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Should I stay or should I go? Natal dispersal in the brown bear

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We studied the causes of natal dispersal of male and female brown bears, *Ursus arctos*, in two study areas in Sweden. Males had a higher dispersal probability (94%) than females (41%). For males, we found no difference in dispersal probability or mean age of dispersal between the study areas, in spite of differences in population density and sex ratio. Male–male competition did not seem to influence subadult male dispersal probability significantly. These results support the inbreeding avoidance hypothesis as the cause of male natal dispersal. For females, dispersal probability decreased with increasing maternal age and decreased with increasing body size, and an interaction between maternal age and body size suggested that the importance of body size decreased with increasing maternal age. Nondispersing females were closer to their mother than their dispersing sibling sisters were in the period between weaning and dispersal. Female littermates seemed to compete for philopatry, suggesting that a dominance hierarchy among female littermates based on body size may cause the subdominant sister to disperse. If juvenile females are born into matrilineal assemblages, surrounded mostly by related females, the competition for philopatry may not be as severe as when they are born into an area surrounded by mostly nonkin females. This hypothesis is supported by the decreasing importance of body size for dispersal with increasing maternal age. We suggest that natal dispersal in juvenile female brown bears can be explained by the resident fitness hypothesis.

Keywords: brown bear; inbreeding avoidance; natal dispersal; resident fitness; *Ursus arctos*

Dispersal often has multiple causes determined by different factors operating at different ontogenetic stages during an organism's life cycle (Ims & Hjermann 2001). In general, dispersing individuals of most bird and mammal species are young (Greenwood 1980). In contrast to birds, where dispersal is usually female biased, dispersal in mammals is often male biased and females remain philopatric (Pusey 1987).

Dispersal and philopatry can be viewed as behaviours of individual organisms that have demographic and genetic consequences for the population as a whole (Gaines & McCleneghan 1980; Armitage 1991; Byrom & Krebs 1999). Several hypotheses have been proposed to explain the ultimate causes of natal dispersal in a wide range of species: the inbreeding avoidance hypothesis, where individuals disperse to avoid inbreeding with close relatives (Greenwood 1980; Cockburn et al. 1985; Pusey 1987; Wolff 1993, 1994); the intrasexual mate competition hypothesis, where individuals disperse to avoid competition for mates (Dobson 1982; Moore & Ali 1984); the resource competition hypothesis, where individuals disperse to increase access to environmental resources (Greenwood 1980; Waser & Jones 1983; Pusey 1987); and the resident fitness hypothesis, where juveniles compete for philopatry (Anderson 1989). However, the causes of dispersal can differ between species, between populations and between the sexes (Waser & Jones 1983; Moore & Ali 1984; Lidicker & Stenseth 1992), and the various proposed hypotheses are not mutually exclusive (Dobson & Jones 1985).

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We studied a solitary large carnivore, the brown bear, *Ursus arctos*, a species with a polygynous mating system (Schwartz et al. 2003; Bellemain et al. 2006). Natal dispersal in brown bears has been reported to be sex biased, with highly philopatric females establishing their home ranges in or adjacent to their natal areas and males dispersing long distances from their mother's home range (McLellan & Hovey 2001; Støen et al. 2006). Almost no female natal dispersal has been reported in brown bear populations in North America (e.g. McLellan & Hovey 2001), but 32–46% of females disperse from their natal home ranges in Scandinavian brown bear populations (Støen et al. 2006).

We examined a data series from a long-term study (20 years) of brown bears in two areas in Scandinavia. The study areas have different population densities (Zedrosser et al. 2006), and human influence (poaching) has resulted in a skewed sex ratio in one of the areas (Swenson et al. 2001a). These differences and the large geographical distance (600 km) between the study areas enabled us to use a 'quasiexperimental design' for our study. We defined a juvenile as a bear aged 1–4 years (both females and males), because the mean age at which bears had their first successful litter was 5 years in both study areas (Swenson et al. 2001a; Støen et al. 2006). Our aims were to investigate the causes of natal dispersal in brown bears, and also to examine which life history traits make individuals more prone to disperse. From the three main hypotheses to explain natal dispersal we made several predictions.

(1) Hypothesis 1: male brown bears disperse to avoid intrasexual mate competition (mate competition hypothesis). Because of the polygynous mating system of brown bears, females are unlikely to disperse to avoid mate competition, as has also been suggested for polygynous arctic ground squirrels, *Spermophilus* spp. (Dobson 1982; Byrom & Krebs 1999). The following predictions of the mate competition hypothesis therefore apply only to male brown bears: (1a) dispersal probability should be lower in the area with lower density and with fewer males per female (northern study area); (1b) mean dispersal age should be higher in the area with the uneven sex ratio (northern study area); and (1c) dispersal probability of juvenile males in both study areas should be positively related to the number of adult males in the vicinity of a given juvenile male.

(2) Hypothesis 2: juvenile male brown bears disperse to avoid inbreeding with close relatives (inbreeding avoidance hypothesis). Juvenile female brown bears disperse about 28 km from their natal area as 2–4 year olds in Scandinavia (Støen et al. 2006). Bellemain et al. (2006) found that 95% of all breeding brown bear pairs (i.e. a female and the father of her current offspring) were located within 40 km of each other in Scandinavia. Hence, dispersing juvenile females do not seem to settle in areas outside the reproductive reach of their father. However, inbreeding between philopatric females and their fathers does not seem to be a major problem in brown bears, because in our study areas only 2% of all litters resulted from incestuous matings between father and daughter (Bellemain et al. 2006). The following predictions of the inbreeding avoidance hypothesis therefore apply only to male brown bears: (2a) there should be no differences in the probability of dispersal between the study areas, even with differences in density and sex ratio; (2b) mean dispersal age of juvenile males should not differ between the study areas; and (2c) dispersal probability of juvenile males in both study areas should not be related to the number of adult males in the vicinity of a given juvenile male.

(3) Hypothesis 3: juvenile female brown bears compete for philopatry (the resident fitness hypothesis). The prevalent hypothesis in the literature to explain the causes of female dispersal in mammals is the resource competition hypothesis, where individuals disperse to increase access to environmental resources, such as food or territories (Greenwood 1980; Waser & Jones 1983; Pusey 1987). However, female brown bears show some dispersal characteristics that argue against this hypothesis: related females form matrilineal assemblages, where members have more home range overlap than unrelated females (Støen et al. 2005). This implies that subadult females benefit from remaining philopatric, despite an increase in resource competition caused by the home range overlap.

Anderson (1989) formulated the resident fitness hypothesis as an ultimate explanation for dispersal in rodents. According to this hypothesis, it is selectively advantageous for adult female rodents to retain their maturing daughters near the natal site and to behave cohesively towards them, provided competition for essential resources is below the point at which these resources become limiting to the mothers' reproductive success. Sibling daughters should compete for philopatry, and the more dominant sibling is expected to force the subdominant sibling to emigrate (Wiggett & Boag 1992). Although formulated specifically to explain dispersal in rodents, the resident fitness hypothesis may fit the expectations of female brown bear dispersal better than the resource competition hypothesis does. Matrilineal assemblages in brown bears may be formed by philopatry or short-distance dispersal of juvenile female offspring (Støen et al. 2005). As more related females settle around a mother throughout time, this may decrease the competition with unrelated females. We therefore predicted from the resident fitness hypothesis that (3a) the probability of juvenile female dispersal should be negatively related to maternal age, when the effects of population density and environmental conditions are controlled; and (3b) the dispersal probability of juvenile females should be positively related to litter size and the number of female littermates, because competition for philopatry should increase with increasing litter size of females. If female offspring compete for philopatry, then physical advantages may influence the outcome; we therefore predicted that (3c) body size should be negatively related to dispersal probability. To assess whether there is competition among female littermates for philopatry, we predicted that (3d) in sibling pairs containing female dispersers and nondispersers, the nondispersing sibling should be geographically more closely associated with the mother than the dispersing sibling after separation but before dispersal.