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Maternal effect and interactions with philopatry in subadult female American black bear, *Ursus americanus*, den selection

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The selection of suitable locations to fulfil life history requisites is an important process that can influence the survival and development of individuals and the persistence of populations. The impacts of site selection are well documented across taxa, but the driving forces behind site selection, especially regarding transgenerational behaviour, are less well understood. Philopatry (the tendency for an individual to remain near its natal home range) and maternal effect (a nongenetic transfer of phenotypes from mother to offspring) are two factors often thought to influence birth site selection behaviours. We investigated black bear, *Ursus americanus*, transgenerational den type selection behaviour by analysing a long-term data set containing den selection data of 168 2-year-old subadult females during 1984–2013 at four study sites in Maine, U.S.A. to determine whether there is evidence of philopatry and maternal effect on den type selection. Using logistic regression and model selection, we found evidence that both mechanisms play a role in subadult den type selection. Bears that spent the last winter with their mother in a high-protection den were more likely to select that den type as a subadult. Furthermore, in instances of differences in transgenerational den type selection, most subadults (79%) transitioned from a yearling den of lower protection to a subadult den of higher protection. Transitional behaviour might indicate that subadult black bears also account for environmental plasticity and mediate their den selection accordingly, without the benefit of prior independent denning experience. Future research should evaluate the relationship between den type and offspring recruitment to examine whether an individual-level maternal effect is manifested at the population level. Our results suggest that behavioural maternal effects, in part, influence transgenerational den type selection in black bears, and by extension may influence the behavioural phenotypes of other species with extended periods of maternal care.

The ability to select suitable sites during key periods in an animal's life can significantly influence the fate of individuals and the persistence of populations. Birth site selection, for example, may allow animals to cope with risky environments and provides protection from both predation and environmental pressures (Bowyer, Van Ballenberghe, Kie, & Maier, 1999; Wesolowski, 2002; Wilson, 1998). Nest site selection serves in predator avoidance and reproductive success of many species of birds (Davis, 2005; Joern & Jackson, 1983; Wesolowski, 2002), embryonic development, offspring survival and behaviour and temperature-dependent sex determination influencing sex ratios of reptiles (Burger, 1993; Schwarzkopf & Brooks, 1987; Wilson, 1998), offspring growth and population structure of amphibians (Petranka, 1990) and survival and growth of embryonic and juvenile fish (Phelps, Lohmeyer, Wahl, Zeigler, & Whitledge, 2009; Scott, Kosick, Clement, Noakes, & Beamish, 2005). Similarly, den site selection imparts protection from predators, energy conservation during gestation and lactation, offspring survival and successful recruitment in many mammal species (Henner, Chamberlain, Leopold, & Burger, 2004; Person & Russell, 2009; Ross, Kamnitzer, Munkhtsog, & Harris, 2010). While the importance of site characteristics has been demonstrated at both an individual and population level across several taxa of animals, whether and how site selection behaviour is transmitted from mothers to offspring is less well documented. These pieces of information are important components for understanding a species' ecology, its life history and its management and conservation needs.

Two factors associated with transgenerational site selection behaviour are natal philopatry and maternal behaviour (Benson & Chamberlain, 2007; Bowyer et al., 1999; Skeel, 1983; Waser & Jones, 1983). Natal philopatry (philopatry hereafter) is defined as an individual's continued use of, or return to, its natal home range

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past the age of independence from its parents (Waser & Jones, 1983). Philopatry can decrease exposure to mortality risks associated with dispersal and increase the probability of survival by allowing individuals to reside in a familiar environment (Weatherhead & Forbes, 1994). Philopatry is evident in a wide range of mammals, both social (Boydston, Kapheim, Van Horn, Smale, & Holekamp, 2005; Gompper, Gittleman, & Wayne, 1998; Hoogland, 1999) and solitary species (Davis, 1996; Jones, 1984; Ratnayeke, Tuskan, & Pelton, 2002). In most philopatric mammal species, philopatry is sex biased, and females are typically the philopatric sex, while males disperse (Clutton-Brock & Lukas, 2012; Greenwood, 1980; Waser & Jones, 1983).

Maternal effects result from a nongenetic transfer of phenotypes from a mother to her offspring, including physiological and behavioural phenotypes (Rödel, Prager, Stefanski, von Holst, & Hudson, 2008), and can be viewed as the causal influence of maternal behavioural phenotypes on the offspring's behavioural phenotype (Wolf & Wade, 2009). Behavioural maternal effects are mediated by both the mother's phenotype and her environment, allowing for transgenerational adaptive behavioural phenotypic plasticity (Hoyle & Ezard, 2012; Maestripieri & Mateo, 2009; Mousseau & Fox, 1998; Wolf & Wade, 2009). By adjusting to environmental change, a mother can affect her offspring's phenotype, which can be beneficial if that offspring is likely to encounter a similar environment (Bernardo, 1996; Maestripieri & Mateo, 2009; Mousseau & Fox, 1998). Mammals show the largest and most significant influence of maternal effects (Reinhold, 2002), likely owing to the extended period of parental care found throughout the taxon.

Experimental studies on mice (*Mus musculus*), for example, have shown female transgenerational transmission of behavioural phenotypes related to maternal care, specifically the speed with which a mother will seek out and retrieve offspring that have been removed from the nest (Curley, Champagne, Bateson, & Keverne, 2008). The neonatal mice that were retrieved more quickly were then observed to retrieve their own offspring quickly, despite the fact that they did not have the opportunity to simply imitate or copy their mother's behaviour as would be seen with social learning. Instead, this transmitted behaviour was the result of a maternal effect, mediated by the mother's phenotype (proclivity to quickly retrieve displaced offspring) and the environment in which the study was conducted. Mateo (2014) has shown behavioural maternal effects associated with foraging (leading to an increase in offspring weight), predator avoidance (increasing offspring survival) and vigilance (leading to improved predator avoidance) in Belding's ground squirrel, *Urocitellus beldingi*. Furthermore, differences in microhabitat-specific maternal effects have been observed within populations and among species of ground squirrels, including Belding's ground squirrels (Mateo & Holmes, 1999), Arctic ground squirrels, *Urocitellus parryii*, California ground squirrels, *Otospermphilus beecheyi*, and rock squirrels, *Otospermphilus variegatus* (Mateo, 2014, and references therein).

Learning is another mechanism of information and behaviour acquisition that can be achieved independently by an individual (asocial learning) or through observation of or interaction with another individual (social learning) (Breck et al., 2008; Heyes, 1994). Social learning is an efficient means of behaviour transmission among conspecifics, including via vertical transmission from mother to offspring as seen in black bears, *Ursus americanus* (Hopkins, 2013; Kendal, Kendal, Hoppitt, & Laland, 2009; Mazur & Seher, 2008). Food conditioning and other conflict behaviours have been suggested to be socially learned behaviours passed on via vertical transmission as opposed to genetically inherited traits in black bears (Breck et al., 2008; Hopkins, 2013; Mazur & Seher, 2008) and grizzly bears, *Ursus arctos* (Morehouse, Graves, Mikle, & Boyce, 2016). The importance of social learning in black bears should not be understated, as it is partially responsible for an offspring's acquisition of behaviours necessary for survival, including learning what and where to eat, what to fear and how to escape from danger (Breck et al., 2008; Galef & Laland, 2005; Hopkins, 2013; Mazur & Seher, 2008).

Although the concepts of social learning and maternal effect are similar and, at times, one and the same (Avital & Jablonka, 1994; Bernardo, 1996; Maestripieri & Mateo, 2009; Storm & Lima, 2010), it is important to distinguish between the two concepts as the present study specifically addresses maternal effects and not social learning. Rather than simply passing a behaviour on through teaching or social learning (Caro & Hauser, 1992; Heyes, 1994; Laland, 2004; Thornton & Raihani, 2010), behavioural maternal effects are mediated by phenotype and the environment (Hoyle & Ezard, 2012; Maestripieri & Mateo, 2009; Mousseau & Fox, 1998; Wolf & Wade, 2009). With behavioural transmission via maternal effects, offspring do not necessarily need to copy or imitate behaviours as with social learning, but can simply be passive recipients of maternal effects (Maestripieri & Mateo, 2009). Within this construct, a mother leading her offspring to a food source and then eating the most nutritious food at the site, prompting active imitation and learning by the offspring regarding food habits, would be an example of social learning (Laland, 2004). Conversely, maternal effects can be transmitted passively and do not require active perception by the offspring, as shown with the previously described offspring retrieval in mice (Curley et al., 2008). Similarly, mothers do not need to play an active role in the behaviour transmission as would be the case with social learning mechanisms such as teaching (Maestripieri & Mateo, 2009; Thornton & Raihani, 2010). Social learning has been empirically identified using an option-bias method, which states that social learning will result in greater homogeneity within a population for a given behaviour than expected in the absence of social learning (Kendal et al., 2009, 2010). Conversely, the phenotypic plasticity offered by maternal effects allows for heterogeneity and alternative behavioural phenotypes to be favoured dependent upon environmental changes (Maestripieri & Mateo, 2009).

In this study, we examine the relative importance of philopatric effects and maternal effects on transgenerational site selection using a long-term data set on den site selection in American black bears in Maine, U.S.A. The American black bear is an omnivorous mammal that ranges across much of North America. Within dens, black bears undergo a period of annual winter dormancy known as torpor, which is a mechanism by which bears avoid periods of extreme cold, heavy snowfall and low food supplies (Johnson & Pelton, 1980). Regardless of the climate, female black bears need to den for several months to successfully reproduce (Davis, 1996; Wooding & Hardisky, 1992), to protect themselves and their young during torpor and to provide thermal buffering from the external environment (Crook & Chamberlain, 2010; Davis, 1996). Consequently, concealment from predators and protection from thermal exposure are key attributes of a den site (Beecham, Reynolds, & Hornocker, 1983). Cubs stay with their mother through their first summer and den with her once again as a yearling (from age 1 to age 2), and therefore, protection benefits extend to the yearling den as well (Hopkins, 2013; Miller, 1994).

Philopatry plays an important role in black bear home range selection, or second-order selection, and therefore may also play an important role in eventual den site selection, or third-order selection (Johnson, 1980). Shortly after the yearling denning period, when offspring are about 18 months of age, family groups separate (Ryan, 1997). Male offspring typically disperse as subadults (2-year-olds) whereas females are philopatric, often inheriting a portion of their mother's home range (Davis, 1996).