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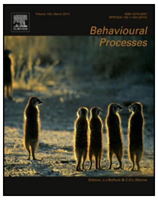

Mating-related behaviour of grizzly bears inhabiting marginal habitat at the periphery of their North American range

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ABSTRACT

In comparison to core populations, peripheral populations have low density and recruitment, and are subject to different selective pressures, such as environmental conditions, food type and availability, predation, disease, etc., which may result in behavioural modifications to mating. We test the roam-to-mate hypothesis for a peripheral population of grizzly bears (*Ursus arctos*) at the northern extent of their North American range, in Canada's Arctic. If bears are roaming-to-mate, we predicted greater range size and daily displacement, and more linear movements for receptive animals during the mating period compared to post-mating. In contrast to our predictions, we found that in general range size and displacement increased from mating to post-mating regardless of reproductive status. When considered across both periods, females with cubs-of-the-year had smaller range use metrics than other reproductive groups, which we attribute to a counter-strategy against sexually selected infanticide and the reduced mobility of cubs. Linearity of movements remained near zero during both periods across all groups, suggesting tortuous movements more characteristic of foraging than of mate-searching. We suggest that for this population, finding quality habitat takes precedence over mate-searching in this marginal Arctic landscape. Alternatively, a more monogamous mating system and sequestering behaviour may have obscured movement differences between the two periods. The behavioural differences in mating that we observed from what is typical of core populations may reflect local adaptation to marginal conditions and could benefit the species in the face of ongoing environmental change.

1. Introduction

Interest in the conservation value of populations on the periphery of their core distribution has increased despite their often having lower density, lower recruitment, and being at greater risk of extinction from stochastic events than core populations (Kawecki, 2008; Petersen et al., 2010). The lower density of peripheral populations is believed to be largely driven by spatial patterns of quality habitat (Vucetich and Waite, 2003). In comparison to core populations, peripheral populations may exhibit variation in specific behavioural traits from core populations with habitat-specific consequences for fitness (Kawecki, 2008). These behavioural modifications can include differences in spacing behaviour and range use resulting from the characteristically lower population density and reproductive rate, and is most pronounced among large mammals (Petersen et al., 2010). The conservation value of peripheral populations is being re-evaluated due to the discovery that these populations may add to the genetic diversity of the population as a whole (Scudder, 1989; Lesica and Allendorf, 1995; Hampe and Petit, 2005). The added genetic diversity is the result of peripheral populations being exposed to different selective pressures that might influence behaviour and reproductive success and could result in phenotypic changes.

The selective pressure experienced by peripheral populations, such as harsh environmental conditions, reduced availability of quality foods and other resources, increased predation risk and sources of disease, etc., may be such that individuals within the population adapt to these marginal environments by changing their behaviours in order to persist (Kawecki, 2008; Edwards et al., 2009). Survival and reproductive success is often lower in marginal environments (Kawecki, 2008). However, if individuals can adapt and survival and reproductive success increases, once marginal environments may become source habitats for species emigration and range expansion. By examining behavioural variation across a species' range, we may gain insight into the evolution of range

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dynamics and ecological niches. Because of the low density and low reproductive rates exhibited by peripheral populations (Bond and Wolff, 1999), variation in mating behaviour is pertinent to examine (Kokko and Rankin, 2006). Four main mating systems have been documented, including defence of individual females during all or part of their receptive period, defence of feeding areas that partially or entirely overlap female or female group home ranges, defence of a group of females during the mating period or throughout the year without defence of a particular area, and defence of mating-specific territories within part of the females' ranges (Clutton-Brock, 1989). At their core, a primary determining factor of these forms of mating is the spatial-temporal availability and defensibility of limited resources, be it the potential mate or the mating-specific area (Clutton-Brock and Harvey, 1978; Clutton-Brock, 1989; Whitehead, 1990; Shuster and Wade, 2003). Although animal mating systems may differ, they all share the common goal of maximizing reproductive success. For females, maximum reproductive success is achieved through provisioning and protecting offspring, whereas for males it is achieved through access to females, and the number of mates (Trivers, 1972; Emlen and Oring, 1977; Sandell and Liberg, 1992; Shuster and Wade, 2003).

During the mating period, ranging behaviour may be influenced by the age and reproductive status of individuals, and for females, the presence and age of dependent young (Bateman, 1948; Clutton-Brock and Harvey, 1978; Harestad and Bunnell, 1979; Sandell, 1989). For reproductively receptive individuals, greater range use during the mating period has been observed in both sexes, but primarily in males (Schwagmeyer, 1988; San Jose and Lovari, 1998; Fisher and Lara, 1999). For polygamous species, a large range during the mating period may be advantageous, because of the increased probability of encountering asynchronously receptive mates (Clutton-Brock, 1989). Where male parental care is absent, female home range size, which may be reduced in the presence of dependent young, is expected to be a function of the spatial dispersion of forage (Clutton-Brock and Harvey, 1978), reduced mobility of younger offspring (Lindzey and Meslow, 1977), and an increased risk of infanticide by conspecifics (Hrdy, 1979; Ebensperger, 1998). Outside the mating period, animals should switch their focus from mating to procuring food (Erlinge and Sandell, 1986). Males, however, may consistently use larger areas than females to obtain information on conspecifics and to meet the higher energy demands of their generally larger mass (Dahle and Swenson, 2003a).

The mating system of grizzly bears (*Ursus arctos*) has been described as scramble competition polygamy (Radespiel et al., 2001; Dahle and Swenson, 2003b; Steyaert et al., 2012), with males both roaming in search of and guarding mates (Shuster and Wade, 2003; Steyaert et al., 2012). Males generally have larger home ranges than females (Hilderbrand et al., 1999; McLoughlin et al., 2000). A male home range will often overlap that of several females and both males and females can have larger ranges during the mating period compared to the post-mating period, which may support the hypothesis that grizzly bears roam-to-mate (McLoughlin et al., 1999; Swenson et al., 2000; Dahle and Swenson, 2003a,b). However, region-specific selective pressure may result in alternate behaviour among peripheral populations, and local research is needed to understand if these behavioural differences affect a population's reproductive success (Steyaert et al., 2012). In this study, we examine the mating behaviour of grizzly bears in the Mackenzie Delta region (Northwest Territories), in the Arctic of northwest Canada, in particular the roam-to-mate hypothesis.

The Mackenzie Delta bears are a peripheral population at the northern extent of their North American geographical distribution. Grizzly bear foods in the Mackenzie Delta are patchy and dispersed, and only available for a short period, with low inter-annual predictability (Edwards et al., 2013). In the spring following den-emergence, available foods include overwintered berries, sweetvetch roots (*Hedysarum alpinum*), moose (*Alces alces*) neonates in some areas, and ungulate overwinter mortality primarily from a small herd of semi-domesticated reindeer (*Rangifer tarandus tarandus*). Alternate foods available for short periods are broad whitefish moving between water bodies along perennial streams (Barker and Derocher, 2009), muskrat and beaver, and hibernating Arctic ground squirrels (Barker and Derocher, 2010; Barker et al., 2014). As spring changes to early summer, grizzly bears will begin foraging on the fresh new shoots of hedysarum and horsetail (*Equisetum arvense*), before switching to berries for the hyperphagic period of relative food abundance in late July when they are at their peak (Nagy et al., 1983; Edwards et al., 2013).

To test the roam-to-mate hypothesis we examined variability in range use of grizzly bears during mating and post-mating periods. The mating period for grizzly bears lasts about 2.5 months (Schwartz et al., 2003; Spady et al., 2007), beginning shortly after den-emergence in the spring for our study area (Nagy et al., 1983) and we predicted that range use by solitary males and females would decrease from the mating period to the post-mating period as the behavioural focus switches from mating to foraging. Encounter theory suggests that where the density of targets is low, the chance of encountering a receptive mate is increased by moving with more linear persistence and thus covering more ground (Gurarie and Ovaskainen, 2013). The bears in this peripheral population occur at low density, and we predicted that the median daily displacement and directional persistence would be greater and less tortuous during the mating period than in the post-mating period.

For non-oestrous females, movements may be encumbered by younger, less mobile offspring, therefore, we predicted that range size and daily displacement of females with cubs-of-the-year would increase from the mating to the post-mating season as young become more mobile. However, because foraging and offspring security remain the priority in both periods, we predicted that linearity of movements would remain the same. Offspring survival increases following the first year of life, with the majority of deaths occurring by infanticidal males during the mating period (Swenson et al., 1997; Steyaert et al., 2012). Because the threat to offspring is reduced for older cubs, range size and displacement for females with cubs ≥1 year old should remain constant between mating and post-mating periods. Danger to offspring from infanticidal male bears remains a threat (Swenson et al., 1997), which could reduce movements by mothers, but finding adequate food for the family is necessary and may require greater movements. Because foraging and not mate searching is the priority for females with cubs ≥1 year old, linearity of movement should be the same across both mating and post-mating.

2. Methods

2.1. Study area

This study was conducted in 2003–2006 in the Mackenzie Delta region, Northwest Territories, in Canada's western Arctic and encompassed approximately 23,000 km^2 (Fig. 1). Climatic conditions in the Arctic are characteristically extreme, primary productivity is low, seasonality high, and with less climatic predictability habitat quality is marginal (Ferguson and McLoughlin, 2000). Water is a dominant feature on the landscape with numerous lakes and rivers, and the Mackenzie Delta in the west (MacKay, 1963; Edwards et al., 2013). Other geographical features include landforms that transition from coastal ecosystems along the Beaufort Sea in the north, to tundra and boreal forest dominated by spruce (*Picea glauca* and *Picea mariana*), and larch (*Larix laricina*) in the south (MacKay, 1963). Dense stands of willow (*Salix* spp.)