Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density

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Summary

1. We studied male yearly reproductive success (YRS) and its determinants (phenotypic characteristics, age, population density) in two Scandinavian brown bear populations, using molecular techniques to determine paternity.

2. We found a significant difference in male YRS between the study areas, with lower YRS in the south than in the north.

3. In general, older and larger males had higher YRS. Older males may be more experienced in competition for reproduction (male dominance). Large body size is of direct benefit in male–male competition and of advantage in endurance competition for the access to females.

4. Age was relatively more important for YRS in the north and body size was more important in the south, due perhaps to differences in male age structure due to illegal killing. A single old male dominated the reproduction in the north during the study, which resulted most probably in the relatively higher importance of age in the north. In the south, with a more even male age structure, no single male was able to dominate, probably resulting in a more intense competition among males, with body size as the deciding factor.

5. Male YRS was correlated positively with population density. This may be related to the structure of the expanding bear population, with female densities declining towards the population edge.

6. Internal relatedness, a measure of genetic heterozygosity, was correlated negatively with YRS, suggesting that outbred individuals have a higher YRS. Individual heterozygosity at key or many loci may reflect male physical qualities and condition-sensitive traits, which may benefit males directly in contest or in sperm competition.

Key-words: age, annual reproductive success, body size, brown bear, density, heterozygosity, *Ursus arctos*.

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Introduction

Ecological and evolutionary change is generated by variation in individual performance (Coulson *et al.* 2006). Yearly reproductive success (YRS) can be defined

as the total number of offspring produced in a year by each member of a set of known individuals (Grafen 1988). Analysing the factors related to individual variation in YRS, and identifying the characteristics of successful individuals, provides insight into the selective pressures affecting evolutionary processes, especially if summed over a lifetime (but see also Coulson *et al*. 2006). YRS is not usually easy to study in natural populations of large mammals, as it requires accurate measures of the number of offspring produced per individual. This is especially difficult in species that occur at low densities and are difficult to observe and capture. However, molecular techniques can be used to determine paternity (Clutton-Brock 1988; Clutton-Brock, Albon & Guinness 1988; Clapham & Palsboll 1997; Coltman *et al*. 2001).

Due to the absence of paternal care in most mammals, male reproductive success is constrained only by the ability to sire offspring (Trivers 1972). Thus, male mammals usually compete intensely for mates, creating the potential for a high variance in male mating success (Emlen & Oring 1977) and thus an opportunity for sexual selection (Wade & Arnold 1980; Arnold & Wade 1984), but only if variation in mating success is correlated with phenotypical variation (Andersson 1994).

Intrasexual selection favours traits that confer an advantage on males in access to females (Andersson 1994), such as large body size, because of its advantage during combat and endurance rivalry (Andersson 1994). When male mating success is influenced strongly by fighting, sexual selection promotes sexual size dimorphism, with larger males. Male reproductive success is then expected to be biased towards a few large adults with superior competitive abilities. Large male size may also be favoured if females prefer large males (Andersson 1994). Body size has often been found to be a major contributing factor to male reproductive success (e.g. red deer *Cervus elaphus*, Clutton-Brock, Guiness & Albon 1982; Clutton-Brock *et al*. 1988; bridled nailtail wallaby *Onochyogalea fraenata*, Fisher & Lara 1999; common brushtail possum *Trichosurus vulpecula*, Clinchy *et al*. 2004), but not always (harbour seal *Phoca vitulina*, Coltman, Bowen & Wright 1998; Coltman *et al*. 1999).

Body size and age are linked closely in many large mammals, and age is often associated with male reproductive success (e.g. Clutton-Brock *et al*. 1982, 1988; Hogg & Forbes 1997; McElligott, Altwegg & Hayden 2002). Older males are often more experienced (East *et al*. 2003) and dominant (Clutton-Brock *et al*. 1988; Le Boeuf & Reiter 1988), and therefore superior competitors in male–male competition. Due to viability selection, older males may also have higher genetic quality (Trivers 1972), but younger males may use alternative mating strategies (e.g. Hogg 1984).

Population density may influence YRS, with mating skew increasing or decreasing with density (Kokko & Rankin 2006). In red deer male lifetime breeding success was correlated positively with the local female density (Clutton-Brock *et al*. 1988). In an expanding population of brown bears (*Ursus arctos*), the relative female population density declined more rapidly than for males from the centre of the distribution towards the edge (Swenson, Sandegren & Söderberg 1998a; Swenson *et al*. 1998b), which may affect male YRS.

Superior reproductive competitors may have greater multilocus heterozygosity, which is often correlated with fitness-associated traits (David 1998; Hansson & Westerberg 2002). Significant correlations between multilocus heterozygosity and fitness have been found in birds (Hansson *et al*. 2001) and mammals (Coltman *et al*. 1998; Slate *et al*. 2000). Brown (1997) suggested that the expression of vigour, condition-sensitive ornaments and symmetry in males may directly reflect individual heterozygosity at key loci or many loci.

Here we evaluate YRS and its determinants in male brown bears using genetic paternity analysis in an 18-year study of two bear populations in Sweden. To our knowledge, this is the first report of male reproductive success in a wild non-social large carnivore. The brown bear is thought to be a non-social and non-territorial species, exhibiting a sequentially polygynous and promiscuous mating system, in which males compete for access to individual oestrous females (Schwartz, Miller & Haroldson 2003). Our objectives were to estimate the influence of phenotypical factors, age and population density on variation in YRS of males. We predict that (a) body size, (b) age and (c) population density are correlated positively with male YRS, and that (d) internal relatedness (a measure of genetic heterozygosity; Amos, Worthington Wilmer & Kokko 2001) is correlated negatively with male YRS.

Methods

STUDY AREA AND FIELD METHODS

The study areas were in south-central Sweden (approximately 61° N, 14° E, south) and northern Sweden (approximately 67° N, 18° E, north). The rolling south consists of 13 000 km^2 of intensively managed boreal forest and contains a hunted bear population. The mountainous north encompasses 8000 km^2 and includes mountainous national parks and adjacent forested lands. Bears are not hunted legally in the national parks. For a detailed description of the study areas see Zedrosser, Dahle & Swenson 2006).

We immobilized bears from a helicopter in April–May, shortly after den emergence. A tissue sample was taken for genetic analysis and, for bears of unknown age, the vestigial first premolar was extracted for age determination (Matson *et al*. 1993). The head circumference (maximum circumference at the zygomatic arches) was measured with a tape measure and used as a measure of overall size of a male. Derocher & Stirling (1998) suggested that head measurements rather than body length might provide the most useful measures to compare populations of polar bears (*Ursus maritimus*).

INDIVIDUAL POPULATION DENSITY INDEX AND SPATIAL DISTRIBUTION

In the south a population size estimate, based on a DNA analysis of non-invasive sampling of scats, was carried out in 2001 and 2002 (Bellemain *et al.* 2005a). Following the procedures described by Zedrosser *et al.* (2006) we calculated an individual density index (within a radius of 17·84 km, i.e. 1000 km^2) around each radio-marked individual in our analysis. The procedures used by Zedrosser *et al.* (in press) are based on the location of individuals identified genetically by the scat sampling, the location of the radio-marked bears [71% of the radio-marked bears were represented in the genetic samples from scats (Bellemain *et al.* 2005a)] and the growth rate in the population (used to temporally correct the density estimate throughout the study period).

In the north virtually every adult male and female and all subadult female bears were radio-marked from 1995 to 2002 (Swenson *et al.* 2001). We used these data and data on growth rate of the population to calculate an individual density index, as in the south (Zedrosser *et al.* 2006). We regard the indices in both study areas as comparable, because we are confident that virtually all individuals (except subadult males and cubs-of-the-year, which were accounted for) were radio-marked in the north, and the density estimates based on the genetic sampling in the south were corrected by dividing it by the proportion of radio-marked bears identified in the genetic sample. The average population density index was 11·1 bears per 1000 km^2 in the north and 29·3 bears per 1000 km^2 in the south (Støen *et al.* 2006).

To ensure that estimates of YRS were not affected by temporal changes in male spatial distribution, we compared mean and median home range diameters and the mean distance between adult male annual home range centres in our study areas. If adult males commonly shift their home ranges between years, mean distances between annual home range centres should be large in relation to the mean home range diameters. The mean distance between adult male brown bear annual home range centres were calculated based on radio-telemetry locations and 95% minimum convex polygon home ranges. Corresponding home range diameters have been published previously (Dahle & Swenson 2003).

PATERNITY ANALYSIS, DATA SELECTION AND INTERNAL RELATEDNESS

Eighteen microsatellite loci, described in Patkeau & Strobeck (1994) and Taberlet *et al.* (1997), were amplified using polymerase chain reaction. The amplification and analysis of microsatellites follow the protocol described in Waits *et al.* (2000). Our database consisted of 738 multilocus genotypes, including radio-marked and hunter-killed individuals.

We estimated YRS for each individual male as the genetically detected number of offspring surviving to 1 year of age per year. For most of the offspring the mother was known, because yearlings were captured with their mother. For bears with unknown pedigree, we determined parentage using the software PARENTE (Cercueil, Bellemain & Manel 2002). Paternity probabilities were calculated using the same software, taking into account allelic frequencies, global error rate and sampling rate of the population (Cercueil *et al.* 2002). One allelic incompatibility of 18 loci was allowed comparing the father–offspring genotype to consider the 0·8% error rate in the genetic data set (Bonin *et al.* 2004).

The probabilities of identity (PI), i.e. the probability to obtain two identical genotypes, from two different individuals by chance (Patkeau & Strobeck 1994; PIsib, for siblings, Waits *et al.* 2000) was very low: $PI = 3·1 \times 10^{-17}$ and $PIsib = 2·4 \times 10^{-7}$. We considered only fathers that were geographically possible (i.e. males with home range centres or kill locations within 40 km of a given female (Bellemain *et al.* 2006) and had a probability of paternity > 0·75, to prevent incorrect paternity assignments and artefactual relationships between heterozygosity and paternity assignment.

For all individuals in this study, we calculated an internal relatedness (IR) index, which reflects a quantity measured between parental half-genotypes that weights allele sharing by the frequencies of the alleles involved. It estimates heterozygosity, giving more weight to homozygotes involving rare alleles and reflects parental similarity more effectively than commonly used heterozygosity indices (Amos *et al.* 2001). It is calculated as:

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

where *H* represents the number of an individual's homozygous loci; *N* the number of loci genotyped and *fi* the frequency of the *i*th allele contained in the genotype within the subpopulation (Amos *et al.* 2001).

STATISTICAL ANALYSES

To estimate absolute size in the years a male was not captured, we calculated the von Bertalanffy growth curve for each study population, because it has been used previously to describe the growth of bears (Kingsley, Nagy & Reynolds 1988; Derocher & Stirling 1998; Zedrosser *et al.* 2006). The von Bertalanffy size-at-age equation was used in the form:

$$s_a = S(1 - e^{-k(a-A)})^3$$

where s_a = head circumference (cm) at age *a*, *S* = asymptotic head circumference (cm), *k* = size growth rate constant (years^{-1}), *A* = fitting constant (extrapolated age at zero size) (years). For individuals captured more than once we used only the measurement at the highest age to construct the population's growth curve. Because all bears were captured within a 2-week period in each study area, we did not adjust body size for capture date. The average individual deviation in size of an individual from the population growth curve was used

Table 1. Comparison of mean and median home range diameters and the mean distance between adult male brown bear annual home range centres in two study areas in Scandinavia in the period 1984–2001. Males were aged 3–30 years (north: 22 males with radio-locations from together 74 years; south: 34 different males with radio-locations from together 126 years). Home range sizes are in km², the distances calculated are in km. Median diameter = median home range diameter as calculated from the median home range. Mean diameter = mean home range diameter as calculated from the mean home range. Mean distance = the mean distance between male annual home range centres

| Study area	Median home range	Mean home range	Range	Median diameter	Mean diameter	Mean distance
North	833 km²*	1137 km²*	245–2029 km²*	16·28 km	19·02 km	12·7 km**
South	1055 km²*	4289 km²*	314–8264 km²*	18·33 km	36·95 km	11·6 km**

*Data from Dahle & Swenson (2003), based on 95% minimum convex polygon home ranges; **based on radio-telemetry locations and 95% minimum convex polygon home ranges.

to calculate an individual growth curve, from which we derived body size at a given age.

Differences in male age structure, YRS and proportion of successful males per age class between study areas were tested using independent-samples *t*-tests. To examine the relationship between YRS success and several categorical and covariate factors, while controlling for dependences, we used general linear mixed models (GLMM). We first analysed the whole data set (global GLMM) before analysing each area separately (GLMM). We assumed a Poisson data distribution and composed global models that accounted for the effects of multiple explanatory variables on YRS. Overdispersion in our data set was handled by using random effects (McCulloch & Searle 2001). The least significant terms were excluded in a backward stepwise manner until the final model consisted of only significant ($P = 0.05$) or suggestive terms ($P = 0.1$). We used the statistical software R version 1·9·0 (R Development Core Team 2004; http://www.R-project.org) in all analyses.

Results

During 1984–2001, we obtained reproductive data from 68 males (24 in the north, 44 in the south) for 417 individual mating seasons (the number of mating seasons the males in our sample were alive during the 18-year study period). Males were spatially stable over time, because the mean distance between male annual home range centres was shorter than both the mean and median home range diameters of adult males in both areas (Table 1). Male age ranged from 3 to 30 years, and ages of successful males ranged from 3 to 27 years. The male age structure differed between the areas (Fig. 1), with mean age significantly higher in the south than in the north (South: $\bar{X} = 9.55$ years ± 5.93 (*SD*), North: $\bar{X} = 6.88$ years ± 4.51, $t_{58} = 2.08$, $P = 0.042$). Mean YRS was significantly higher in the north than in the south (North: $\bar{X} = 1.02 \pm 1.59$, South: $\bar{X} = 0.42$ genetically detected offspring per year ± 0.95, $t_{134} = 3.69$, $P < 0.001$). There was also a statistically significant difference in the proportion of reproductively successful males per age class (3 years of age and older) between the study areas (south: age classes 3–30, $\bar{X} = 21.4\% \pm 32.6$, north: age classes 3–24, $\bar{X} = 56.8\% \pm 42.1$, $t_{38} = 2.56$, $P = 0.014$, Fig. 2).
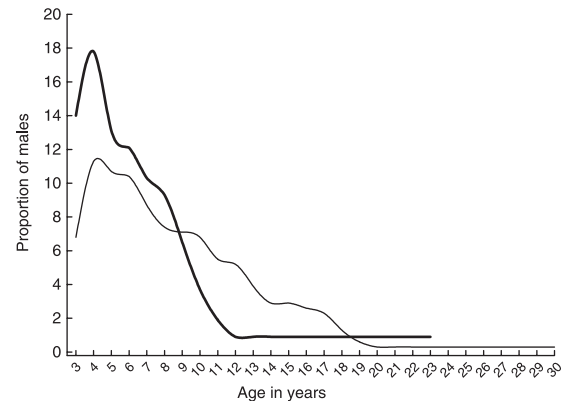
Fig. 1. Proportions based on the composite age structure of marked adult (≥ 3 years) male brown bears in two study areas in Scandinavia from 1984 to 2001. The thick solid line represents males in the north and the thin solid line males in the south. Due to capture methods a relatively lower proportion of 3- and 4-year old males are represented in the figure.
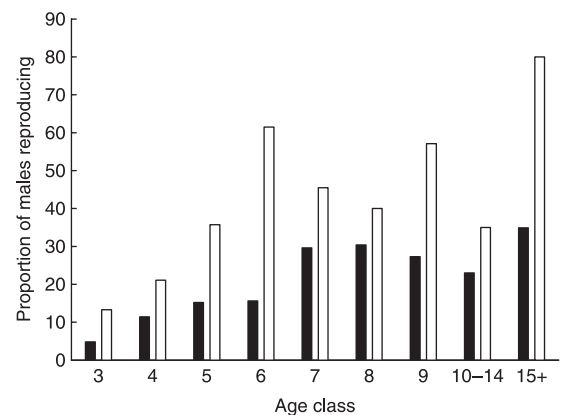

Fig. 2. Proportion of adult (≥ 3 years) male brown bears reproducing annually per age class in two study areas in Scandinavia from 1984 to 2001. The black bars represent the south, the white bars the north.

The area-specific von Bertalanffy curves (based on 74 individuals in the north and 152 in the south) were not significantly different (Table 2, Fig. 3) and were used to calculate the body size of the individuals in further analyses. The overall model showed that YRS was significantly lower in the south (Table 3). Age and

Table 2. Parameter estimates for the von Bertalanffy size-at-age curves for head circumference of male Scandinavian brown bears (± SE) in two study areas in Scandinavia. S: asymptotic head circumference; K: size growth constant; A: theoretical age at which the animal would have size zero; n: sample size

Study area	S (cm)	K (year^{-1})	A (years)	n
North	78·28 ± 1·81	0·384 ± 0·047	−3·25 ± 0·48	74
South	77·68 ± 0·80	0·335 ± 0·018	−3·83 ± 0·24	152
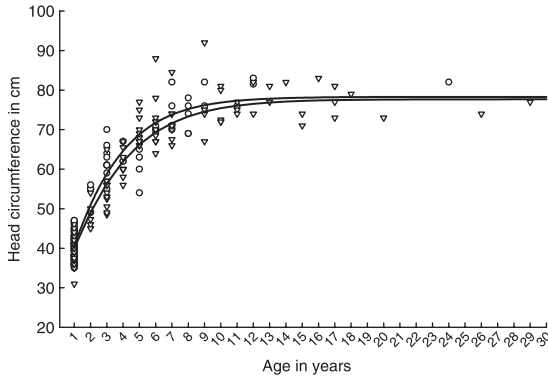
Fig. 3. The von Bertalanffy growth curve fitted to age and head circumference of male Scandinavian brown bears. The thick solid line and the circles represent males in the north ($n = 74$) and the thin solid line and triangles males in the south ($n = 152$).

population density were positively related, and internal relatedness was negatively related to YRS. The interaction study area × body size suggested that body size was more important in the south, whereas the interaction study area × age showed that age was more important in the north (Table 3). The separate analysis of the study areas showed that YRS was related significantly to age and population density in the north and related significantly to body size and tended to be related to population density in the south (Table 4).

Discussion

YRS measures an individual's short-term (seasonal) production of offspring. In general, YRS in this study might be underestimates, because males could have sired offspring outside the study area or produced young within the study area that were not detected. Age patterns or spatial organization in natural, non-hunted brown bear populations and the importance of some factors influencing male YRS may differ between unhunted and hunted populations. We studied hunted (legally and illegally) populations; in Sweden no age or sex classes, except females with young, are protected and bear hunters show little selection (Fujita 2000).

YRS was significantly lower in the south (Table 3, Fig. 2), due perhaps to better sampling in the north. However, this should affect only the absolute but not the relative measures of YRS. Another explanation may be the lower operational sex ratio in the south (fewer adult females per adult male; Swenson *et al.* 2001). Due to illegal killing, especially in spring, only one old and reproductively dominant male and several young adult males were present in the north for several years (Swenson *et al.* 2001). Males ≥ 9 years were largely missing (Fig. 1). This uneven age distribution apparently enabled a relatively higher proportion of young males (3–4 years) to gain reproductive success in the north, and achieve relatively higher YRS than in the south (Fig. 2). In the south bears were usually

Table 3. A global generalized mixed linear model explaining the detected number of offspring produced annually by a male brown bear in two study areas in Scandinavia in the period 1984–2001. Variables included are study area, age, body size, internal relatedness, density and relevant interactions. Male identity was included as a random effect. After a successive exclusion of the least significant terms, the final model is shown in the table; d.f.: degrees of freedom, β: logistic regression coefficient, SE: standard error; t: t-value; P: significance level; $n = 417$, number of groups: 68

Explanatory variables	d.f.	β	SE	t	P
Study area	66			−2·284	0·026
South		−6·086	2·665		
North		0	0		
Age	343	0·079	0·040	1·988	0·048
Body size	343	−0·008	0·029	−0·272	0·786
Internal relatedness	343	−1·869	0·798	−2·343	0·020
Density	343	0·016	0·007	2·322	0·021
Study area × body size	343			1·954	0·051
South × body size		0·079	0·041		
North × body size		0	0		
Study area × age	343			−2·007	0·046
South × age		−0·104	0·052		
North × age		0	0		

Table 4. Separate global generalized mixed linear models explaining the detected number of offspring produced annually by a male brown bear in two study areas in Scandinavia in the period 1984–2001. Variables included are age, body size, internal relatedness, population density and relevant interactions. Male identity was included as a random effect. After a successive exclusion of the least significant terms, the final models are shown in the table; d.f.: degrees of freedom; β: logistic regression coefficient; SE: standard error; *t*: *t*-value; *P*: denotes the significance level. North: *n* = 108, number of individuals = 24; south: *n* = 309, number of individuals = 44

Study area	Explanatory variables	d.f.	β	SE	*t*	*P*
North						
	Age	82	0·063	0·024	2·632	0·010
	Population density	82	0·039	0·016	2·399	0·019
South						
	Body size	263	0·063	0·022	2·841	0·005
	Population density	263	0·014	0·008	1·826	0·069

killed during a regulated autumn hunting season. This resulted in a more evenly distributed age structure and increasing YRS with age classes (Figs 1 and 2).

Generally, YRS was correlated positively with age. We found no evidence of reproductive senescence in male brown bears, as occurs in male red deer (Clutton-Brock *et al.* 1988) and female brown bears (Schwartz *et al.* 2003b), because all males over 20 years reproduced regularly. Females of many species choose to mate with old males, possibly because they pass superior genes to their offspring (Brooks & Kemp 2001). Male age may reflect genetic quality (the viability selection hypothesis, Trivers 1972), and/or older males may be more selected by females (the good gene hypothesis, Brown 1997). However, this latter hypothesis (Brown 1997) may not be applicable to our study, because both study populations were under heavy hunting pressure and therefore survival may not depend on genetic quality. Additionally the mortality rates of adult bears (≥ 3 years) are independent of age (Sæther *et al.* 1998).

Several studies show that male age is often correlated strongly with rank (Clutton-Brock *et al.* 1982, 1988; Le Boeuf & Reiter 1988; Pelletier & Festa-Bianchet 2006); however, all these studies dealt with social species. Brown bears are considered to be a non-social species, although a spatial male dominance hierarchy based on age and size cannot be excluded, as suggested for brown bears at garbage dumps (Craighead, Sumner & Mitchell 1995), and for American black bears (*Ursus americanus*) (Kovach & Powell 2003) and polar bears (Derocher & Stirling 1990).

The brown bear mating system is based on male contest competition for females (Schwartz *et al.* 2003a), which is also indicated by the large sexual size dimorphism (Andersson 1994). As predicted, age-corrected male body size was correlated positively with YRS. This suggests that larger males are able to dominate and exclude smaller males physically when competing for oestrous females, as has been found in several other species (Clutton-Brock *et al.* 1988; Le Boeuf & Reiter 1988; McElligott *et al.* 2001; Wilson *et al.* 2002). An alternative explanation is that females select larger males, as suggested for brown bears (Bellemain *et al.* 2006). An advantage of body size in endurance compe-

tition may also be involved. In general, energy storage capacity should increase with body size more rapidly than metabolic costs (Andersson 1994). Large size and stored energy may enable a male to roam wider and longer in search of females. In bighorn sheep (*Ovis canadensis*) younger or subdominant males that were not able to attend an oestrous female employed alternative mating tactics more often than adult males, which successfully attended oestrous females (Hogg 1984). However, to our knowledge, no alternative mating tactics have been observed in brown bears, although some young males may mate with an unguarded oestrous female.

The separate analyses of the study areas and the interactions of study area × age and study area × body size suggest that age was more important for YRS in the north and body size was more important in the south. Body size and age are highly correlated in our study areas (Bellemain *et al.* 2006). These study-area differences are probably related to the aforementioned differences in male age structure due to human-caused mortality. A single old male dominated the reproduction in the north during the study period (Fig. 2), which resulted most probably in the relatively higher importance of age there. In the south, with a more even male age structure, no single male dominated. This resulted most probably in a more intense competition among males, with body size as the deciding factor.

As predicted, population density had a positive effect on YRS. The Scandinavian bear population is expanding in size and range (Swenson *et al.* 1995), and Swenson *et al.* (1998a,b) showed that the relative density of females declined more rapidly than for males from the centre of the distribution towards the edge, and that males dominated low-density areas into which bears are expanding. The declining female density towards the population edge decreases the chances to obtain mating opportunities and therefore also their YRS (Swenson *et al.* 1998b).

As predicted, IR was correlated negatively with YRS. Negative values suggest relatively outbred individuals, whereas high positive values suggest inbreeding. The negative correlation in our results suggests that outbred individuals have higher YRS. IR was probably not correlated significantly with male YRS when the

study areas were analysed separately because of sample size, because the effects of measures of heterozygosity are typically evident only with large sample sizes (David 1998). Individual heterozygosity at key or many loci may be reflected in male physical qualities and condition-sensitive traits (Brown 1997), which may directly benefit males in competition. However, heterozygosity may also be selected via female choice; a female might choose the most heterozygous male through physical cues because it may favour the production of diverse and superior offspring. In brown bears, females seem to select genetically diverse males for mating (Bellemain *et al.* 2006), as also suggested in grey seals (*Halichoerus grypus*) (Amos *et al.* 2001). In red deer male and female lifetime breeding success was correlated positively with heterozygosity (Slate *et al.* 2000). Less inbred, and thus more heterozygous, males may also have an advantage in sperm competition (Andersson 1994). Multiple paternities are frequent in Scandinavian brown bears, occurring in 14·5% litters with ≥ 2 and 28% of litters with ≥ 3 (Bellemain, Swenson & Taberlet 2005b). Internal relatedness as a measure of heterozygosity probably reflects male quality due to the functional overdominance hypothesis (Bellemain *et al.* 2006).

Acknowledgements

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