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The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide

Eva Bellemain[1,2], Andreas Zedrosser[2,3], Stéphanie Manel[1], Lisette P. Waits[4], Pierre Taberlet[1] and Jon E. Swenson[2,5,*]

[1]*Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université Joseph Fourier, BP 53,*
38041 Grenoble Cedex 9, France
[2]*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences,*
PO Box 5003, 1432 Ås, Norway
[3]*Department of Integrative Biology, Institute for Wildlife Biology and Game Management,*
University of Natural Resources and Applied Life Sciences, Vienna, Peter Jordan Strasse 76, 1190 Vienna, Austria
[4]*Fish and Wildlife Resources, University of Idaho, PO Box 441136, Moscow, ID 83844-1136, USA*
[5]*Norwegian Institute for Nature Management, Tungasletta 2, 7485 Trondheim, Norway*

Because of differential investment in gametes between sexes, females tend to be the more selective sex. Based on this concept, we investigate mate selection in a large carnivore: the brown bear (*Ursus arctos*). We hypothesize that, in this species with sexually selected infanticide (SSI), females may be faced with a dilemma: either select a high-quality partner based on phenotypic criteria, as suggested by theories of mate choice, or rather mate with future potentially infanticidal males as a counter-strategy to SSI. We evaluated which male characteristics were important in paternity assignment. Among males available in the vicinity of the females, the largest, most heterozygous and less inbred and also the geographically closest males were more often the fathers of the female's next litter. We suggest that female brown bears may select the closest males as a counter-strategy to infanticide and exercise a post-copulatory cryptic choice, based on physical attributes, such as a large body size, reflecting male genetic quality. However, male–male competition either in the form of fighting before copulation or during the post-copulatory phase, in the form of sperm competition, cannot entirely be ruled out.

Keywords: female choice; infanticide; mating system; microsatellites; parentage analysis; *Ursus arctos*

1. INTRODUCTION

Mate selection is defined as the process leading to the tendency of members of one sex to mate non-randomly with respect to one or more varying traits in members of the other sex (Heisler *et al.* 1987). It is a component of the intersexual conflict and an evolutionary force driving mating systems (Darwin 1871; Andersson 1994). Females are usually the more selective sex in mate selection, because of the higher reproductive investment of females than males (Darwin 1871; Clutton-Brock 1989). Females may gain direct benefits (increased fecundity or amelioration of a cost) and/or indirect benefits (increased fitness of their offspring) by choosing a high-quality reproductive partner (e.g. Kokko *et al.* 2003). However, female choice is rarely obvious and can even be very subtle or cryptic, occurring during or even after mating (Birkhead & Møller 1993; Eberhardt 1996). Why and how females select their partners and how mating preferences have evolved remains under debate among evolutionary biologists and understanding these mechanisms is one of the greatest tasks in behavioural ecology (for a review see Cordero & Eberhard 2003).

Several surrogate measures of male quality have been used to evaluate female choice. Morphological traits, such as body size, weaponry and intense signals of fighting ability, are essential in male–male competition and are expected to be important cues in female choice (Andersson 1994), as is male age (viability selection theory; Trivers 1972), provided that survival rates are not age-dependent (Beck & Powell 2000). Females may also gain genetic benefits by selecting the most heterozygous males (the 'good genes' hypothesis; Brown 1997). Assuming a correlation between heterozygosity and fitness-associated traits (Hansson & Westerberg 2002), females may base their choice on traits directly reflecting heterozygosity at key loci or at many loci, such as the expression of vigour, symmetry or condition-sensitive ornaments. Also, by choosing mates based on compatible genes such as the Major Histocompatibility Complex (MHC), females may enhance their offspring viability and performance (Penn & Potts 1999; Trezenga & Wedell 2000). Finally, mate selection directed towards less related individuals has been suggested as an efficient mechanism for inbreeding avoidance (Blouin & Blouin 1998). Generally, these surrogate measures of male quality are tested separately. Limited by the availability of field or genetic data, and also by appropriate statistical models, very few studies have included several of these factors in the same model to determine the extent each factor influences female mate selection.

Female choice may also be context-dependent. For example, female choice may differ for species in which young are vulnerable to sexually selected infanticide (SSI), i.e. where males kill dependent offspring, but not their

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[*] Author for correspondence (jon.swenson@umb.no).

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own progeny, to gain access to breeding opportunities with the mother (Hrdy 1979). This phenomenon is rarely of benefit to females, and may lead to a dilemma: select a high-quality mating partner or prioritize mating strategies to counter infanticide. A potential counterstrategy to SSI is multiple mating, or 'promiscuity', in which the female attempts to confuse paternity. This idea has received much support in recent decades, and paternity uncertainty has been hypothesized as a major factor explaining multi-male mating by female mammals (Wolff & Macdonald 2004). Based on this hypothesis, females would tend to mate with any males they are likely to meet in the future, while accompanied by their dependent young, rather than trying to select a high-quality partner. Wolff & Macdonald (2004) pointed out that future studies should quantify the role of female choice to elucidate the evolutionary significance of multi-male mating in female mammals.

The mating system of bears, including mate selection, is poorly known. To our knowledge, only a few studies have examined this question in brown bears (*Ursus arctos*; Craighead *et al.* 1995*a*, 1998) and American black bears (*Ursus americanus*; Schenk & Kovacs 1995; Kovach & Powell 2003), all with a limited number of genetic samples and field observations. Female bears are induced ovulators, i.e. eggs are released after behavioural, hormonal or physical stimulation (Craighead *et al.* 1995*b*; Boone *et al.* 1998). This may allow females to evaluate male quality inside the reproductive tract and may provide them with more control over the paternity of their offspring than with spontaneous ovulation (Larivière & Fergusson 2003).

Based on the assumption that female bears may be choosy, we investigated female mate selection in two subpopulations of Scandinavian brown bears that have been studied for about 20 years and for which good field and genetic data are available. SSI has been documented in these subpopulations (Swenson *et al.* 1997; Swenson 2003), and it has been shown that infanticidal males were not related to the cubs they killed (Bellemain *et al.* 2005*a*). Males seem to be able to differentiate their own cubs from unrelated cubs, perhaps by recognizing the females they mated with the year before.

Based on paternity assignment of the female's litter, we tested the following predictions:

(1) females select males based on morphological, age or genetic criteria to maximize their reproductive output or inclusive fitness (direct or indirect benefits). Based on theory and the literature review described above, we predicted that paternity assignment would be positively correlated with male age, body size, and negatively correlated with a male's internal relatedness (an index reflecting both heterozygosity and inbreeding; see §2) and his relatedness to the female; and
(2) females use a strategy to minimize the risk of SSI by confounding paternity, i.e. mating with the geographically closest males, which have the highest potential to kill their future cubs.

2. MATERIAL AND METHODS

(a) *Study species, study areas and sampling*

During the mating season, male and female brown bears remain together for a few hours to several days, or even several weeks (Craighead *et al.* 1995*b*), and both males and females mate promiscuously, with females mating with up to eight males in a mating season (Craighead *et al.* 1995*b*). Both sexes roam to mate, increasing their home range during the early May to mid-July mating season (Dahle & Swenson 2003*a*). Implantation is delayed until November (Renfree & Calaby 1981). After 6–8 weeks of effective gestation, females give birth to 1–4 small cubs in January, while still hibernating in dens (Pasitschniak-Arts 1993). Young bears receive extended maternal care, staying with the mother for 1.5–2.5 years in the studied populations (Dahle & Swenson 2003*b*). Females do not mate while caring for their young (Schwartz *et al.* 2003) and there is no paternal investment in rearing of the offspring. A previous study (Bellemain *et al.* 2005*a*) showed that multiple paternities were frequent in this population, occurring in 14.5% of 69 litters with greater than or equal to two young and 28% of 32 litters with greater than or equal to three young. Scandinavian brown bears exhibit a sex ratio close to 50 : 50 (Bellemain *et al.* 2005*b*). Cub mortality averages 35% annually in the southern study area and 4% in the northern study area (Swenson *et al.* 2001). A study examining nutritional, social (SSI), and den disturbance factors found that the patterns of cub mortality were best explained by social factors in both populations (Swenson *et al.* 2001).

Table 1. Number and percentage of brown bears for whom the mother and/or father have been determined genetically or verified (from prior field observations) with a parentage probability greater than 80%, in two study areas in Scandinavia.

		maternities	
	determined paternities	genetically determined	verified from field data
north study area ($n=148$)	96 (64.8%)	12 (8.1%)	113 (76.3%)
south study area ($n=248$)	146 (58.9%)	31 (12.5%)	160 (64.5%)
total ($n=396$)	242 (61%)	41 (10.4%)	273 (68.9%)

The study areas are located in southcentral Sweden (49 000 km^2) and northern Sweden (8000 km^2) and are described by Bjärvall & Sandegren (1987). The two subpopulations located in each study area differed in mortality regimes and in their male age structure. Bear hunting was, generally, allowed during the autumn in both areas, but the northern area included three national parks, where bear hunting was illegal during the study period, although there was evidence of intensive poaching (Swenson & Sandegren 1999). There were few large adult males in the northern study area and a more evenly distributed male age structure in the southern study area (Swenson *et al.* 2001).

We used radio-telemetry for long-term monitoring of adult bears. Between 1984 and 2003, brown bears, including females accompanied by their yearling offspring, were immobilized in the spring and received radio-transmitters. Home ranges of radio-marked bears were estimated using 95% Minimum Convex Polygon as described by Dahle & Swenson (2003*a*). In addition, we obtained teeth for age determination and location of death from all killed bears (legally hunted or traffic-killed) in Sweden. Tissue samples

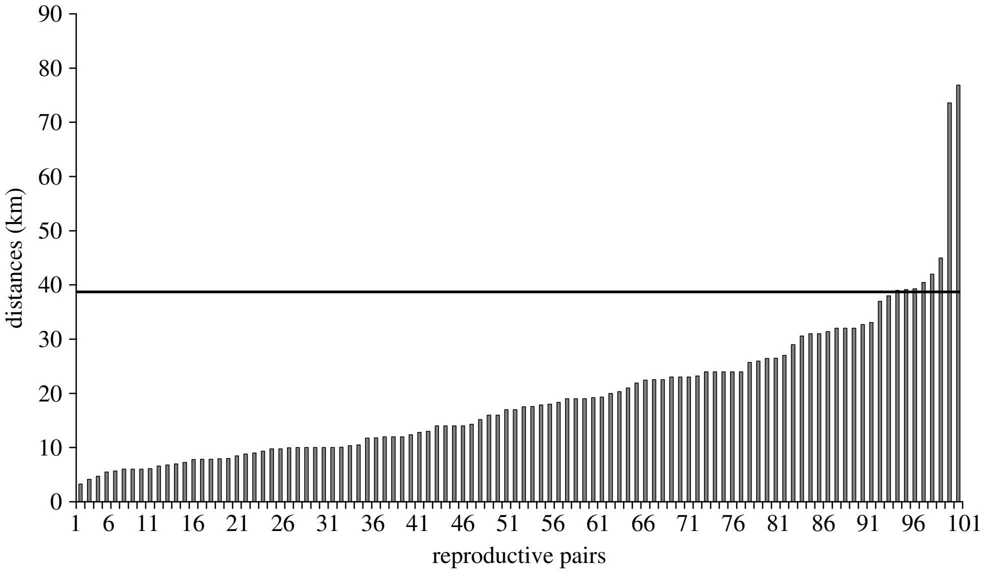

Figure 1. Geographical distances between the centres of the home ranges (or kill location) of 102 reproductive pairs (determined from parentage analysis) of brown bears in two populations in Scandinavia. The horizontal black line represents the distance corresponding to the 95% of the distribution of the distance between reproductive pairs (40 km).

were collected from both marked and killed bears and stored in 95% alcohol until extraction for genetic typing.

(**b**) *DNA extraction and typing*

Our genetic database contained 977 bear genotypes, of which 396 were from marked animals. The amplification and analysis of microsatellites were carried out following the protocol described by Waits *et al.* (2000). The following 18 microsatellite loci were used: G1A, G1D, G10B, G10C, G10L, G10P, G10X, G10H, G10O, G10J (Paetkau & Strobeck 1994; Paetkau *et al.* 1995) and Mu05, Mu10, Mu15, Mu23, Mu50, Mu51, Mu59, Mu61 (Taberlet *et al.* 1997).

(**c**) *Parentage analysis*

Based on the multilocus genotypes of mothers, offspring and males, we analysed parentage using the software PARENTE (Cercueil *et al.* 2003, available at http://www2.ujf-grenoble.fr/leca/membres/manel.html). One allelic incompatibility of 18 loci was allowed in the comparison of the parent–offspring genotypes to account for possible genotyping errors or mutations. We assessed the proportion of individuals for which parentage was assigned in the population (table 1). The results were checked with observational field data and for geographical consistency.

(**d**) *Evaluation of female choice*

We evaluated selection of reproductive partners by radio-marked oestrous females based on the comparison of characteristics of males that became fathers of the subsequent litter and other males in the vicinity of the female that did not become fathers. We proceeded in two steps:

1. we considered geographical information (radio-telemetry data for marked bears or kill location for unmarked bears) of all males in the vicinity of each radio-marked oestrous female as potential reproductive partners (hereafter referred to as 'large dataset'); and
2. to evaluate further if females actually had the opportunity to choose among males, we considered only observed (visually or radio-telemetry) cases of female–male encounters during the mating season (hereafter referred to as 'behavioural dataset').

The data selection and evaluation of female mate selection is detailed below for each of the datasets.

(i) *Data selection for the large dataset*

A male was considered available for potential reproduction with a given female if three criteria were fulfilled: (i) he was at least 3 years old (age of sexual maturity in male Scandinavian brown bears; our unpublished data) during the year the female was in oestrus; (ii) he was known to be alive during the female oestrous year (based on radio-tracking or killed-bear data); (iii) his home range centre (or kill location for unmarked males) was located within 40 km of the home range centre of the oestrous female. This 40 km distance corresponds to the 95% distribution of the distances between all reproductive pairs, known from parentage analysis (i.e. distance between the centres of the respective home ranges or kill locations; figure 1). This distance was chosen rather than the maximum distance between reproductive pairs to avoid overestimation of the number of males available in the vicinity of the female. Also, this distance seems reasonable based on behavioural data from both males and oestrous females during the mating season; oestrous females travelled a mean of 5.25 ± 0.47 km per day (range 0–24.9 km) and males travelled a mean of 13.25 ± 1.05 km per day (range 0.1–42.4 km) in our southern study area (Kristoffersen 2002).

Female choice was evaluated in relation to the following explanatory variables: (i) *study area*, as a factor variable; (ii) *number of males available around the oestrous female*, i.e. the number of males at a distance less than or equal to 40 km from the centre of the female's home range; (iii) *Male age*, as determined from field data. For all bears that were not captured as yearlings of radio-marked females, we collected a first premolar for age estimation based on the cementum annuli in the tooth root (Matson *et al.* 1999); (iv) *Male internal relatedness* (IR). This IR index reflects a quantity measured between parental half-genotypes. It is an estimator of heterozygosity, giving more weight to homozygotes

Table 2. Summary of a generalized mixed linear model analysis of female brown bear choice in Scandinavia as a function of: number of males available (within a radius of 40 km around the female), study area, geographical distance between the home range centres of the male and female, male body size, male IR and relatedness between the male and female. (The response variable was assumed to be binomial, given random effect for female identity. After a successive exclusion of the least significant terms ($p \geq 0.05$), the significance values of the final model are shown in the table. Non-significant terms are presented with the values they were removed from the model with. d.f. is degrees of freedom, β is the logistic regression coefficient, s.d. is the standard deviation, s.e. is the standard error, t denotes the t-value and p the significance level. Number of observations, 837 and number of groups, 48.)

explanatory variables	β	s.d.	s.e.	t	d.f.	P
fixed effects						
area	−0.0238		0.3226	0.0738	46	0.9415
relatedness	0.3182		0.5619	0.5662	773	0.5714
number of males available	−0.1375		0.0251	−5.4823	773	<0.0001
male IR	−2.426		0.7189	−3.374	773	0.0008
male body size	0.0485		0.0163	2.9699	773	0.0031
geographical distance	−0.0373		0.0112	−3.3157	773	0.0010
intercept	−2.7080		1.2509	−2.1648	773	0.0307
random effects						
female identity		0.0114				
residual		1.0219				

involving rare alleles. It is calculated as:

$$IR = \frac{2H - \sum fi}{2N - \sum fi}$$

(Amos *et al.* 2001), where H represents the number of homozygous loci within an individual, N the number of loci genotyped and fi the frequency of the ith allele contained in the genotype; (v) *Male body size*, using head circumference (at the widest part of the skull using a tape measure) as a surrogate measurement of absolute size of an individual. To estimate absolute size in the years a male was not captured, we calculated the von Bertalanffy growth curve (von Bertalanffy 1938) for each subpopulation. The average deviation in size of an individual from the mean population growth curve was used to calculate an individual growth curve, from which we derived absolute body size at a given age (our unpublished data); (vi) *Genetic relatedness between a female and her potential reproductive partners*, pairwise relationship coefficients (‘r’ as defined by Wang 2002 and recommended in Blouin 2003) were calculated for any two individuals by comparing the shared alleles of these individuals with the allele frequencies in each subpopulation, using the software SPAGeDi (Hardy & Vekemans 2002, available at http://www.ulb.ac.be/sciences/lagev/spagedi.html); and (vii) *Geographical distance between potential reproductive partners*, calculated as the distance (in km) between the centres of the respective home ranges or kill sites.

Variables i and ii were used as control variables; female choice might differ between study areas, as those areas differed in their male age structure and mortality regimes, and may be influenced by the density of males available in the vicinity. Using variables iii–vi, we tested whether female choice was influenced by male quality (prediction 1) and, using variable vii, whether female choice was influenced by SSI (prediction 2).

(ii) *Data selection for the behavioural dataset (see table 3)*

We selected visual or radio-telemetry observations of oestrous radio-marked females with at least one known male during a mating season and when the father of her next year’s litter was genetically determined. Female choice was evaluated in relation to the following explanatory variables (as described above): male age; male IR; male absolute body size; genetic relatedness between the female and her potential reproductive partners. In this case, comparing the other variables described above (study area, number of males in the area, geographical distance) was meaningless.

(e) ***Statistical analysis***

We evaluated female choice based on paternity assignment of the female’s next litter, i.e. whether or not a particular male was the father of a female’s cubs (binomial process). For the large dataset, we used a generalized linear mixed model (GLMM) with a logit link and binomial error distribution (McCullagh & Nelder 1989) to account for the effects of the explanatory variables on the probability of paternity assignment. The response variable (paternity assignment) was assumed to be binary (‘1’ for a male(s) genetically determined as a father(s) or ‘0’ for all other males within a 40 km radius), given random effects for female identity. Models were fitted using a penalized quasi likelihood method (Venables & Ripley 1999) in the statistical software R 1.9.1 (R Development Core Team 2004, http://www.R-project.org). After a stepwise exclusion of the least significant term ($p \geq 0.05$), the final model was revealed. Models were compared using the AIC criterion (Burnham & Anderson 1998).

For the behavioural dataset, we used pairwise t-tests to compare characteristics of males that were observed with oestrous females during the mating season with characteristics of the actual father(s) of the females’ next litter. The software SPSS (SPSS 12.0.1, SPSS Inc., Chicago, IL) was used for those statistical analyses.

3. RESULTS

(a) ***Parentage analysis***

All mother–offspring combinations known from field observations ($n = 314$) were genetically confirmed (table 1). In addition, we genetically determined the maternity for 41 marked bears with unknown pedigree (table 1). Paternity was genetically determined for 242 (61%) of the marked individuals; 6% of those fathers were unmarked.

Table 3. Observations (visual or radio-telemetry) of radio-marked female brown bears for which the paternity of the next year's litter was determined.

case[a]	female[b]	year	father(s)[b,c]	males observed together with the female[b,d]
1	BD01	1991	BD06	BD06 on May 16, 17; BD34 on June 2, 4
2	BD01	1997	BD59; 01BD02	BD59 on May 29; both BD50 and BD38 on June 11
3*	BD01	2000	unmarked	BD105 on June 8
4	BD07	1993	BD06; BD43	BD43 on May 26, 27 and June 15
5	BD07	1995	BD35	BD35 on May 16, 24, 28 and June 2; BD06 on June 8, 13
6*	BD10	1988	unmarked	BD17 on May 25, 30 and June 1, 3
7*	BD104	2000	BD06; BD38	Both BD36 and BD73 on May 18; BD73 on May 22
8*	BD12	1990	BD60	BD32 on May 31 and June 3
9*	BD18	1988	unmarked	BD09 on June 6, 7
10*	BD23	1994	unmarked	BD35 on May 12, 16, 19, 25
11	BD23	2001	BD36	BD36 on June 1; both BD36 and BD97 on June 4
12*	BD24	1992	BD34	BD40 on May 15, 18, 21; BD34 on May 20, 23, 25; BD06 on June 1
13	BD27	1990	BD06	BD06 on May 17, 18, 21, 22, 23, 25; BD34 on June 5, 8
14	BD37	1995	BD36; BD61	BD36 on June 2; BD38 on June 8
15*	BD47	1996	BD06	BD38 on May 28, 29 and June 3
16	BD71	2000	BD88	BD88 on May 18, 22, 31; BD36 on June 8
17*	W8802	1988	03ZZ17; unmarked	W8801 on May 21
18*	W8808	1990	W8503	W8903 on July 4, 7
19*	W8808	1994	W9011; unmarked	both W9301 and W8607 on May 20; W9301 on May 29; W9301 on June 16, 17
20*	W8904	1995	99X02	W9202 on June 24
21*	W8906	1989	W8607	W8903 on May 21; W8503 on May 28
22*	W8906	1993	W8607	W9301 on May 18, 21; W8607 on May 24; W8607, W9301 and 2 unmarked males on May 28, 29; W8607 on May 30; W9301 on June 4, 5, 8
23*	W8906	1995	unmarked	both W8607 and W9511on June 21; W8607 on June 23
24*	W8906	2001	W0012	W9301 on May 21
25*	W9003	1997	W0108; unmarked	both W8807 and 1 unmarked male on May 21
26	W9008	1998	W9505	W9505 on May 19 and June 12, 13; both W9311 and W9505 on May 24
27*	W9403	2000	W0232; unmarked	W0016 on May 31
28*	W9615	2001	W0233	W9921 on June 6, 9

[a] Asterisks indicate situations where the father, or one of the fathers, was not the first male observed with the mother during the mating season.

[b] Identification numbers: BD, from the northern study area; W, from the southern study area; numerical, unmarked bears killed during the hunting season (their data was subsequently recorded).

[c] Male(s) genetically identified as the father(s) of the female's next litter (cases 1, 4, 7, 14, 17, 19, 25, 27 represent cases of multiple paternity).

[d] If the female was observed with an unmarked bear and this individual showed obvious mating behaviour (copulation, tending, fighting with marked males), then this bear is referred to as observed.

(b) *Female choice*

The large dataset included 43 litters in the southern subpopulation (24 mothers) and 52 litters in the northern subpopulation (24 mothers). Totally, 107 different males were considered available (of which 20 were unmarked) for a total of 825 bear-years, and 102 reproductive pairs were considered (including 7 litters with multiple paternity with both fathers known). Two litters (*ca* 2%) resulted from incestuous matings (reproduction between the daughter and her father). The distance between reproductive pairs ranged from 3.3 to 76.8 km (figure 1). A minimum mean of 12.48 ± 5.33 (s.e.) males (range 3–25) in the south and 7.82 ± 3.81 (s.e.) males (range 2–16) in the north were known to be available in the vicinity of a given female (within a radius of less than or equal to 40 km) during her oestrous year.

Male age and male body size were highly correlated (Pearson correlation; $r=0.657$; $P \leq 0.001$). We therefore analysed these variables in separate models, including all other explanatory variables. The model including male body size was kept instead of the one including age, as it had a lower AIC value. The results of the final GLMM (table 2) showed that paternity assignment was positively correlated with male body size and negatively correlated with male IR, with geographical distance and with the number of males available within a 40 km radius. The explanatory variables 'study area' and 'genetic relatedness' did not significantly influence paternity assignment. All possible interactions making biological sense were tested in the model, but none of them were significant. The random effect of female identity was small (s.d. $=0.0114$) in our study, and it only slightly modified the estimates of the final model. All other models (results not shown) had a difference in the AIC value greater than 2 and were thus not considered in the discussion.

The behavioural dataset (table 3) included 12 litters in the southern subpopulation (eight mothers) and 16 litters in the northern subpopulation (12 mothers). There was considerable variation in the observations of female–male encounters. In eight of 28 cases (28.5%), females were observed with two or more males at the same time; in all other cases, they encountered males sequentially. Thirteen females were observed with only one male, 13 females with two, one female with three males and one female with five different males during the mating season. Overall, 54% of the females were observed with more than one male during the course of a mating season. In 12 cases (43%), the female was observed with the father of her next years' litter. We did not observe any cases of females rejecting a male, nor have other observational studies of brown bear mating behaviour (Craighead *et al.* 1995*b*), however this is extremely difficult to document. We observed several instances of apparent long-term association (greater than 4 days) between a male and a female, without the male becoming a father (table 3). Most of the time (in 68% of the cases), the first male to be observed with the female was not the father of the subsequent litter. Females observed in more than one mating season did not always reproduce with the same male (e.g. BD07 reproduced with BD06 and BD43 in 1993 and with BD35 in 1995).

Pairwise *t*-tests showed that paternal males were significantly older ($t_{20}=3.36$; $p=0.003$) and larger ($t_{14}=3.28$; $p=0.005$) than males that did not become fathers. We did not find a difference in IR ($t_{27}=-0.25$; $p=0.808$) nor relatedness to the female ($t_{27}=-0.58$; $p=0.568$) between the fathers and other males.

4. DISCUSSION

(a) *Distinguishing between female choice and male–male competition in paternity assignment*

Sexual selection predicts that the fundamental reproductive asymmetries between males and females give rise to a conflict between sexes (Darwin 1871). In mammals, females are typically choosy, as they invest the most into reproduction (Darwin 1871; Clutton-Brock 1989). Even if females do not choose their mate before mating, they may still have the post-mating opportunity to choose between the sperm of several males (cryptic female choice; Eberhardt 1996). However, male–male competition can also occur during the post-copulatory phase via sperm competition (Ginsberg & Huck 1989). It is extremely difficult to distinguish between those two aspects of sexual selection and to evaluate their relative importance. For instance, sperm selection by females (oocytes selecting sperm bearing compatible genes; e.g. Ehlers *et al.* 2000) can only be differentiated from sperm competition (the fittest sperm out-compete other sperm; Gomendio & Roldan 1993) under controlled conditions (e.g. Hugues *et al.* 1999).

In this paper, we chose to focus on the evaluation of female mate selection in brown bears, based on the background that, in mammals, females are the more selective sex, and, in species with induced ovulation, females might be able to control paternity. Our results are consistent with the female choice hypothesis; however they do not exclude a role of males in determining paternity. During the pre-copulatory phase, both sexes seem to play a role in paternity determination. Brown bears show large size dimorphism, with males being 1.2–2.2 times heavier than females (Stringham 1990), revealing the importance of intra-sexual selection, through male–male competition, for gaining access to females (Andersson 1994). Meanwhile, females roam extensively during the mating season (Dahle & Swenson 2003*a*), suggesting that they are actively searching for copulations, perhaps to confound paternities in the context of SSI. We did not observe females rejecting any males, which otherwise would argue against the SSI hypothesis. We documented that some highly reproductive males (our unpublished data), which, under a sperm competition hypothesis would have highly competitive sperm, were not always fathering the cubs after being observed with a female (e.g. table 3, cases 5 and 12 for male BD06). Thus, the sperm of dominant males does not always result in paternity, perhaps due to sperm selection by the female. Females encountered males simultaneously as well as sequentially. In the first case, females may be able to assess male quality by direct comparison. In the second case, selection inside the female reproductive tract via sperm selection or sexual stimulation may allow a female to gather information to compare several males simultaneously. We suggest that, by being promiscuous, females might mate with the geographically closest partners (as a counter-strategy to infanticide), and select a father for their offspring via post-copulatory choice. In the following section (§4b), we concentrate on mechanisms influencing female mate selection, although sperm competition cannot be ruled out.

(b) *Factors influencing female choice*

Optimal choosiness should be affected by at least three variables: distribution of mate quality, cost of searching for mates, and the chooser's quality (Gibson & Langen 1996). We were not able to evaluate the costs of searching for mates. However, the other two variables (distribution of mate quality and chooser's quality) were considered in our model. In our study, some observations were made of the same individual in different years and are consequently correlated, because both are modelled as a function of the same random effect, female identity. The GLMM considers the effects of 'female identity' (the chooser here) as a random factor (predicted as individual-specific deviations from a population mean once the independent effects of other variables are accounted for) and removes the effect of statistical dependence among repeated measures. As predicted, the number of males available around a given female had a significant effect on female choice. Therefore, by including this variable in the model, the effects of the other explanatory variables were corrected for.

Paternity assignment was negatively correlated with male's IR in the large dataset. This index reflects parental similarity better than commonly used heterozygosity indices (Amos *et al.* 2001). For example, negative values are suggestive of relatively outbred individuals, whereas high positive values suggest inbreeding. This negative correlation suggests that females would select both highly heterozygous and less inbred males, which will in turn favour the production of diverse and superior offspring (Brown 1997). Heterozygosity is probably linked to male quality via the functional overdominance hypothesis (Hansson & Westerberg 2002) and females might select their partners based on condition-sensitive traits in the male, such as body size, symmetry or other external features. This paternity bias toward more heterozygous and less inbred males may be explained by post-copulatory mechanisms inside the female reproductive tract. Either the most heterozygous sperm outcompete the rest by being the fittest (Ginsberg & Huck 1989), or a female is able to evaluate male sperm quality and select the most heterozygous sperm (Birkhead & Møller 1993). Nuclear heterozygosity might also be linked to polymorphism in MHC, with females obtaining indirect benefits from choosing males with the most compatible MHC genes (Penn & Potts 1999; Trezenga & Wedell 2000). MHC-based disassortative mating preferences would reduce homozygosity throughout the genome, and particularly within loci linked to the MHC. Progeny derived from such matings would have an increased

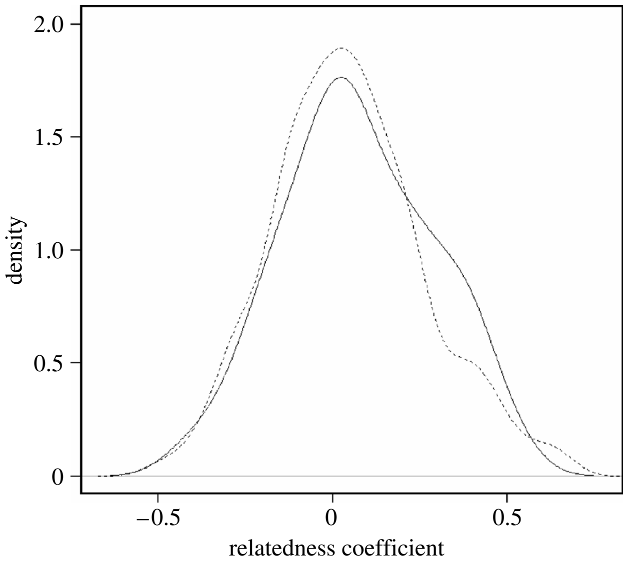

Figure 2. Distribution of relatedness coefficients between reproductive pairs (solid line) or potential pairs (dotted line) of brown bears in Scandinavia within a 40 km radius.

fitness, because of reduced levels of inbreeding and increased resistance to infectious diseases arising from their increased MHC heterozygosity. This hypothesis has, to our knowledge, only been tested with laboratory animals (e.g. Yamazaki *et al.* 1978) and remains to be investigated in wild mammals. The finding of interactions between parental male and female genotypes calls for studying the physiological mechanisms involved (Bernasconi *et al.* 2004). The lack of significance of the IR factor in our behavioural dataset could be due to low power caused by small sample size.

The morphological factor 'body size' was positively correlated with paternity assignment both in the final model of the large dataset analysis and in the 'behavioural data' analysis. As previously suggested, large body size in males could reflect their genetic quality and females may select their reproductive partner based on this criteria. Body size is age-dependent in bears (male age and male body size were highly correlated in our data; see results), therefore females choosing the largest males also select for the oldest males, although the age variable was less important than body size in paternity assignment. In several mammals, age is correlated with dominance rank and it has been shown that dominant males obtain higher reproductive success (e.g. in red deer (*Cervus elaphus*); Clutton-Brock 1988). We have no data on dominance status of males in our subpopulations, however male bears do not defend exclusive territories but have overlapping home ranges (McLellan & Hovey 2001). Thus they may interact with each other throughout the year and a male dominance hierarchy may be established, as suggested in American black bears (Kovach & Powell 2003). Therefore, selection of older males by females might also reflect selection of dominant males.

Among all males available within a 40 km radius, paternity assignment was negatively correlated with geographical distance to potential reproductive partners. In these subpopulations, where SSI is prevalent and where infanticidal males are mostly residents (Swenson *et al.* 1997, 2001; Swenson 2003), it has been proposed that females use promiscuity as a counterstrategy to SSI (Swenson 2003; Bellemain *et al.* 2005*a*). In this study, we further suggested that female mating behaviour is influenced by the occurrence of SSI as the geographically closest males, i.e. potentially infanticidal males, were preferentially selected as fathers of the offspring. We suggest that females may chose to mate with as many close males as possible, which could be viewed as females making 'the best of a bad job' (Wolff & Macdonald 2004). In brown bears, both sexes roam to mate over large distances (Dahle & Swenson 2003*a*), thus individuals whose home range centres are separated by 40 km can easily meet. Therefore, we are confident that our results concerning the selection of geographically closest males is not due to bias, i.e. females would come into contact with close-living males more frequently than with more distant males. However, we cannot exclude the possibility that choosing the closest males also reduces the cost of searching for potential mates, and this may partly explain the effect of distance on female choice. Paternity assignment was not influenced by the factor study area, suggesting that females tended to use the same selection criterion in both subpopulations, independently of the male age structure or mortality regime of the area.

Paternity assignment was not influenced by relatedness between a female and her potential mates in both datasets, indicating that female bears neither prefer genetically distant nor close males. Following the 'optimal outbreeding' theory (Bateson 1983), females should preferentially select males with intermediate relatedness. Relatedness of fathers was not significantly different from non-fathers, either in the large dataset (Mann–Whitney *U* test; $p=0.21$; figure 2), nor in the behavioural dataset. This indicates a random mating scheme in relation to relatedness and suggests that mate choice is not a mechanism to avoid overall inbreeding or outbreeding. The spatial organization of bears may explain this pattern. Bears usually exhibit sex-biased natal dispersal: females are highly philopatric and establish their breeding home ranges in or near their natal areas, whereas males disperse from their mothers' home range and can move long distances (McLellan & Hovey 2001). In Scandinavia, about 36% of the females and 85% of the males have dispersed by 4 years of age (O. G. Støen, personal communication). Consequently, the probability of females mating with closely related males is low (except their father, which happened in *ca* 2% of the litters in our dataset) and they do not have to actively avoid inbreeding.

5. CONCLUSIONS

The high number of marked individuals and the large proportion of parentage assignments (table 1) allowed us to study behavioural characteristics in this brown bear population, and to improve our knowledge about female choice in this species. Due to the occurrence of SSI, the optimal strategy for female bears may be to mate with potentially future infanticidal males and exercise a postcopulatory cryptic choice of the father on her offspring. Our findings support this hypothesis, because not only geographical distance, but also male morphological, genetic, and age criteria were important in determining paternity. Females may be able to increase the survival of their offspring by choosing good genes in their reproductive partners (Brown 1997); we suggest that they use morphological traits such as age or body size and perhaps also dominance status as indicators for male genetic quality. Although our results might partly be explained by male intra-sexual competition, they are consistent with the female choice hypothesis in relation to SSI.

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