126**	265	237	**102**
			133	**157**	**161**	**148**	**181**	**125**	128	**275**	**239**	102

Year	**Den ID**
2006	**204**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	111	113	153	151	142	175	121	124	271	235	94
			137	155	155	148	179	123	130	277	235	102
Adult	Female	123	125	155	159	146	169	121	128	269	225	98
			129	155	161	152	177	121	128	273	237	100
Juvenile	Female	112	*125*	**153**	**155**	*146*	*169*	*121*	*128*	*269*	*237*	*100*
			131	*155*	*161*	154	173	125	**130**	275	237	**102**
Juvenile	Female	119	*125*	*155*	157	*146*	173	*121*	**124**	*269*	*225*	*98*
			129	**155**	*159*	154	*177*	127	*128*	**271**	*237*	**102**
Juvenile	Male	120	*125*	*155*	157	*146*	*169*	*121*	*128*	*273*	231	*98*
			131	**155**	*161*	154	173	125	**130**	275	*237*	104
Juvenile	Male	121	*129*	**153**	157	*152*	*169*	*121*	*128*	*273*	231	*100*
			131	*155*	*161*	154	*177*	125	**130**	275	*237*	**102**
Juvenile	Female	122	*129*	**153**	**155**	*152*	*169*	*121*	*128*	*269*	*225*	*100*
			129	*155*	*159*	154	173	125	**130**	**271**	231	**102**

Year	**Den ID**
2007	**105**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	64	123	151	155	148	175	121	124	275	219	100
			131	155	163	148	181	121	132	277	237	102
Adult	Female	77	119	153	155	148	177	121	130	271	227	98
			129	161	159	152	179	123	132	275	241	104
Juvenile	Male	130	*129*	**151**	*155*	**148**	*179*	**121**	**132**	*271*	**237**	**100**
			131	*153*	**163**	*152*	**181**	*121*	*132*	**277**	*241*	*104*
Juvenile	Male	135	*129*	**155**	*155*	**148**	**175**	**121**	*130*	*271*	*227*	**102**
			131	*161*	**163**	*148*	*177*	*123*	**132**	**277**	**237**	*104*
Juvenile	Male	136	*119*	**151**	**155**	**148**	**175**	**121**	**124**	*275*	**219**	**102**
			123	*153*	*159*	*148*	*177*	*123*	*130*	**277**	*227*	*104*
Juvenile	Male	137	*129*	**155**	**155**	144	169	**121**	126	*271*	231	98
			129	*161*	*159*	*152*	*177*	*123*	*132*	**275**	*241*	*98*
Juvenile	Female	138	*129*	*153*	*155*	**148**	**175**	**121**	**132**	**275**	**237**	**102**
			131	**155**	**163**	*152*	*177*	*123*	*132*	*275*	*241*	*104*
Juvenile	Female	139	**123**	*153*	**155**	144	169	**121**	**124**	*271*	**237**	**102**
			129	**155**	*159*	*148*	*177*	*123*	*130*	**275**	*241*	*104*

Year	**Den ID**											
2007	**106**											
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	190	131	153	155	146	177	123	122	271	225	100
			131	155	157	148	177	127	124	279	231	106
Adult	Female	33	129	151	155	146	177	121	130	275	237	100
			131	155	157	148	181	121	132	275	241	102
Juvenile	Male	140	119	*151*	*155*	*146*	175	*121*	*130*	**271**	*237*	*102*
			131	**155**	159	**148**	*181*	**123**	130	*275*	*241*	102
Juvenile	Male	141	119	*151*	*155*	*146*	175	*121*	*130*	**271**	227	*102*
			129	**155**	**155**	**146**	*177*	**123**	130	*275*	*241*	102
Juvenile	Female	142	119	*151*	*155*	144	175	*121*	*130*	**271**	*237*	**100**
			129	**155**	**157**	*146*	*177*	**127**	*132*	*275*	237	*102*
Juvenile	Female	143	119	*151*	*155*	144	175	*121*	*130*	**271**	*237*	**100**
			129	151	**155**	*148*	*181*	**127**	*132*	*275*	237	*102*
Juvenile	Male	144	119	*151*	*155*	*146*	173	*121*	*130*	**271**	*237*	**100**
			129	151	**155**	**146**	*177*	**127**	*132*	*275*	237	*102*
Juvenile	Female	145	119	*151*	*157*	*146*	173	*121*	*130*	**271**	*237*	**100**
			131	151	159	**148**	*177*	**123**	130	*275*	*241*	*102*
Juvenile	Female	146	119	*151*	*157*	144	175	*121*	*130*	*275*	*237*	**100**
			131	**155**	159	*146*	*177*	**123**	*132*	277	237	*100*

Year	**Den ID**											
2007	**111**											
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	20	113	151	155	142	175	125	124	265	219	96
			131	151	157	148	181	127	132	271	237	102
Juvenile	Female	147	121	**151**	**157**	**148**	**175**	121	**124**	**271**	**237**	**96**
			131	155	163	148	**181**	**125**	130	279	241	**102**
Juvenile	Male	149	**131**	**151**	**157**	**148**	**181**	121	**124**	**265**	**237**	**96**
			131	155	157	148	183	**125**	130	279	241	**102**
Juvenile	Female	151	121	**151**	**155**	**142**	**181**	121	130	**271**	**219**	**96**
			131	155	163	**148**	181	**127**	**132**	277	241	**102**
Juvenile	Male	152	121	**151**	**157**	**142**	**181**	121	**124**	**265**	**219**	**102**
			131	155	163	**148**	181	**125**	123	275	**237**	102

Year	**Den ID**
2007	**114**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	173	133	151	155	148	175	125	126	269	235	94
			133	151	155	148	175	127	128	269	237	102
Adult	Female	154	113	151	157	140	173	121	132	271	235	100
			129	155	157	148	175	123	132	277	237	100
Juvenile	Female	153	*129*	**151**	**155**	**148**	**175**	*123*	**126**	**269**	**235**	**94**
			133	*155*	*157*	*148*	*175*	**125**	*132*	*271*	*237*	*100*

Year	**Den ID**
2007	**115**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	116	129	155	153	152	171	121	122	271	231	98
			137	155	155	156	181	121	126	271	241	102
Juvenile	Male	155	**129**	151	**153**	148	**171**	**121**	**122**	**271**	**231**	100
			133	**155**	**155**	**156**	177	125	124	277	235	**102**
Juvenile	Female	156	133	151	**153**	146	**171**	**121**	**122**	269	**231**	**98**
			137	**155**	**155**	**152**	**181**	125	124	**271**	**241**	100
Juvenile	Male	157	**129**	151	**153**	148	**171**	**121**	**122**	269	**231**	100
			133	**155**	**155**	**152**	177	125	124	**271**	235	**102**
Juvenile	Female	158	133	**155**	**155**	148	**171**	**121**	**122**	**271**	**231**	100
			137	155	155	**152**	**181**	125	124	277	235	**102**
Juvenile	Male	159	**129**	151	**153**	146	**171**	**121**	**122**	269	**231**	100
			133	**155**	**155**	**152**	177	129	124	**271**	235	**102**
Juvenile	Male	160	**129**	151	**153**	146	**181**	**121**	124	269	**241**	**98**
			137	**155**	**155**	**156**	181	125	**126**	**271**	241	100
Juvenile	Male	161	**129**	151	**153**	148	177	**121**	**122**	269	**231**	100
			137	**155**	**155**	**152**	**181**	129	124	**271**	235	**102**

Year	**Den ID**											
2007	**123**											
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	125	129	155	159	136	171	121	126	269	229	98
			129	157	161	140	177	127	132	277	231	100
Juvenile	Female	162	125	151	155	**136**	173	**121**	128	**269**	235	**100**
			129	153	**159**	148	175	125	140	275	235	102
Juvenile	Male	163	125	151	155	**136**	175	123	130	**269**	235	94
			129	**155**	157	142	175	125	140	275	237	**100**
Juvenile	Male	164	**129**	151	155	**136**	175	123	130	**269**	235	94
			131	**155**	157	148	181	125	138	269	237	**100**
Juvenile	Male	165	**129**	151	155	**136**	175	**121**	128	**269**	237	94
			131	**155**	**159**	148	181	125	138	275	237	**100**
Juvenile	Female	166	125	151	155	142	175	**121**	128	**269**	237	**100**
			129	**155**	**159**	146	175	125	140	275	237	102
Juvenile	Male	167	125	151	155	142	175	**121**	128	**269**	237	**100**
			125	153	157	146	175	125	140	275	237	100
Juvenile	Male	168	125	**155**	155	146	173	123	-	**269**	237	**100**
			131	155	**159**	148	181	125	-	275	237	102
Juvenile	Male	169	125	151	155	**136**	175	123	128	**269**	235	**100**
			131	153	**159**	148	175	125	138	275	237	102
Juvenile	Male	170	125	153	155	**136**	173	**121**	130	**269**	235	96
			131	**155**	**159**	142	175	125	140	275	237	**100**
Juvenile	Male	171	**129**	151	155	**136**	175	**121**	128	**269**	235	**100**
			131	153	**159**	142	181	125	138	269	235	100
Juvenile	Female	172	125	151	155	142	175	123	130	**269**	235	**100**
			131	153	157	146	175	125	140	269	237	102

Year	**Den ID**

2007 **131**

Age	Sex	ID	5	9	15	140	147	173	250	745	758	771
Adult	Male	179	125	151	155	148	171	123	122	277	233	96
			133	155	155	148	175	129	130	277	239	104
Adult	Female	181	123	151	155	146	169	121	136	275	225	104
			135	155	155	156	177	125	138	279	235	104
Juvenile	Female	174	*123*	**151**	**155**	*146*	*169*	*121*	**122**	*275*	*235*	**96**
			125	*151*	*155*	**148**	**171**	**129**	*138*	**277**	**239**	*104*
Juvenile	Male	175	**133**	**151**	**155**	**148**	*169*	*121*	**122**	*275*	*235*	**104**
			135	*155*	*155*	*156*	**171**	**123**	*136*	**277**	**239**	*104*
Juvenile	Male	176	**133**	**151**	**155**	**148**	*169*	*125*	**122**	**277**	*235*	**104**
			135	*155*	*155*	*156*	**175**	**129**	*136*	*279*	**239**	*104*
Juvenile	Female	177	**125**	**151**	**155**	**148**	*169*	*125*	**122**	*275*	*225*	**104**
			135	*151*	*155*	*156*	**175**	**129**	*136*	**277**	**233**	*104*
Juvenile	Female	178	*123*	**151**	**155**	*146*	*175*	**123**	**130**	*275*	*225*	**96**
			133	*155*	*155*	**148**	**177**	*125*	*136*	**277**	**239**	*104*
Juvenile	Female	180	**125**	**155**	**155**	**148**	*169*	*121*	**122**	*275*	**233**	**104**
			135	*155*	*155*	*156*	**175**	**129**	*138*	**277**	*235*	*104*
Juvenile	Female	182	*123*	**151**	**155**	**148**	*169*	*121*	**130**	*275*	*235*	**96**
			125	*155*	*155*	*156*	**175**	**123**	*136*	**277**	**239**	*104*

Year **Den ID**

2007 **137**

Age	Sex	ID	5	9	15	140	147	173	250	745	758	771
Adult	Female	185	125	151	155	148	165	121	126	265	237	104
			133	159	155	152	175	125	126	273	239	108
Juvenile	Female	148	113	151	*155*	144	169	*121*	124	*273*	231	102
			125	159	155	*148*	*175*	127	*126*	277	*239*	*108*
Juvenile	Female	183	113	155	*155*	*148*	169	*121*	124	*273*	225	98
			133	*159*	155	*152*	*175*	121	*126*	275	*239*	*104*
Juvenile	Male	184	127	155	*155*	146	*175*	*125*	*126*	271	*237*	98
			133	*159*	155	*148*	175	125	132	*273*	*239*	*104*
Juvenile	Male	186	121	*151*	*155*	146	*175*	*121*	*126*	*265*	*237*	106
			133	155	155	*152*	181	*125*	132	271	*239*	*108*

Year **Den ID**

2007	**204**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	49	121	155	155	146	175	121	122	271	225	98
			127	155	157	154	179	125	132	281	237	106
Adult	Female	123	125	155	159	146	169	121	128	269	225	98
			129	155	161	152	177	121	128	273	237	100
Juvenile	Female	187	**121**	**155**	**155**	*152*	**175**	**121**	**122**	*269*	**237**	*98*
			129	*155*	*161*	**154**	*177*	*121*	*128*	**281**	*237*	**106**
Juvenile	Male	188	**127**	**155**	**157**	**146**	*169*	**121**	**122**	*273*	**225**	**98**
			129	*155*	*161*	*146*	**175**	*121*	*128*	**281**	*237*	*98*
Juvenile	Female	189	*125*	**155**	**155**	*146*	**175**	**121**	*128*	*269*	**225**	*98*
			127	*155*	*161*	**154**	*177*	*121*	**132**	**271**	*225*	**106**

Year	**Den ID**												
2008	**001**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Female	249	121	151	155	136	167	123	122	277	235	100
			131	155	155	152	181	125	136	279	239	102
Juvenile	Female	247	*121*	*151*	*155*	148	177	*123*	126	275	*235*	*102*
			133	*155*	155	*152*	*181*	123	*136*	*279*	241	104
Juvenile	Female	248	*121*	*151*	151	*136*	*167*	*123*	126	275	*235*	98
			133	157	*155*	148	*181*	123	*136*	*277*	241	*102*
Juvenile	Female	224	*121*	*155*	*155*	*136*	*167*	*125*	-	275	*239*	*100*
			133	157	155	148	167	127	-	*279*	241	104
Juvenile	Male	225	*121*	*151*	151	148	*167*	*123*	*122*	271	*235*	98
			133	157	*155*	*152*	167	123	126	*277*	235	*100*

Year	**Den ID**												
2008	**003**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Juvenile	Female	223	125	155	155	148	167	123	126	275	235	100
			131	157	155	152	177	125	136	277	241	104
Juvenile	Female	226	121	155	155	136	167	123	126	271	235	100
			125	157	155	146	177	125	136	277	241	104
Juvenile	Male	227	131	151	155	148	177	125	122	271	235	100
			131	151	155	152	181	127	126	277	239	100

Year	**Den ID**												
2008	**106**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	190	131	153	155	146	177	123	122	271	225	100
			131	155	157	148	177	127	124	279	231	106
Adult	Female	33	129	151	155	146	177	121	130	275	237	100
			131	155	157	148	181	121	132	275	241	102
Juvenile	Female	215	*129*	*151*	**155**	**148**	**177**	*121*	**124**	**271**	**225**	**100**
			131	**155**	*155*	*148*	*177*	**123**	*130*	*275*	*241*	*100*
Juvenile	Female	216	*129*	*151*	**155**	**146**	**177**	*121*	**122**	*275*	**225**	**100**
			131	**153**	*155*	*148*	*177*	**123**	*132*	**279**	*241*	*102*
Juvenile	Female	217	*129*	**155**	**157**	**146**	**177**	*121*	**122**	**271**	**231**	*100*
			131	*155*	*157*	*148*	*177*	**127**	*132*	*275*	*237*	**106**
Juvenile	Female	218	**131**	*151*	**155**	**146**	**177**	*121*	**122**	*275*	**231**	*102*
			131	**155**	*157*	*146*	*181*	**127**	*130*	**279**	*241*	**106**
Juvenile	Male	219	123	**155**	*157*	**148**	175	*121*	**124**	*275*	219	**100**
			129	*155*	163	*148*	*181*	121	*132*	275	*237*	*102*
Juvenile	Female	220	*129*	*151*	**157**	**146**	**177**	*121*	**122**	**271**	**231**	*102*
			131	**155**	*157*	*148*	*177*	**127**	*130*	*275*	*241*	**106**

Year	**Den ID**												
2008	**111**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	237	113	151	155	142	177	127	124	265	225	100
			117	155	159	144	181	127	126	269	237	106
Adult	Female	238	121	155	157	148	181	121	126	275	219	100
			131	157	163	148	181	121	132	275	241	102
Juvenile	Female	228	**117**	**151**	**155**	**144**	**181**	*121*	**124**	**265**	*219*	*102*
			121	*155*	*157*	*148*	*181*	**127**	*132*	*275*	**237**	**106**
Juvenile	Female	229	**113**	**155**	**155**	**144**	**181**	*121*	**124**	**269**	**237**	**100**
			121	*157*	*163*	*148*	*181*	**127**	*132*	*275*	*241*	*102*
Juvenile	Female	230	**117**	**151**	**159**	**144**	**177**	*121*	**124**	**269**	*219*	**100**
			131	*155*	*163*	*148*	*181*	**127**	*126*	*275*	**237**	*102*
Juvenile	Male	231	**113**	**155**	**155**	**144**	**177**	*121*	**126**	**265**	*219*	**100**
			121	*157*	*163*	*148*	*181*	**127**	*126*	*275*	**225**	*102*
Juvenile	Male	232	**117**	**155**	**159**	**142**	**181**	*121*	**124**	**269**	**237**	*102*
			131	*157*	*163*	*148*	*181*	**127**	*132*	*275*	*241*	**106**
Juvenile	Female	233	**117**	**151**	**155**	**142**	**181**	*121*	**126**	**265**	**225**	*102*
			121	*155*	*157*	*148*	*181*	**127**	*126*	*275*	*241*	**106**
Juvenile	Male	234	**117**	-	**155**	**142**	**181**	*121*	**124**	**265**	*219*	**100**
			131	-	*163*	*148*	*181*	**127**	*126*	*275*	**237**	*100*
Juvenile	Female	235	**117**	**151**	*157*	**142**	**177**	*121*	**124**	**269**	**237**	*100*
			131	*155*	**159**	*148*	*181*	**127**	*132*	*275*	*241*	**106**
Juvenile	Male	236	**113**	**155**	**155**	**144**	**177**	*121*	**124**	**269**	**237**	**100**
			131	*157*	*163*	*148*	*181*	**127**	*132*	*275*	*241*	*100*

Year	**Den ID**
2008	**113**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	197	113	151	155	142	175	121	124	269	233	94
			133	155	157	152	181	127	126	273	237	110
Juvenile	Male	191	**113**	*153*	***155***	*136*	*173*	**121**	122	265	*235*	*98*
			129	157	159	*144*	177	**127**	***126***	277	235	106
Juvenile	Female	192	**113**	*153*	***155***	*136*	*171*	123	**124**	265	223	106
			123	157	159	**142**	177	**127**	***126***	277	***233***	*118*
Juvenile	Female	193	119	**151**	***155***	*136*	*171*	**121**	*126*	*275*	**233**	102
			123	*151*	155	*144*	*173*	123	130	275	*235*	*118*
Juvenile	Male	194	123	**151**	**155**	136	171	**121**	**126**	**269**	**233**	**94**
			133	151	**157**	**152**	**175**	121	126	275	**237**	118
Juvenile	Female	195	**113**	153	**155**	144	173	**121**	**126**	**269**	235	**94**
			129	**155**	**157**	**152**	**181**	121	136	275	**237**	98
Juvenile	Male	196	119	***151***	***155***	*144*	*173*	123	***126***	*275*	*235*	*98*
			129	*153*	155	146	173	**127**	130	275	235	102

Year	**Den ID**
2008	**115**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	116	129	155	153	152	171	121	122	271	231	98
			137	155	155	156	181	121	126	271	241	102
Juvenile	Female	250	**129**	**155**	**155**	146	169	**121**	124	269	235	100
			131	155	155	**156**	**181**	129	**126**	**271**	**241**	**102**
Juvenile	Female	251	**129**	151	**155**	146	177	**121**	124	**271**	**241**	**98**
			129	**155**	155	**156**	**181**	125	**126**	275	241	100

Year	**Den ID**
2008	**131**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	179	125	151	155	148	171	123	122	277	233	96
			133	155	155	148	175	129	130	277	239	104
Adult	Female	181	123	151	155	146	169	121	136	275	225	104
			135	155	155	156	177	125	138	279	235	104
Juvenile	Female	251	*123*	**151**	**155**	*146*	**171**	*121*	**130**	*275*	**233**	**96**
			125	*151*	*155*	**148**	*177*	**129**	*136*	**277**	*235*	*104*

Year	**Den ID**												
2008	**145**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	64	123	151	155	148	175	121	124	275	219	100
			131	155	163	148	181	121	132	277	237	102
Adult	Female	201	127	151	157	142	173	125	124	265	235	102
			131	151	159	142	177	125	126	275	237	106
Juvenile	Female	199	*127*	*151*	*159*	*142*	*173*	**121**	*126*	**275**	**237**	**102**
			131	**155**	**163**	**148**	**181**	*125*	**132**	*275*	*237*	*106*
Juvenile	Female	200	**131**	*151*	151	*142*	*177*	*125*	122	*265*	*235*	*102*
			131	153	*157*	**148**	**181**	125	*124*	265	235	104
Juvenile	Male	202	*127*	*151*	**155**	*142*	**175**	**121**	**124**	*265*	**219**	**100**
			131	**155**	*159*	**148**	*177*	*125*	*126*	**275**	*237*	*102*
Juvenile	Male	203	**123**	*151*	*157*	*142*	*173*	**121**	*124*	**275**	*235*	**102**
			131	**155**	**163**	**148**	**181**	*125*	**132**	*275*	**237**	*102*
Juvenile	Female	204	*127*	**151**	**155**	*142*	**175**	**121**	**124**	**275**	**219**	**100**
			131	*151*	*159*	**148**	*177*	*125*	*126*	*275*	*235*	*106*
Juvenile	Male	205	*127*	*151*	*159*	*142*	*173*	**121**	*126*	**275**	*235*	**102**
			131	**155**	**163**	**148**	**181**	*125*	**132**	*275*	**237**	*102*
Juvenile	Female	206	**131**	*151*	*159*	*142*	**175**	**121**	**124**	*265*	**219**	**102**
			131	**155**	**163**	**148**	*177*	*125*	*126*	**275**	*237*	*102*
Juvenile	Female	207	*127*	**151**	**155**	*142*	*177*	**121**	**124**	**275**	**219**	**100**
			131	*151*	*157*	**148**	**181**	*125*	*124*	*275*	*237*	*102*
Juvenile	Male	208	*131*	*151*	151	*142*	*173*	*125*	*124*	*265*	*235*	*102*
			131	153	*159*	144	**181**	125	128	**275**	**237**	104
Juvenile	Female	209	**123**	*151*	*157*	*142*	*177*	**121**	**124**	**275**	**219**	**100**
			131	**155**	**163**	**148**	**181**	*125*	*124*	*275*	*235*	*106*
Juvenile	Male	210	*131*	*151*	**155**	*142*	169	**121**	**124**	*275*	231	**102**
			133	**155**	*157*	144	*177*	*125*	*128*	279	*235*	*102*

Year	**Den ID**												
2008	**204**												
Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Juvenile	Male	214	125	153	151	144	175	-	126	269	237	94
			131	155	155	148	181	-	128	281	237	96

Year	**Den ID**
2008	**207**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	212	121	155	155	148	175	121	124	269	219	102
			137	155	157	150	181	121	132	275	239	102
Adult	Female	213	127	155	155	144	175	127	126	275	231	100
			137	155	155	152	181	127	126	275	241	102
Juvenile	Female	211	*127*	**155**	*155*	*144*	**175**	**121**	*126*	**269**	**239**	**102**
			137	*155*	**157**	**150**	*175*	*127*	**132**	*275*	*241*	*102*

Year	**Den ID**
2008	**327**

Age	**Sex**	**ID**	**5**	**9**	**15**	**140**	**147**	**173**	**250**	**745**	**758**	**771**
Adult	Male	245	133	151	155	146	175	121	122	275	235	100
			133	155	155	148	181	125	132	279	237	116
Juvenile	Male	239	125	**151**	151	136	**181**	**121**	**122**	271	**235**	**100**
			133	**155**	**155**	**146**	181	123	**132**	**279**	239	106
Juvenile	Female	240	125	**155**	**155**	**146**	**175**	123	**122**	271	**235**	100
			133	155	155	**148**	175	**125**	124	**275**	239	**116**
Juvenile	Male	241	125	**151**	**155**	136	**175**	**125**	**122**	**279**	**237**	**100**
			133	**151**	155	**146**	**181**	127	**132**	279	239	106
Juvenile	Male	242	113	**151**	**155**	136	**181**	123	124	271	**235**	100
			133	**155**	155	**148**	181	**125**	**132**	**279**	**237**	**116**
Juvenile	Female	243	125	**151**	**155**	136	**181**	123	**122**	**279**	**235**	**100**
			133	**155**	155	**146**	181	**125**	124	279	235	100
Juvenile	Female	244	**133**	**151**	**155**	136	**181**	**125**	**122**	**279**	**235**	100
			133	151	155	**148**	181	127	124	279	235	**116**

Appendix 3 - Summary of den attendance and food provisioning by social parents at arctic fox reproductive dens on Bylot Island, Bylot Island, Nunavut, Canada, 2007-2008 recorded from direct observations and analysis of automatic cameraphotographs.

			Direct observations			Automatic cameras			Mean	
	Year	Den ID	Frequency of den attendance (times/hour)	Frequency of food provisioning (times/hour)	Duration of the observation period (hours)	Frequency of den attendance (times/hour)	Frequency of food provisioning (times/hour)	Duration of the observation period (hours)	Frequency of den attendance (times/hour)	Frequency of food provisioning (times/hour)
Mothers	2007	105	8.8	2.9	16.3	4.7	1.9	76.8	6.8	2.4
	2007	106	10.5	6.75	32.0	14.9	4.2	81.6	12.7	5.5
	2007	114	6.9	1.7	13.9	-	-	-	6.9	1.7
	2007	131	2.3	0.6	38.3	-	-	-	2.3	0.6
	2007	137	4.8	0	4.8	-	-	-	4.8	0
	2007	204	0	0	18.5	0.5	0.5	48.0	0.25	0.3
	2008	001	-	-	-	8.3	0.7	55.2	8.3	0.7
	2008	106	23.2	2.8	25.9	5.1	0	72.0	14.2	1.4
	2008	111	-	-	-	4.2	0.8	62.4	4.2	0.8
	2008	131	2.3	0	10.5	8.5	1.1	583.2	5.4	0.6
	2008	145	14.1	4.4	27.2	9.2	3.1	156.0	11.7	3.8
	Mean ± SD		8.1 ± 7.2	2.1 ± 2.3	20.8 ± 10.8	6.9 ± 4.3	1.5 ± 1.4	141.6 ± 182.4	7.0 ± 4.4	1.6 ± 1.7
Fathers	2007	105	0	0	16.3	0.6	0.3	76.8	0.3	0.2
	2007	106	0	0	32.0	0.3	0.3	81.6	0.2	0.2
	2007	115	6.3	3.8	18.9	4.5	1.8	52.8	5.4	2.8
	2007	123	7.6	7.6	6.3	1.0	0.2	115.2	4.3	3.9
	2007	131	3.1	0.6	38.3	-	-	-	3.1	0.6
	2007	204	3.9	1.3	18.5	2.6	1.5	48.0	3.3	1.4
	2008	106	13.0	5.6	25.9	3.6	0.3	72.0	8.3	3.0
	2008	111	-	-	-	0.4	0.4	62.4	0.4	0.4
	2008	113	5.0	0.8	28.7	16.9	5.4	31.2	11.0	3.1
	2008	115	1.8	0.6	40.8	-	-	-	1.8	0.6
	2008	131	4.6	0	10.5	4.1	3.1	583.2	4.4	1.6
	2008	145	11.5	1.8	27.2	7.1	3.1	156.0	9.3	2.5
	2008	327	7.0	0.6	37.8	1.7	1.2	165.6	4.4	0.9
	Mean ± SD		5.3 ± 4.1	1.9 ± 2.5	25.2 ± 11.2	3.9 ± 4.8	1.6 ± 1.7	132.0 ± 156.0	4.3 ± 3.5	1.6 ± 1.3