

1 **Title**

2 Evidence of adoption, monozygotic twinning, and low inbreeding rates in a large genetic  
3 pedigree of polar bears

4

5 **Authors**

6 René M. Malenfant<sup>a,\*</sup>, David W. Coltman<sup>a</sup>, Evan S. Richardson<sup>b</sup>, Nicholas J. Lunn<sup>b</sup>, Ian  
7 Stirling<sup>a,b</sup>, Elizabeth Adamowicz<sup>a</sup>, Corey S. Davis<sup>a</sup>

8

9 **Affiliations**

10 <sup>a</sup> Department of Biological Sciences, University of Alberta, Edmonton AB T6G 2E9, Canada

11 <sup>b</sup> Wildlife Research Division, Science and Technology Branch, Environment Canada, CW405  
12 Biological Sciences Centre, University of Alberta, Edmonton AB T6G 2E9, Canada

13 \* Corresponding author (email: rene.malenfant@ualberta.ca, fax: 1-780-492-9234)

14

15

16 Note: Pre-review copy. A modified version of this article was accepted in Polar Biology on Dec.

17 15, 2015. DOI to be provided.

## 18 **Abstract**

19           Multigenerational pedigrees have been developed for free-ranging populations of many  
20 species, are frequently used to describe mating systems, and are used in studies of quantitative  
21 genetics. Here, we document the development of a 4449-individual pedigree for the Western  
22 Hudson Bay subpopulation of polar bears (*Ursus maritimus*), created from relationships inferred  
23 from field and genetic data collected over six generations of bears sampled between 1966 and  
24 2011. Microsatellite genotypes for 22–25 loci were obtained for 2945 individuals, and parentage  
25 analysis was performed using the program FRANZ, including additional offspring–dam  
26 associations known only from capture data. Parentage assignments for a subset of 859 individuals  
27 were confirmed using an independent high-density set of single nucleotide polymorphisms. To  
28 account for unsampled males in our population, we performed half-sib–full-sib analysis to  
29 reconstruct males using the program COLONY, resulting in a final pedigree containing 2957  
30 assigned maternities and 1861 assigned paternities with only one observed case of inbreeding  
31 between close relatives. During genotyping, we identified two independently captured two-year-  
32 old males with identical genotypes at all 25 loci, showing—for the first time—a case of  
33 monozygotic twinning among polar bears. In addition, we documented six new cases of cub  
34 adoption, which we attribute to cub misidentification or misdirected maternal care by a female  
35 bereaved of her young. Importantly, none of these adoptions could be attributed to reduced  
36 female vigilance caused by immobilization to facilitate scientific handling, as has previously been  
37 suggested.

38

## 39 **Keywords**

40 Ursidae, Western Hudson Bay, alloparenting, relatedness, microsatellites, identical twins

## 41 **Introduction**

42           Multigenerational pedigrees are useful in studies describing mating systems and for  
43 quantitative genetics research (Pemberton 2008) and large pedigrees have been developed for  
44 wild populations of many species, including red deer (*Cervus elaphus*; Slate et al. 2002), bighorn  
45 sheep (*Ovis canadensis*; Poissant et al. 2010), song sparrows (*Melospiza melodia*; Reid et al.  
46 2011), and American red squirrels (*Tamiasciurus hudsonicus*; Taylor et al. 2012). However,  
47 because of the great effort and expense of sampling large carnivores, few pedigrees have been  
48 developed for ursid species, with most parentage analyses containing no more than a few hundred  
49 individuals, which are typically sampled non-invasively (Cronin et al. 2005; De Barba et al.  
50 2010; Itoh et al. 2012; Onorato et al. 2004; however, cf. Proctor et al. 2004; Bellemain et al.  
51 2006). To date, the largest parentage analysis of polar bears (*Ursus maritimus*) was based on 583  
52 individuals in the Barents Sea (Zeyl et al. 2009a; Zeyl et al. 2009b), which showed that polar  
53 bears exhibit serial monogamy, male-biased dispersal, and that inbreeding between close relatives  
54 is rare.

55           Polar bears are large carnivores that occur at low densities throughout the circumpolar  
56 Arctic and subarctic regions. They have a polygynous mating system (Derocher et al. 2010),  
57 typically breeding between late March and June, with females giving birth to 1–3 cubs in  
58 November–December while overwintering in maternity dens. Females emerge from dens in early  
59 spring, and are the only providers of parental care until their cubs become independent—typically  
60 at about 2.5 years old (Ramsay and Stirling 1988). Though family groups tend to avoid other  
61 bears—perhaps to avoid cannibalism and other conspecific aggression (Taylor et al. 1985)—  
62 cases of adoption have previously been documented (Atkinson et al. 1996; Belikov 1976;  
63 Derocher and Wiig 1999; Lunn et al. 2000; Saunders 2005; Vibe 1976). Although adoption has

64 been known to occur in the Barents Sea subpopulation (Derocher and Wiig 1999), Zeyl et al.  
65 (2009a, 2009b) did not report any cases of adoption, perhaps because of the infrequency of  
66 occurrence, combined with the study's comparatively small sample size.

67 Adoption has been observed in more than 60 mammalian species (Gorrell et al. 2010), and  
68 its occurrence requires special explanation due to the extremely high cost of milk provision to  
69 adopted young (e.g., Clutton-Brock et al. 1989). Allonursing and adoption may be explained  
70 adaptively through kin selection, reciprocal altruism, evacuation of excess milk, or through a gain  
71 in parenting experience (Roulin 2002). Alternately, adoption and allonursing may simply be the  
72 result of error, occurring especially when a reproductive individual is already hormonally or  
73 behaviourally primed to provide parental care and is bereaved of their young (Riedman 1982).  
74 Most empirical studies support the kin selection, milk evacuation, or misdirected parental care  
75 hypotheses (Roulin 2002). Amongst polar bears, adoption has been attributed to misdirected  
76 parental care caused by cub misidentification (Lunn et al. 2000), which may be caused by  
77 confusion due to the immobilization of adult females, which is necessary for scientific handling  
78 (Derocher and Wiig 1999).

79 Like adoption, monozygotic twinning is taxonomically widespread but infrequent, and  
80 although well described in humans (e.g., Bulmer 1970) and cattle (e.g., Silva del Río et al. 2006),  
81 few cases have been documented in wildlife species. Monozygotic quadruplets are the normal  
82 mode of reproduction among some species of armadillos (Hardy 1995), and monozygotic twins  
83 have been identified in lesser flat-headed bats (*Tylonycteris pachypus*; Hua et al. 2011), in wolves  
84 (*Canis lupus*; Carmichael et al. 2009), among some species of pinnipeds (Spotte 1982), including  
85 Antarctic fur seals (*Arctocephalus gazella*; Hoffman and Forcada 2009), and possibly in mule  
86 deer (Anderson and Wallmo 1984). The apparent scarcity of monozygotic twins is partially

87 attributable to the difficulty of identifying them, as this requires genetic or embryological  
88 confirmation. For instance, conjoined twins, which develop from monozygotic twins and are  
89 therefore far rarer, are phenotypically conspicuous, and at least 20 cases of conjoined twinning in  
90 wildlife species have been published (Kompanje and Hermans 2008). To our knowledge,  
91 identical twinning (or conjoined twinning) has never been detected in any species of bear,  
92 although no studies have had large enough sample sizes to reliably detect such a rare event.

93 In this paper, we present a large pedigree of polar bears comprising 4449 individuals from  
94 the Western Hudson Bay subpopulation captured over six bear generations in northeastern  
95 Manitoba, Canada between 1966 and 2011. We document six new cases of cub adoption, and  
96 show—for the first time—an instance of monozygotic twinning among polar bears. Further, we  
97 find no cases of inbreeding between first-degree relatives. This pedigree is now being used to  
98 determine the mating system of polar bears (Richardson 2014), and in future studies, this  
99 pedigree will be used to determine the heritabilities of various body size metrics, some of which  
100 have been declining in this subpopulation for decades (Stirling and Derocher 2012).

101

## 102 **Methods**

### 103 *Sample collection*

104 Most tissue samples were collected from bears that were immobilized and handled as part  
105 of long-term ecological studies of polar bears in Western Hudson Bay. However, a small number  
106 of samples were collected from bears captured by Manitoba Conservation staff near the  
107 community of Churchill as part of the Polar Bear Alert Program (Kearney 1989) or from polar  
108 bears harvested each year as part of a legal, regulated subsistence hunt by Inuit living along the  
109 coast of western Hudson Bay (Derocher et al. 1997; Taylor et al. 2008). Sampling locations are

110 shown in Figure 1. During the first handling of each captured individual, he/she was assigned a  
111 unique ID applied as a permanent tattoo on the inside of the upper lip and affixed as a plastic tag  
112 in each ear. Skin samples were collected by retaining leftover pinnal tissue from ear-tagging or  
113 from adipose tissue samples collected using a 6-mm biopsy punch of superficial fat on the rump  
114 (Ramsay et al. 1992; Thiemann et al. 2008). A temporary paint mark is also applied to avoid  
115 recapture of the same individual twice in one season. Blood samples were collected by drawing  
116 blood from a femoral vein into a sterile vacutainer. All samples were stored at  $-80^{\circ}\text{C}$  until DNA  
117 extraction. If the age of a newly sampled individual was unknown (i.e., not a cub-of-the-year or a  
118 dependent yearling), a vestigial premolar tooth was extracted for age determination using  
119 measurement of cementum annulus deposition (Calvert and Ramsay 1998). All individuals  
120 handled by Environment Canada were sampled in autumn and were selected for handling  
121 indiscriminately of age or sex; however, in every year from 1980 onward (except for 1985 and  
122 1986), a springtime sampling effort was also included, in which only adult females and their  
123 cubs-of-the-year—which had recently emerged from maternity dens—were handled.

124

#### 125 *DNA extraction and microsatellite genotyping*

126 Total genomic DNA was extracted from fat, skin, or leukocytes recovered from ACK-  
127 lysed blood using DNeasy Blood & Tissue Kits (Qiagen, Hilden, Germany). We genotyped 2945  
128 individuals born between 1960 and 2011, including duplicate samples from 69 individuals  
129 included to estimate genotyping error rates. Individuals born before 2006 were genotyped at all  
130 25 microsatellite loci (Table S1, Supplementary Material); however, because of changes to the  
131 genotyping protocol made in 2012 to streamline microsatellite multiplexing, individuals born  
132 from 2006 onward were genotyped at 24 loci (excluding CXX173). PCR products from

133 microsatellite amplifications were resolved on an Applied Biosystems 377 DNA Sequencer,  
134 3100-Avant DNA Analyzer, or a 3730 DNA Analyzer, and sized relative to Genescan size  
135 standards. Genotyping was performed using the programs Genotyper and Genemapper (Applied  
136 Biosystems, Foster City, CA, USA).

137

### 138 *Genetic diversity, tests of disequilibrium, and statistics*

139 The number of observed alleles ( $N_A$ ), observed heterozygosities ( $H_O$ ), expected  
140 heterozygosities ( $H_E$ ), probabilities of exclusion ( $P_{ex}$ ), and probabilities of identity ( $P_{ID}$ ) were  
141 calculated using GENALEX 6.5 (Peakall and Smouse 2006; Peakall and Smouse 2012);  $P_{ex}$  was  
142 calculated using the formula for single unknown parent exclusion from Jamieson and Taylor  
143 (1997). Departures from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD)  
144 were assessed with exact tests (Guo and Thompson 1992) and a Markov chain (dememorization  
145 number = 5000, number of batches = 1000, number of iterations per batch = 2000) using  
146 GENEPOP ON THE WEB 4.2 (Raymond and Rousset 1995; Rousset 2008). The total genotyping  
147 error rate (calculated as the sum of the allelic dropout rate (E1) and false allele rate (E2), Table  
148 S1) was calculated from duplicate samples using the program PEDANT 1.0 (Johnson and Haydon  
149 2007) using 100,000 replicates. Unless otherwise indicated, all other statistics were calculated in  
150 R 3.1.3 (R Core Team 2015), and a significance level of  $\alpha=0.05$  was used for all tests.

151

### 152 *Pedigree generation and adoption detection*

153 We used the program FRANZ 2.0 (Riester et al. 2009; Riester et al. 2010) to generate an  
154 initial pedigree from our microsatellite data, using a sub-pedigree comprising known mother–cub  
155 relations from field data, individuals' years of birth (and death, if known) and the settings

156 specified in Table 1. FRANZ generates a multigenerational pedigree in a single step, using  
157 simulations to determine expected parent–offspring mismatch rates, simulated annealing to  
158 estimate the maximum-likelihood pedigree, and Metropolis-coupled Markov chain Monte Carlo  
159 sampling to calculate parentage posterior probabilities. As part of its simulation step, FRANZ  
160 uses the empirical distribution of parent–offspring mismatch rates to identify problematic  
161 parental assignments in the sub-pedigree (Figure 2), which we have classified here as adoptions.  
162 Although our field records contain no instances of females younger than four years old (or older  
163 than 28 years old) having successfully given birth, we specified a possible reproductive age range  
164 of 2–32 (at time of parturition) to account for outliers amongst unobserved maternities as well as  
165 possible errors in tooth aging. For simplicity, we also used this same age range for males; males  
166 generally do not become reproductively active until at least their fifth or sixth year, though they  
167 may begin to produce spermatozoa at age two (Rosing-Asvid et al. 2002). The oldest female and  
168 male polar bears captured from the Western Hudson Bay subpopulation were 32 and 29 years  
169 old, respectively.

170 To detect the genetic mothers of adopted individuals, we removed their links from our  
171 field-data sub-pedigree and re-ran FRANZ. Then, to validate and error-correct the resultant  
172 pedigree, we used the program VIPER 1.01 (Paterson et al. 2012) to examine the inheritance of  
173 4,475 single-nucleotide polymorphisms (SNPs) genotyped in a 859-individual subset of  
174 pedigreed bears. These SNPs were developed from transcriptomic and RAD sequencing and were  
175 genotyped with high fidelity in all individuals using a recently developed 9K Illumina BeadChip  
176 for polar bears (Malenfant et al. 2015). We removed all pedigree links displaying more than one  
177 SNP inheritance error, which we determined as a cutoff based on the empirical distribution of  
178 inheritance errors.



179 Finally, to account for a lower proportion of males than females being sampled in our data  
180 (which led to proportionally fewer paternity than maternity assignments), we used the program  
181 COLONY 2.0 (Jones and Wang 2010) to generate hypothetical sires and differentiate between  
182 full siblings and maternal half siblings. To reduce false paternity assignments, we limited  
183 candidate offspring in this analysis to 760 individuals having unassigned sires but genetically  
184 assigned dams. All individuals were pooled in a single analysis irrespective of birth year to allow  
185 for the possibility that a hypothetical male had sired multiple offspring across years. We allowed  
186 for male and female polygamy, using maternal and paternal sibship priors of 3.655 and 2.968  
187 respectively, which were determined empirically from the pedigree. All pedigree statistics were  
188 calculated using the package PEDANTICS 1.5 (Morrissey and Wilson 2010).

189

#### 190 *Genetic relatedness*

191 Asocial animals such as polar bears might choose to adopt nearby orphans if they are  
192 genetically related, as this can provide an inclusive fitness advantage to the foster parent (e.g.,  
193 Gorrell et al. 2010). To determine if adopted cubs were genetically related to their foster mothers,  
194 we used the program COANCESTRY 1.0.1.2 (Wang 2011) to obtain the Queller-and-Goodnight  
195 (1989), Lynch-and-Ritland (1999), and Wang (2002) relatedness metrics using allele frequencies  
196 and error rates estimated from the full microsatellite dataset. Because all estimators gave similar  
197 results, only the Queller-and-Goodnight estimator results are presented. This estimator was  
198 designed for studies of kin selection and has the property that unrelated individuals are expected,  
199 on average, to have a relatedness of zero.

200

#### 201 **Results**

202 *Microsatellite genotypes*

203 Complete 25-locus genotypes were obtained for 2418 individuals, 24-locus genotypes  
204 were obtained for 478 individuals, 23-locus genotypes were obtained for 34 individuals, and 22-  
205 locus genotypes were obtained for 15 individuals. The mean number of observed alleles ( $N_A$ ) was  
206 7.6 (range: 3–10), and mean observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosities were both 0.672  
207 (ranges: 0.112–0.847 and 0.112–0.840, respectively). Two loci, G1A and G10L, deviated from  
208 HWE ( $P_{G1A} = 0.0028$ ,  $P_{G10L} = 0.0064$ ) but were not significantly out of HWE following a strict  
209 Bonferroni correction for multiple tests ( $\alpha_{corrected} = 0.002$ ). Complete summary statistics for  
210 microsatellite loci are presented in Table S1. Thirty pairwise tests of LD were significant  
211 following strict Bonferroni correction, however, this was likely because our dataset contained  
212 many groups of related individuals. Combined probability of exclusion ( $P_{ex}$ ) over all loci is  
213 0.99991; this drops to 0.99988 if CXX173 is excluded. Combined probability of identity ( $P_{ID}$ )  
214 was  $7.102 \times 10^{-23}$  for unrelated individuals and  $1.562 \times 10^{-9}$  for full siblings; these increase to  
215  $5.020 \times 10^{-22}$  and  $3.551 \times 10^{-9}$  respectively if CXX173 is excluded. Total genotyping error rate was  
216 estimated at 0.36%. Fourteen successfully genotyped individuals were removed prior to pedigree  
217 generation because their year of birth was unknown.

218

219 *Pedigree statistics and inbreeding*

220 We supplemented the remaining 2931 genotyped-and-aged individuals with 1225  
221 individuals known only from field observation. FRANZ assigned 2972 maternities using field  
222 and/or genetic data and 1105 paternities using genetic data alone. Based on SNP inheritance  
223 errors identified in VIPER, 4 offspring–sire links out of 163 ( $\approx 2.5\%$ ) and 15 offspring–dam links  
224 out of 465 ( $\approx 3.2\%$ ) were removed. In all 15 of these cases, offspring–dam relationships had been

225 inferred using genetic data only (i.e., they were not based on field observations). COLONY  
226 reconstructed 293 sires, which collectively accounted for 760 paternal assignments (mean  $\pm$  SD  
227 offspring per reconstructed sire =  $2.6 \pm 1.4$ ), and brought the pedigree to 4449 individuals in  
228 total. Nine females aged 3 years or younger and males aged 2 years or younger (at time of  
229 conception) were assigned as parents in the final version of the pedigree, though the ages of 17 of  
230 these 18 individuals were uncertain as they were derived from tooth-aging estimates. The oldest  
231 dam and sire assigned in the pedigree were 28 and 30 respectively at the time of conception.

232 Including COLONY-reconstructed individuals, the pedigree contains 1381 founders (i.e.,  
233 individuals of unknown parentage) and extends to six generations for some individuals. Of 382  
234 mating events in which the identities of both parents and at least one grandparent on each side  
235 were known (a necessity for detecting inbreeding), only three individuals had non-zero  
236 inbreeding coefficients: X11088, X11089, and X11389. X11088 and X11089 are littermates born  
237 in 1989 to X10668 after mating with her half-brother X10497; X11389 was supposedly born to  
238 X09396 and her brother X09398 (however, cf. the Discussion regarding this mating). A graphical  
239 view of the pedigree and complete pedigree statistics and are given in Figure 3 and Table S2 of  
240 the Supplementary Material, respectively.

241

#### 242 *Monozygotic twinning*

243 We detected one pair of identical twins among 574 genotyped twin litters and 37  
244 genotyped triplet litters: cubs X17324 and X17326 match at all 25 loci (Supplementary Material  
245 2). Both individuals were independent two-year olds at the time of capture (November 10 and 11,  
246 2003, respectively), and were handled ~3.5 km apart on opposite sides of the Churchill airport.  
247 They were known not to have been recaptures of the same individual because the second-

248 captured individual (X17326) lacked the temporary paint mark and did not have a permanent  
249 tattoo or ear tags. If dizygotic, the probability of these cubs sharing a genotype at all 25 loci is  
250  $1.64 \times 10^{-11}$ , as calculated from the full genotypes of both parents. To discount the possibility that  
251 these identical genotypes were the result of sample mix-up, we reconfirmed the genotype of  
252 X17324 using a second, independently collected tissue sample; unfortunately, a second sample  
253 for X17326 was not available. However, because these individuals were handled on different  
254 days, the probability of sample mix-up during fieldwork is extremely low.

255

#### 256 *Cases of adoption*

257 We identified six previously undetected cases of adoption occurring between 1981 and  
258 2004 and identified four of the six genetic mothers (Table 2, Supplementary Material S2). In five  
259 of these cases, cubs were adopted during their first year of life; in the remaining case (X09059), it  
260 was unclear if the cub was adopted during its first or second year. In two cases, adoptive mothers  
261 were observed to have fostered cubs for at least a year, and from later capture and harvest  
262 records, it is known that at least five of six adopted cubs survived to independence (though the  
263 fate of X11097 is unknown.) Although five of the six adopted cubs were female, there was no  
264 statistical evidence of preference to adopt females over males (binomial test of 1:1 ratio:  $P =$   
265  $0.2188$ ). All adopted cubs appeared to be unrelated to their adoptive mothers: average adoptee–  
266 adopter relatedness is  $-0.038$ , and 95% confidence intervals for the Queller-and-Goodnight  
267 relatedness estimators are not significantly different from 0 in all cases. In two of the six adoption  
268 cases, females were also accompanied by their own genetic offspring.

269

#### 270 **Discussion**

271 *Inbreeding*

272 Active inbreeding avoidance is often presumed to be common amongst animals because  
273 of reduced fitness of inbred offspring (Keller and Waller 2002), though tolerance of—or even  
274 preference for—inbreeding may occur because of inclusive fitness benefits (Szulkin et al. 2013).  
275 When inbreeding avoidance does occur, it is generally attributed to mate choice or sex-biased  
276 dispersal (Pusey and Wolf 1996). However, sex-biased dispersal may also occur for reasons  
277 unrelated to inbreeding, such as sex differences in the benefits of retaining a productive territory  
278 or avoidance of intersexual competition (Moore and Ali 1984). Little is known about inbreeding  
279 in polar bears, and primary among the motivations for developing this pedigree was the  
280 characterization of inbreeding in this subpopulation (Richardson et al. 2006).

281 We detected only two instances of incestuous mating: one between half-siblings X10668  
282 and X10497 (producing X11088 and X11089), and another putative case between full-siblings  
283 X09396 and X09398 (producing X11389). However, in this latter case, X09398 is almost  
284 certainly a false paternity assignment: X09396 is an ungenotyped dam that was assigned using  
285 only field data, causing X09398 to be incorrectly assigned as a father because of allele-sharing  
286 with his sister. Therefore, after excluding this case, inbreeding among close relatives appears to  
287 be extremely rare in the Western Hudson Bay subpopulation, occurring only once among 382  
288 mating events in which it could have been observed. For comparison, in a study of the Barents  
289 Sea subpopulation, a single instance of father–daughter inbreeding was detected amongst 22  
290 matings between parents of known identity (Zeyl et al. 2009a), suggesting that the rate of mating  
291 between first-degree relatives was ~4.5%.

292 Polar bears exhibit low variation at major histocompatibility loci (Weber et al. 2013),  
293 which are thought to play an important role in kin recognition (Villinger and Waldman 2012),

294 and it has also been suggested that polar bears have undergone little selection for kin recognition  
295 because of low population densities (Lunn et al. 2000). If this is the case, then mate choice is  
296 unlikely to explain low inbreeding rates amongst polar bears. In contrast, our finding of little-to-  
297 no inbreeding in the Western Hudson Bay subpopulation may result from substantial dispersal  
298 and interbreeding between Western Hudson Bay and adjacent management units (Richardson  
299 2014). Studies of American black bears (*Ursus americanus*; Costello et al. 2008) and brown  
300 bears (*U. arctos*; Bellemain et al. 2006) have found similar rates of close inbreeding, which were  
301 attributed to lack of opportunity resulting from low population density and male-biased dispersal.  
302 In another study, inbreeding avoidance was cited as the most likely cause of male natal dispersal  
303 among brown bears (Zedrosser et al. 2007). These findings are also likely to hold true for polar  
304 bears, which occur at even lower densities, and for which limited genetic evidence also suggests  
305 male-biased dispersal in some subpopulations (Zeyl et al. 2009b). However, because radio  
306 telemetry data for male polar bears is scarce, little is known about dispersal patterns in male polar  
307 bears and further study is needed.

308

### 309 *Monozygotic twinning*

310 Inclusive fitness theory predicts the possible spread of genes for monozygotic twinning  
311 (Gleeson et al. 1994; Williams 1975), and though the reason for the rarity of monozygotic  
312 twinning is not well understood, it may be partially attributable to higher rates of spontaneous  
313 abortion for monozygotic twins (Livingston and Poland 1980) and lower survival of twins in  
314 species that normally bear only one offspring (e.g., Fricke 2001). Based on observed sex ratios of  
315 multi-cub litters, Ramsay and Stirling (1988) determined that monozygotic twinning was likely  
316 rare or absent among polar bears. Our study confirms that monozygotic polar bear twins are

317 extremely rare, being found in less than 1/600 litters ( $\approx 0.17\%$ ) in our data. To our knowledge,  
318 this is the first confirmed record of monozygotic twinning among polar bears or any other ursid,  
319 and previous genetics studies of bears (e.g., Bellemain et al. 2006; Proctor et al. 2004; Zeyl et al.  
320 2009a) likely failed to detect twins because of smaller sample sizes. Slightly higher rates of  
321 monozygotic twinning have been found for humans (0.35–0.4%; Bulmer 1970) and for cattle  
322 (0.33%; Silva del Río et al. 2006). In part, the lower estimate for polar bears may result from  
323 discounting the “invisible fraction” (Grafen 1988) of identical twins that were never observed  
324 because at least one cub died prior to emergence from the maternity den.

325

### 326 *Adoption*

327         According to Hamilton’s (1964) theory of kin selection, natural selection will favour a  
328 heritable predisposition for altruistic behaviour when  $C < rB$ , where  $C$  is the fitness cost to the  
329 altruist,  $B$  is the fitness benefit to recipient, and  $r$  is the relatedness between these individuals.  
330 Thus, kin selection requires greater-than-average relatedness between altruist and recipient, and  
331 relatedness must be particularly high to account for such energetically costly behaviours as  
332 adoption and nursing. Lunn et al. (2000) ruled out kin selection as an explanation for three  
333 previous cases of polar bear adoption based on low genetic relatedness. Our results reinforce the  
334 finding that adopted cubs and their foster mothers are unrelated, and that kin selection does not  
335 appear to drive adoption in this population. Though reciprocal care of offspring has been  
336 observed in polar bears (Lunn 1986), given the polar bear’s low population density and generally  
337 asocial nature, reciprocal altruism is also extremely unlikely, and no reciprocal cases of adoption  
338 were observed in our data.

339 Milk evacuation may explain allonursing behaviour in some pinnipeds (Riedman and  
340 Boeuf 1982) and bats (Wilkinson 1992), however, it is extremely unlikely to explain adoption in  
341 polar bears. Whereas it is beneficial for pinnipeds and bats to be leaner to increase diving or  
342 flight efficiency (Roulin 2002), lean polar bears lack the energy storage and thermal benefits  
343 (Pond et al. 1992), as well as the reproductive benefits (Stirling et al. 1999) associated with body  
344 condition. This is particularly true in the Western Hudson Bay subpopulation, where mothers  
345 may fast for four or more months during the ice-free period each year. In this subpopulation, a  
346 female's ability to maintain pregnancy (Derocher et al. 1992) and the survival of her own cubs  
347 (Derocher and Stirling 1996) are mass-dependent so that a female would gain no apparent benefit  
348 from milk evacuation. Since it appears that all six foster mothers had birthed genetic litters by the  
349 time of adoption, the parental experience hypothesis is also unlikely to account for any of these  
350 adoptions (Roulin 2002).

351 Adopted cubs were captured alone with their foster mother in four of six cases, and in all  
352 these cases, the adopted cub is known to have survived to independence, implying the  
353 provisioning of milk by the mother to the adoptive offspring, as has been observed directly in at  
354 least once instance of fostering (Belikov 1976). Because spontaneous lactation is not believed to  
355 occur in most species and has only been consistently demonstrated among dwarf mongooses  
356 (*Helogale parvula*) suckling close relatives (Creel et al. 1991), it is highly unlikely to explain  
357 allonursing of alien offspring among polar bears. This suggests that these cubs' adoptions  
358 coincided with the loss of the females' biological litters (either due to death or because of  
359 unintentional cub-swapping with another female), while females were biologically capable of  
360 suckling. In our remaining two adoption cases, cub misidentification is the most likely  
361 explanation, as adopted cubs were accompanied by the female's own biological offspring. Cub



362 mixing sometimes occurs in both polar bears and brown bears (Glenn et al. 1976; Lunn 1986),  
363 and in any of these adoption cases, cub-swapping may have occurred due to simple  
364 misidentification during periods of high bear density, such as springtime den emergence or the  
365 autumn fasting period ashore (Derocher and Stirling 1990; Ramsay and Stirling 1988). However,  
366 we note that in at least one previously observed case of adoption, it has been proposed that a  
367 female with two cubs of her own adopted two of another female's cubs she was killed in a fight  
368 (Vibe 1976), and cubs may also become separated from their mothers if males drive them off in  
369 order to mate with her (I. Stirling, unpublished data).

370         It has been suggested that scientific handling may increase the probability of cub  
371 abandonment or adoption if maternal vigilance is reduced during the time it takes to fully recover  
372 from immobilization (Derocher and Wiig 1999). Importantly, we found no evidence to support  
373 this hypothesis. We were able to identify four of the six genetic mothers, two of which had not  
374 been captured for five years prior to the adoption, and the remaining two of which were not  
375 captured until after the adoption. Likewise, none of the six foster mothers was captured in the  
376 period between the adopted cub's birth and their first observation together. This finding  
377 corresponds with a number of studies that have failed to find a significant negative correlation  
378 between scientific handling and litter size (Amstrup 1993; Lunn et al. 2004), cub survival  
379 (Ramsay and Stirling 1986; Rode et al. 2014), or on the cohesion of family groups (Messier  
380 2000).

381

## 382 **Acknowledgments**

383         The authors would like to thank the Manitoba Department of Conservation and the  
384 Government of Nunavut for providing some of the samples, as well as Dennis Andriashek and

385 Wendy Calvert for long-term data collection and maintenance. We would also like to  
386 acknowledge the contributions of Andrew Derocher and the late Malcolm Ramsay, who gathered  
387 some of the field data used in this study. DNA extractions for most pre-2006 tissue samples were  
388 conducted by Jennifer Bonneville Davis. This project was funded by grants to CSD from  
389 Environment Canada and by a Natural Sciences and Engineering Research Council Discovery  
390 Grant to DWC (Grant ID 312207-2011). RMM is funded by scholarships from Alberta Innovates  
391 Technology Futures, the University of Alberta, and the Province of Alberta. Financial and  
392 logistical support of the long-term study of polar bears in western Hudson Bay have been  
393 provided by Care for the Wild International, the Churchill Northern Studies Centre, Environment  
394 Canada, the Isdell Family Foundation, Manitoba Conservation, Natural Sciences and Engineering  
395 Research Council, Nunavut Wildlife Research Trust Fund, Parks Canada Agency, the Strategic  
396 Technology Applications of Genomics in the Environment (STAGE) funding program, Wildlife  
397 Media Inc., World Wildlife Fund (Canada), and World Wildlife Fund Arctic Programme. Josh  
398 Miller and Jamie Gorrell provided advice and comments on an earlier version of the manuscript.

399

#### 400 **Ethical standards**

401 All applicable international, national, and/or institutional guidelines for the care and use  
402 of animals were followed. Environment Canada's animal-handling procedures were approved  
403 annually by their Prairie and Northern Region Animal Care Committee, and all research was  
404 conducted under wildlife research permits issued by the Province of Manitoba and by Parks  
405 Canada Agency.

406

## References

407

- 408 Amstrup SC (1993) Human disturbances of denning polar bears in Alaska. *Arctic* 46:246–250.
- 409 Anderson AE, Wallmo OC (1984) *Odocoileus hemionus*. *Mammalian Species* 219:1–9.
- 410 Atkinson SN, Cattet MRL, Polischuk SC, Ramsay MA (1996) A case of offspring adoption in  
411 free-ranging polar bears (*Ursus maritimus*). *Arctic* 49:94–96.
- 412 Belikov SE (1976) Behavioral aspects of the polar bear, *Ursus maritimus*. *Bears: Their Biology*  
413 *and Management* 3:37–40. doi: 10.2307/3872752
- 414 Bellemain E, Zedrosser A, Manel S, Waits LP, Taberlet P, Swenson JE (2006) The dilemma of  
415 female mate selection in the brown bear, a species with sexually selected infanticide. *P R*  
416 *Soc B* 273:283–291. doi: 10.1098/Rspb.2005.3331
- 417 Bulmer MG (1970) *The Biology of Twinning in Man*. Clarendon Press, Oxford, UK
- 418 Calvert W, Ramsay MA (1998) Evaluation of age determination of polar bears by counts of  
419 cementum growth layer groups. *Ursus* 10:449–453. doi: 10.2307/3873156
- 420 Carmichael L, Nagy JA, Strobeck C (2009) Monozygotic twin wolves with divergent life  
421 histories. *Arctic* 61:329–331. doi: 10.14430/arctic29  
422 329-331
- 423 Clutton-Brock TH, Albon SD, Guinness FE (1989) Fitness costs of gestation and lactation in wild  
424 mammals. *Nature* 337:260–262.
- 425 Costello CM, Creel SR, Kalinowski ST, Vu NV, Quigley HB (2008) Sex-biased natal dispersal  
426 and inbreeding avoidance in American black bears as revealed by spatial genetic analyses.  
427 *Mol Ecol* 17:4713–4723. doi: 10.1111/j.1365-294X.2008.03930.x
- 428 Creel SR, Monfort SL, Wildt DE, Waser PM (1991) Spontaneous lactation is an adaptive result  
429 of pseudopregnancy. *Nature* 351:660–662.
- 430 Cronin MA, Shideler R, Waits L, Nelson RJ (2005) Genetic variation and relatedness on grizzly  
431 bears in the Prudhoe Bay region and adjacent areas in northern Alaska. *Ursus* 16:70–84.  
432 doi: 10.2192/1537-6176(2005)016[0070:Gvarig]2.0.Co;2
- 433 De Barba M, Waits LP, Garton EO, Genovesi P, Randi E, Mustoni A, Groff C (2010) The power  
434 of genetic monitoring for studying demography, ecology and genetics of a reintroduced  
435 brown bear population. *Mol Ecol* 19:3938–3951. doi: 10.1111/J.1365-294x.2010.04791.X
- 436 Derocher AE, Stirling I (1990) Distribution of polar bears (*Ursus maritimus*) during the ice-free  
437 period in western Hudson Bay. *Can J Zool* 68:1395–1403.
- 438 Derocher AE, Stirling I, Andriashek D (1992) Pregnancy rates and serum progesterone levels of  
439 polar bears in western Hudson Bay. *Can J Zool* 70:561–566. doi: 10.1139/z92-084
- 440 Derocher AE, Stirling I (1996) Aspects of survival in juvenile polar bears. *Can J Zool* 74:1246–  
441 1252.
- 442 Derocher AE, Stirling I, Calvert W (1997) Male-biased harvesting of polar bears in western  
443 Hudson Bay. *J Wildl Manage* 61:1075–1082.
- 444 Derocher AE, Wiig Ø (1999) Observation of adoption in polar bears (*Ursus maritimus*). *Arctic*  
445 52:413–415.
- 446 Derocher AE, Andersen M, Wiig Ø, Aars J (2010) Sexual dimorphism and the mating ecology of  
447 polar bears (*Ursus maritimus*) at Svalbard. *Behav Ecol Sociobiol* 64:939–946. doi:  
448 10.1007/s00265-010-0909-0

- 449 Fricke PM (2001) Review: twinning in dairy cattle. *The Professional Animal Scientist* 17:61–67.
- 450 Gleeson SK, Clark AB, Dugatkin LA (1994) Monozygotic twinning: an evolutionary hypothesis.
- 451 *Proceedings of the National Academy of Sciences* 91:11363–11367.
- 452 Glenn LP, Lentfer JW, Faro JB, Miller LH (1976) Reproductive biology of female brown bears
- 453 (*Ursus arctos*), McNeil River, Alaska. *Bears: Their Biology and Management* 3:381–390.
- 454 doi: 10.2307/3872788
- 455 Gorrell JC, McAdam AG, Coltman DW, Humphries MM, Boutin S (2010) Adopting kin
- 456 enhances inclusive fitness in asocial red squirrels. *Nat Commun* 1:22. doi:
- 457 10.1038/Ncomms1022
- 458 Grafen A (1988) On the Uses of Data on Lifetime Reproductive Success. In: Clutton-Brock TH
- 459 (ed) *Reproductive Success*. University of Chicago Press, Chicago, IL, pp 454–471
- 460 Guo SW, Thompson EA (1992) Performing the exact test of Hardy-Weinberg proportion for
- 461 multiple alleles. *Biometrics* 48:361–372.
- 462 Hamilton WD (1964) The genetical evolution of social behaviour. I. *J Theor Biol* 7:1–16. doi:
- 463 10.1016/0022-5193(64)90038-4
- 464 Hardy ICW (1995) Protagonists of polyembryony. *Trends Ecol Evol* 10:179–180. doi:
- 465 [http://dx.doi.org/10.1016/S0169-5347\(00\)89045-X](http://dx.doi.org/10.1016/S0169-5347(00)89045-X)
- 466 Hoffman JI, Forcada J (2009) Genetic analysis of twinning in Antarctic fur seals (*Arctocephalus*
- 467 *gazella*). *J Mammal* 90:621–628. doi: 10.1644/08-MAMM-A-264R1.1
- 468 Hua P, Zhang L, Zhu G, Jones G, Zhang S, Rossiter SJ (2011) Hierarchical polygyny in
- 469 multiparous lesser flat-headed bats. *Mol Ecol* 20:3669–3680. doi: 10.1111/j.1365-
- 470 294X.2011.05192.x
- 471 Itoh T, Sato Y, Kobayashi K, Mano T, Iwata R (2012) Effective dispersal of brown bears (*Ursus*
- 472 *arctos*) in eastern Hokkaido, inferred from analyses of mitochondrial DNA and
- 473 microsatellites. *Mamm Study* 37:29–41.
- 474 Jamieson A, Taylor SS (1997) Comparisons of three probability formulae for parentage
- 475 exclusion. *Anim Genet* 28:397–400. doi: 10.1111/J.1365-2052.1997.00186.X
- 476 Johnson PCD, Haydon DT (2007) Maximum-likelihood estimation of allelic dropout and false
- 477 allele error rates from microsatellite genotypes in the absence of reference data. *Genetics*
- 478 175:827–842. doi: 10.1534/Genetics.106.064618
- 479 Jones OR, Wang J (2010) COLONY: a program for parentage and sibship inference from
- 480 multilocus genotype data. *Mol Ecol Resour* 10:551–555. doi: 10.1111/J.1755-
- 481 0998.2009.02787.X
- 482 Kahle D, Wickham H (2013) ggmap: spatial visualization with ggplot2. *The R Journal* 5:144–
- 483 161.
- 484 Kearney SR (1989) The Polar Bear Alert Program at Churchill, Manitoba. In: Bromley M (ed)
- 485 *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies*.
- 486 Northwest Territories Department of Renewable Resources, Yellowknife, Northwest
- 487 Territories, Canada, pp 83–92
- 488 Keller LF, Waller DM (2002) Inbreeding effects in wild populations. *Trends Ecol Evol* 17:230–
- 489 241. doi: [http://dx.doi.org/10.1016/S0169-5347\(02\)02489-8](http://dx.doi.org/10.1016/S0169-5347(02)02489-8)
- 490 Kompanje EJO, Hermans JJ (2008) Cephalopagus conjoined twins in a leopard cat (*Prionailurus*
- 491 *bengalensis*). *J Wildl Dis* 44:177–180. doi: 10.7589/0090-3558-44.1.177
- 492 Livingston JE, Poland BJ (1980) A study of spontaneously aborted twins. *Teratology* 21:139–
- 493 148. doi: 10.1002/tera.1420210202

- 494 Lunn NJ (1986) Observations of nonaggressive behavior between polar bear family groups. *Can J*  
495 *Zool* 64:2035–2037. doi: 10.1139/Z86-307
- 496 Lunn NJ, Paetkau D, Calvert W, Atkinson S, Taylor M, Strobeck C (2000) Cub adoption by polar  
497 bears (*Ursus maritimus*): determining relatedness with microsatellite markers. *J Zool*  
498 251:23–30.
- 499 Lunn NJ, Stirling I, Andriashek D, Richardson E (2004) Selection of maternity dens by female  
500 polar bears in western Hudson Bay, Canada and the effects of human disturbance. *Polar*  
501 *Biol* 27:350–356. doi: 10.1007/s00300-004-0604-6
- 502 Lynch M, Ritland K (1999) Estimation of pairwise relatedness with molecular markers. *Genetics*  
503 152:1753–1766.
- 504 Malenfant RM, Coltman DW, Davis CS (2015) Design of a 9K Illumina BeadChip for polar  
505 bears (*Ursus maritimus*) from RAD and transcriptome sequencing. *Mol Ecol Resour*  
506 15:587–600. doi: 10.1111/1755-0998.12327
- 507 Messier F (2000) Effects of capturing, tagging and radio-collaring polar bears for research and  
508 management purposes in Nunavut and Northwest Territories. Department of Biology,  
509 University of Saskatchewan, Saskatoon, SK, Canada, pp 64
- 510 Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? *Anim Behav* 32:94-112.  
511 doi: [http://dx.doi.org/10.1016/S0003-3472\(84\)80328-0](http://dx.doi.org/10.1016/S0003-3472(84)80328-0)
- 512 Morrissey MB, Wilson AJ (2010) PEDANTICS: an R package for pedigree-based genetic  
513 simulation and pedigree manipulation, characterization and viewing. *Mol Ecol Resour*  
514 10:711–719. doi: 10.1111/J.1755-0998.2009.02817.X
- 515 Onorato DP, Hellgren EC, Van Den Bussche RA, Skiles JR (2004) Paternity and relatedness of  
516 American black bears recolonizing a desert montane island. *Can J Zool* 82:1201–1210.  
517 doi: 10.1139/Z04-097
- 518 Paterson T, Graham M, Kennedy J, Law A (2012) VIPER: a visualisation tool for exploring  
519 inheritance inconsistencies in genotyped pedigrees. *BMC Bioinformatics* 13:16. doi:  
520 10.1186/1471-2105-13-s8-s5
- 521 Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic  
522 software for teaching and research. *Mol Ecol Notes* 6:288–295. doi: 10.1111/J.1471-  
523 8286.2005.01155.X
- 524 Peakall R, Smouse PE (2012) GenAIEx 6.5: genetic analysis in Excel. Population genetic  
525 software for teaching and research-an update. *Bioinformatics* 28:2537–2539. doi:  
526 10.1093/Bioinformatics/Bts460
- 527 Pemberton JM (2008) Wild pedigrees: the way forward. *P R Soc B* 275:613–621. doi:  
528 10.1098/rspb.2007.1531
- 529 Poissant J, Hogg JT, Davis CS, Miller JM, Maddox JF, Coltman DW (2010) Genetic linkage map  
530 of a wild genome: genomic structure, recombination and sexual dimorphism in bighorn  
531 sheep. *BMC Genomics* 11. doi: 10.1186/1471-2164-11-524
- 532 Pond CM, Mattacks CA, Colby RH, Ramsay MA (1992) The anatomy, chemical composition,  
533 and metabolism of adipose tissue in wild polar bears (*Ursus maritimus*). *Can J Zool*  
534 70:326–341.
- 535 Proctor MF, McLellan BN, Strobeck C, Barclay RMR (2004) Gender-specific dispersal distances  
536 of grizzly bears estimated by genetic analysis. *Can J Zool* 82:1108–1118. doi:  
537 10.1139/Z04-077

- 538 Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201-206. doi:  
539 [http://dx.doi.org/10.1016/0169-5347\(96\)10028-8](http://dx.doi.org/10.1016/0169-5347(96)10028-8)
- 540 Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*  
541 43:258–275. doi: 10.2307/2409206
- 542 R Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation  
543 for Statistical Computing, Vienna, Austria,
- 544 Ramsay MA, Stirling I (1986) Long-term effects of drugging and handling free-ranging polar  
545 bears. *The Journal of Wildlife Management* 50:619–626. doi: 10.2307/3800972
- 546 Ramsay MA, Stirling I (1988) Reproductive biology and ecology of female polar bears (*Ursus*  
547 *maritimus*). *J Zool* 214:601–634.
- 548 Ramsay MA, Mattacks CA, Pond CM (1992) Seasonal and sex differences in the structure and  
549 chemical composition of adipose tissue in wild polar bears (*Ursus maritimus*). *J Zool*  
550 228:533–544.
- 551 Raymond M, Rousset F (1995) GENEPOP (Version 1.2): population genetics software for exact  
552 tests and ecumenicism. *J Hered* 86:248–249.
- 553 Reid JM, Arcese P, Sardell RJ, Keller LF (2011) Additive genetic variance, heritability, and  
554 inbreeding depression in male extra-pair reproductive success. *The American Naturalist*  
555 177:177–187. doi: 10.1086/657977
- 556 Richardson E, Branigan M, Calvert W, Cattet M, Derocher AE, Doidge W, Hedman D, Lunn NJ,  
557 McLoughlin P, Obbard ME, Stirling I, Taylor M (2006) Research on polar bears in  
558 Canada 2001–2004. In: Aars J, Lunn NJ, Derocher AE (eds) *Polar Bears: Proceedings of*  
559 *the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 20–24 June*  
560 *2005, Seattle, Washington, USA. IUCN, Gland, Switzerland,*
- 561 Richardson ES (2014) *The Mating System and Life History of the Polar Bear. University of*  
562 *Alberta*
- 563 Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. *Q*  
564 *Rev Biol* 57:405–435. doi: 10.1086/412936
- 565 Riedman ML, Boeuf BJ (1982) Mother-pup separation and adoption in northern elephant seals.  
566 *Behav Ecol Sociobiol* 11:203–215. doi: 10.1007/BF00300063
- 567 Riester M, Stadler PF, Klemm K (2009) FRANz: reconstruction of wild multi-generation  
568 pedigrees. *Bioinformatics* 25:2134–2139. doi: 10.1093/Bioinformatics/Btp064
- 569 Riester M, Stadler PF, Klemm K (2010) Reconstruction of pedigrees in clonal plant populations.  
570 *Theor Popul Biol* 78:109–117. doi: 10.1016/J.Tpb.2010.05.002
- 571 Rode KD, Pagano AM, Bromaghin JF, Atwood TC, Durner GM, Simac KS, Amstrup SC (2014)  
572 Effects of capturing and collaring on polar bears: findings from long-term research on the  
573 southern Beaufort Sea population. *Wildl Res* 41:311–322. doi: 10.1071/WR13225
- 574 Rosing-Asvid A, Born E, Kingsley M (2002) Age at sexual maturity of males and timing of the  
575 mating season of polar bears (*Ursus maritimus*) in Greenland. *Polar Biol* 25:878–883. doi:  
576 10.1007/s00300-002-0430-7
- 577 Roulin A (2002) Why do lactating females nurse alien offspring? A review of hypotheses and  
578 empirical evidence. *Anim Behav* 63:201–208. doi: 10.1006/anbe.2001.1895
- 579 Rousset F (2008) GENEPOP'007: a complete re-implementation of the GENEPOP software for  
580 Windows and Linux. *Mol Ecol Resour* 8:103–106. doi: 10.1111/J.1471-  
581 8286.2007.01931.X

- 582 Saunders BL (2005) The Mating System of Polar Bears in the Central Canadian Arctic. Queen's  
583 University
- 584 Silva del Río N, Kirkpatrick BW, Fricke PM (2006) Observed frequency of monozygotic  
585 twinning in Holstein dairy cattle. *Theriogenology* 66:1292-1299. doi:  
586 <http://dx.doi.org/10.1016/j.theriogenology.2006.04.013>
- 587 Slate J, Visscher PM, MacGregor S, Stevens D, Tate ML, Pemberton JM (2002) A genome scan  
588 for quantitative trait loci in a wild population of red deer (*Cervus elaphus*). *Genetics*  
589 162:1863–1873.
- 590 Spotte S (1982) The incidence of twins in pinnipeds. *Canadian Journal of Zoology* 60:2226-2233.  
591 doi: 10.1139/z82-285
- 592 Stirling I, Lunn NJ, Iacozza J (1999) Long-term trends in the population ecology of polar bears in  
593 western Hudson Bay in relation to climatic change. *Arctic* 52:294–306.
- 594 Stirling I, Derocher AE (2012) Effects of climate warming on polar bears: a review of the  
595 evidence. *Global Change Biol* 18:2694–2706. doi: 10.1111/j.1365-2486.2012.02753.x
- 596 Szulkin M, Stopher KV, Pemberton JM, Reid JM (2013) Inbreeding avoidance, tolerance, or  
597 preference in animals? *Trends Ecol Evol* 28:205–211. doi:  
598 <http://dx.doi.org/10.1016/j.tree.2012.10.016>
- 599 Taylor M, Larsen T, Schweinsburg RE (1985) Observations of intraspecific aggression and  
600 cannibalism in polar bears (*Ursus maritimus*). *Arctic* 38:303–309.
- 601 Taylor MK, McLoughlin PD, Messier F (2008) Sex-selective harvesting of polar bears *Ursus*  
602 *maritimus*. *Wildl Biol* 14:52–60.
- 603 Taylor RW, Boon AK, Dantzer B, Réale D, Humphries MM, Boutin S, Gorrell JC, Coltman  
604 DW, McAdam AG (2012) Low heritabilities, but genetic and maternal correlations  
605 between red squirrel behaviours. *J Evol Biol* 25:614–624. doi: 10.1111/j.1420-  
606 9101.2012.02456.x
- 607 Thiemann GW, Iverson SJ, Stirling I (2008) Polar bear diets and arctic marine food webs:  
608 insights from fatty acid analysis. *Ecol Monogr* 78:591–613.
- 609 Vibe C (1976) Preliminary Report on the Second Danish Polar Bear Expedition to North East  
610 Greenland, 1974. Proceedings of the Fifth Working Meeting of the Polar Bear Specialist  
611 Group. IUCN, Morges, Switzerland, pp 91–97
- 612 Villinger J, Waldman B (2012) Social discrimination by quantitative assessment of  
613 immunogenetic similarity.
- 614 Wang JL (2002) An estimator for pairwise relatedness using molecular markers. *Genetics*  
615 160:1203–1215.
- 616 Wang JL (2011) COANCESTRY: a program for simulating, estimating and analysing relatedness  
617 and inbreeding coefficients. *Mol Ecol Resour* 11:141–145. doi: 10.1111/J.1755-  
618 0998.2010.02885.X
- 619 Weber DS, Van Coeverden De Groot PJ, Peacock E, Schrenzel MD, Perez DA, Thomas S,  
620 Shelton JM, Else CK, Darby LL, Acosta L, Harris C, Youngblood J, Boag P, Desalle R  
621 (2013) Low MHC variation in the polar bear: implications in the face of Arctic warming?  
622 *Anim Conserv* 16:671–683. doi: 10.1111/acv.12045
- 623 Wilkinson GS (1992) Communal nursing in the evening bat, *Nycticeius humeralis*. *Behav Ecol*  
624 *Sociobiol* 31:225–235.
- 625 Williams GC (1975) *Sex and Evolution*. Princeton University Press, Princeton, NJ

- 626 Zedrosser A, Støen O-G, Sæbø S, Swenson JE (2007) Should I stay or should I go? Natal  
627 dispersal in the brown bear. *Anim Behav* 74:369–376. doi:  
628 10.1016/j.anbehav.2006.09.015
- 629 Zeyl E, Aars J, Ehrich D, Bachmann L, Wiig Ø (2009a) The mating system of polar bears: a  
630 genetic approach. *Can J Zool* 87:1195–1209. doi: 10.1139/Z09-107
- 631 Zeyl E, Aars J, Ehrich D, Wiig Ø (2009b) Families in space: relatedness in the Barents Sea  
632 population of polar bears (*Ursus maritimus*). *Mol Ecol* 18:735–749. doi: 10.1111/J.1365-  
633 294x.2008.04049.X
- 634



635 **Table 1.** Non-default settings used for pedigree generation in the program FRANZ.

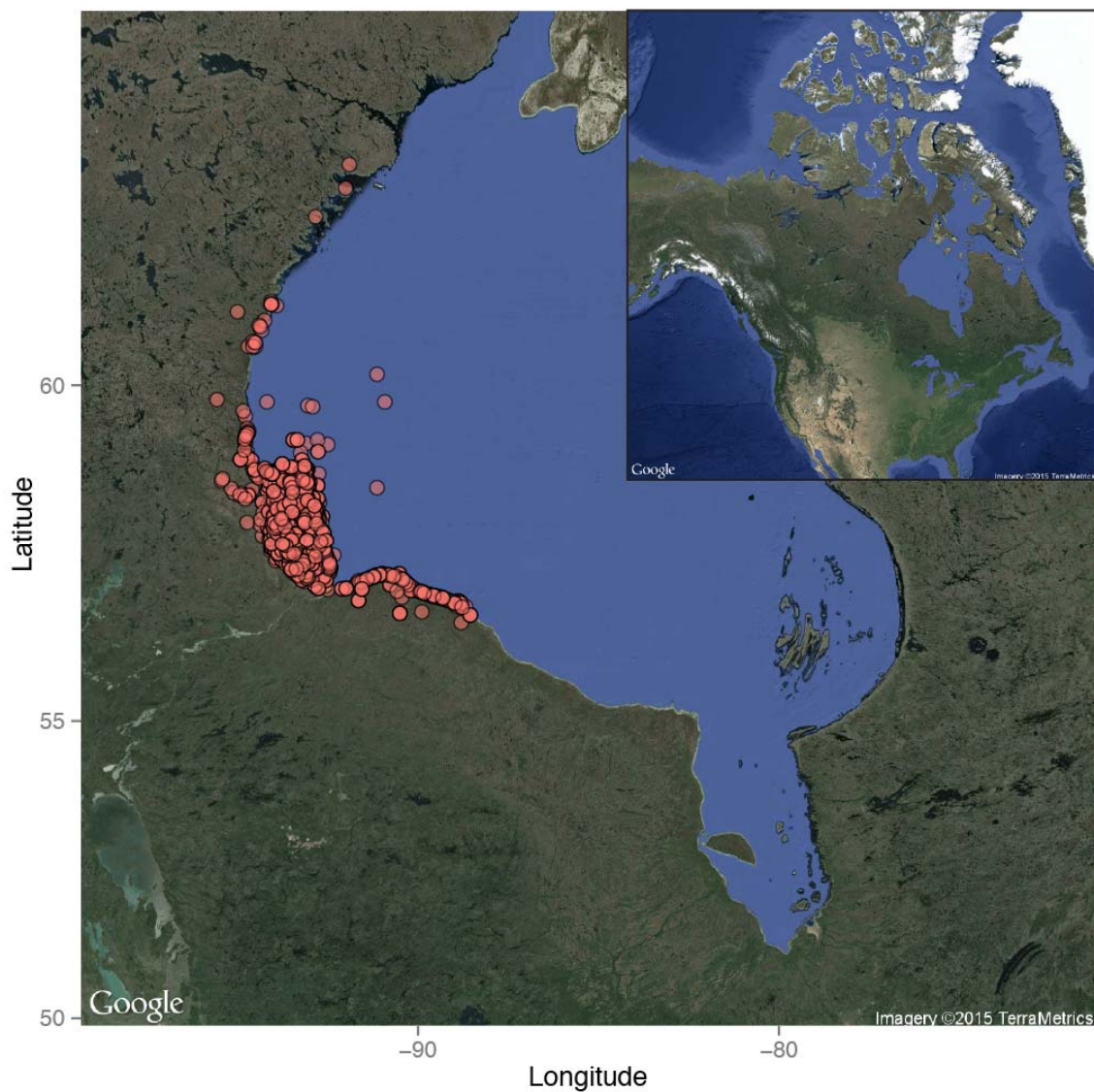
<b>Parameter</b>	<b>Setting</b>
Female reproductive age range	2–32
Male reproductive age range	2–32
Maximum number of candidate mothers	5,000
Maximum number of candidate fathers	5,000
Number of simulation iterations	1,000,000
Maximum number of simulated annealing iterations	1,000,000,000
Number of Metropolis–Hastings burn-in iterations	5,000,000
Number of Metropolis–Hastings iterations	30,000,000
Metropolis–Hastings sampling frequency	100

636

637 **Table 2.** New cases of polar bear adoption reported in this paper.  $P_M$  = proportion of loci mismatched between cub and candidate  
638 mother;  $r_{QG}$  = Queller-and-Goodnight relatedness between cub and the adoptive mother. In two cases (represented as “—”), the true  
639 dam could not be determined. Asterisks denote individuals whose genotypes could be confirmed by genetic assignment of their other  
640 observed offspring to them; most cubs’ genotypes could not be confirmed in this manner because they are not known to have parented  
641 offspring.

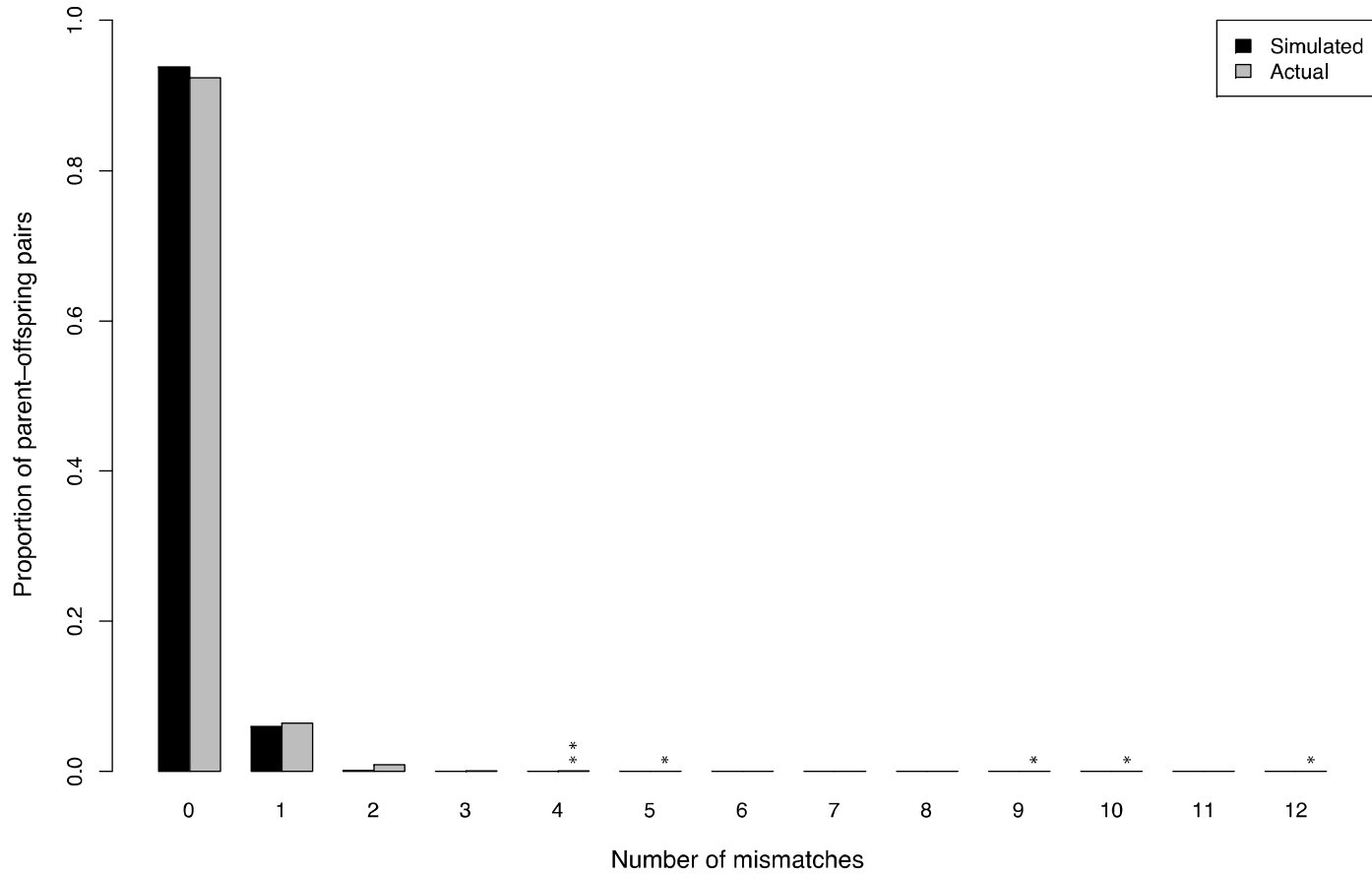
Cub	Sex	Year of birth	Observed dam ( $P_M$ )	Date(s) observed together	Age of observed dam	Other cubs in litter	$r_{QG}$ (95% CI)	Inferred dam ( $P_M$ )	Survived to independence
X09059*	Female	1980	X05562* (10/25)	Aug. 10, 1981	7	0	-0.19 (-0.36 – 0.03)	X09913* (0/25)	Yes
X10608	Female	1987	X10607* (5/25)	Sept. 24, 1987	8	0	-0.05 (-0.22 – 0.12)	—	Yes
X11097	Female	1989	X05668* (9/25)	Mar. 22, 1989	6	2	-0.07 (-0.35 – 0.14)	X11456* (0/25)	Unknown
X17069	Male	1998	X03318* (4/25)	Nov. 30, 1998	24	0	0.17 (0.00 – 0.36)	—	Yes
X17294*	Female	2003	X17082* (4/25)	Sept. 22, 2003 – Nov. 8, 2004	7–8	1	0.03 (-0.12 – 0.21)	X10688* (0/25)	Yes
X19939	Female	2004	X11940* (12/25)	Sept. 18, 2004 – Sept. 18, 2005	11–12	0	-0.12 (-0.38 – 0.10)	X12273* (1/25)	Yes

642

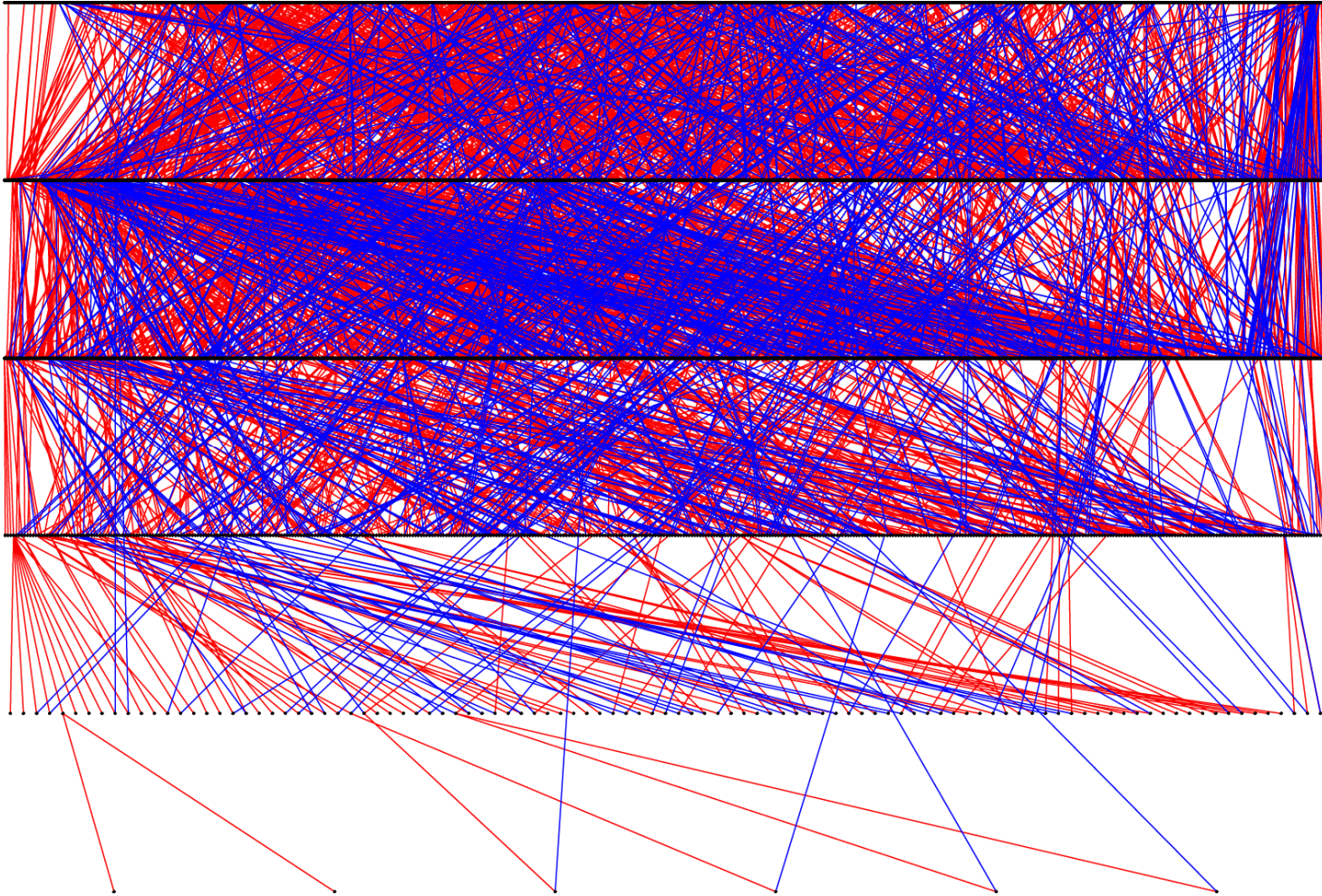


643  
644  
645  
646  
647

**Figure 1.** Sampling locations of bears included in the Western Hudson Bay pedigree. Imagery ©2015 TerraMetrics, Inc. ([www.terrametrics.com](http://www.terrametrics.com)), accessed via Google Maps and ggmap 2.4 (Kahle and Wickham 2013).



648  
649 **Figure 2.** Number of mismatched microsatellite loci for simulated and actual parentage assignments. Simulation results represent  
650 2,000,000 parent-offspring pairs generated in FRANZ using empirically estimated error rates. Asterisks indicate putatively adopted  
651 individuals.



652 **Figure 3.** Graphical representation of the 4449-individual polar bear pedigree described in this paper. Each point is an individual bear.  
653 Maternities are represented by red lines; paternities are represented by blue lines.