Biological Conservation 172 (2014) 190–199

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Thresholds in the capacity of boreal caribou to cope with cumulative disturbances: Evidence from space use patterns

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ARTICLE INFO

Article history:
Received 2 October 2013
Received in revised form 27 February 2014
Accepted 2 March 2014

Keywords:
Boreal caribou
Canadian boreal forest
Disturbance threshold
Forest harvesting
Movement
Roads
Space use

ABSTRACT

Boreal caribou, an ecotype of woodland caribou (*Rangifer tarandus caribou*), are closely associated with the boreal forest, which has been significantly modified by anthropogenic activities over the last century. The species' response to disturbances has been extensively researched – a reflection of the importance of habitat loss in the decline of boreal caribou. We investigated how female caribou cope with disturbances using GPS telemetry data collected on 48 females in a highly managed landscape in Québec, Canada, between 2004 and 2010, using home-range size as a proxy of caribou space use behaviour. Individuals were found to expand their home ranges as the amount of disturbances in their habitat increased, up to a point where further increase caused home range contraction. The density of major roads and the proportion of clearcuts had an important impact on space use throughout the whole year, but the impact of roads was particularly important during calving, summer and rut, while the impact of clearcuts prevailed in spring, early and late winter. Furthermore, we found that a more convoluted shape of cutblocks amplified the effect of clearcuts on caribou space use. These non-linear responses suggest that there is a limit to the adaptability of caribou in coping with anthropogenic disturbances. Although home range expansion could affect survival through the use of unknown habitats, individuals confined in smaller home ranges could be forced into an ecological trap and be more easily detected by predators, making current disturbance levels in the boreal forest and their cumulative amount in the landscape a major issue for the conservation of these boreal caribou populations.

1. Introduction

Human-induced disturbances play a major role in modifying many ecosystems worldwide and the resulting habitat loss, alteration and fragmentation are widely acknowledged as the most important factors impacting wildlife (Venter et al., 2006; Fischer and Lindenmayer, 2007). For instance, in the North-American boreal forest, anthropogenic disturbances have superseded natural disturbances over the last century (Cyr et al., 2009). Forest harvesting, the main anthropogenic activity in the boreal forest, is known to modify the natural age structure of forest stands, greatly alter the quality of natural habitats and decrease overall landscape connectivity for numerous species associated with old-seral forest stands (Burton et al., 1999). Harvesting also results in an increasingly dense road network (Forman et al., 2003), further fragmenting the landscape and impeding many species' movements (Dyer et al., 2002).

Habitat loss (i.e., an overall decrease in a particular habitat's representation in the landscape associated with the increase of other land-cover types; St-Laurent et al., 2009) and habitat fragmentation (i.e., breaking apart of habitats, implying a decrease in habitat connectivity; With et al., 1997; Fahrig, 2003) are both species-specific and their impacts can differ in direction and intensity depending on a species' habitat requirements (Fischer and Lindenmayer, 2007; Smith et al., 2009). At the population level, habitat alterations can lead to the fragmentation and isolation of populations into smaller and more susceptible subpopulations more likely affected by stochasticity and natural stress factors (Fahrig, 2003). At the individual level, disturbances can

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http://dx.doi.org/10.1016/j.biocon.2014.03.002
0006-3207/

modify physiology and behaviour of organisms through a permanent or temporary loss of access to suitable habitats (Eigenbrod et al., 2008). Moreover, a loss of potentially suitable habitats may arise as the impacts of disturbances extend beyond the source of the disturbance (Dyer et al., 2001). Impacts of anthropogenic disturbances can therefore be severe (e.g., Vistnes and Nellemann, 2008), especially for far-ranging species whose movements encompass areas larger than the patches of which the forest mosaic is generally composed (Ims et al., 1993). For such species, changes in habitat-use patterns in response to disturbances may result in important repercussions at multiple biological scales and ultimately affect population viability (Ims et al., 1993; Seip et al., 2007; Johnson and St-Laurent, 2011). Studying behavioural responses to disturbances then appear as a key strategy to ensure species' conservation (Sutherland, 1998; Tuomainen and Candolin, 2011).

Individuals exhibit different space-use patterns in response to varying degrees of disturbance (e.g., Redpath, 1995; Andreassen and Ims, 1998) depending on the amount of suitable habitat left after alteration, landscape connectivity and the propensity of individuals to display range fidelity behaviour (Frair et al., 2008; Faille et al., 2010). For far-ranging species, it is likely that individuals will make more extensive movements and thus expand their home range as disturbance levels increase to access enough suitable resources and compensate for functional habitat loss, relative to the hostility of the matrix, inter-fragment distances and the presence of habitat corridors (Andreassen et al., 1998; Selonen et al., 2001). When movements are hindered by disturbances, however, individuals may become constrained to smaller areas and consequently constrict their home ranges, potentially increasing spatio-temporal overlap with conspecifics and predators (Ims et al., 1993). Numerous wildlife species have been reported to respond in a non-linear manner to disturbances (e.g., Forman et al., 2003; Frair et al., 2008). Therefore, it seems reasonable to expect a non-linear response from individuals from the same population yet occupying different landscape contexts. Primary home-range expansion followed by home-range contraction as the amount of disturbance passes some threshold compromising naturally occurring space-use patterns could thus be expected. We hereafter define a threshold as the disturbance level over which a sudden or gradual shift in wildlife behavioural response is observed and that result in an alternative behavioural state (With and Crist, 1995; Betts and Villard, 2009; Johnson, 2013).

Our objective was to assess the influence of anthropogenic and natural disturbances on space-use behaviour. As a biological model, we used boreal caribou (hereafter referred to as caribou), an ecotype of the woodland caribou subspecies (*Rangifer tarandus caribou*), threatened and declining throughout much of its range (Vors and Boyce, 2009; Environment Canada, 2011). Traditionally evolving under a natural-disturbance regime, the distribution of caribou contracted over the last century and remnant populations now inhabit areas under intensive forest-harvesting activities (Schaefer, 2003; St-Laurent and Dussault, 2012). Logging increases the conversion rate of old-growth coniferous forests, the preferred habitat of caribou, into early-seral stages, which can lead to functional habitat loss that can last up to 60 years (Courtois et al., 2007). Conversely, the resulting early successional forests favour an increase in the distribution and abundance of moose (*Alces alces*), gray wolf (*Canis lupus*) and black bear (*Ursus americanus*; Dussault et al., 2005; Brodeur et al., 2008; Houle et al., 2010). Particularly vulnerable to predation, this change likely jeopardizes caribou's anti-predator strategy (i.e., spacing out; see Bergerud and Page, 1987) by increasing their encounter rates with predators (i.e., apparent competition with moose; Bergerud and Elliot, 1986; Seip, 1992). The caribou thus appears like an ideal candidate to study the impacts of disturbances on wildlife space use at a large scale due to its close association with undisturbed boreal forest (Hins et al., 2009), its known sensitivity to human development (Fortin et al., 2008) and its historical adaptability to natural disturbances (Gustine and Parker, 2008).

We used home-range size as a proxy of caribou space use behaviour (i.e., a synthesis of movements; Andreassen et al., 1998). We predicted that (1) caribou would display a positive relationship between home range size and levels of disturbances in their habitat (i.e., clearcuts, roads and natural disturbances); above some disturbance thresholds, this trend would be reversed and become negative. We also expected that (2) clearcuts associated with a higher degree of fragmentation (measured as edge-to-surface ratio) would have a higher impact than those resulting in less overall fragmentation and that (3) the impact of anthropogenic features would be greater than that of natural disturbances. Finally, we predicted that (4) due to seasonal variations in biological states and environmental conditions, the relative importance of disturbances would differ depending on the period of the year.

2. Material and methods

2.1. Ethics statement

Boreal caribou is recognised as threatened throughout North-America (COSEWIC, 2011), a status that justifies the emergency of understanding more clearly the mechanisms linking anthropogenic disturbances to the species decline. We then captured, collared and released 48 individuals to assess their behavioural responses to disturbances. Our study was carried out in strict accordance with the recommendations of the Canadian Council on Animal Care, and both captures and manipulations of study animals were approved by the Animal Welfare Committee of the Université du Québec à Rimouski (certificate #36-08-67). Captures were conducted on public lands, under the supervision of the Québec government (i.e. Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs, hereafter MDDEFP), so no specific permissions were required.

2.2. Study area

The study area is located north of Lac Saint-Jean and Saguenay River in Québec, Canada, and covers approximately 31,000 km^2 (Fig. 1). The area is centered on Piraube Lake in the north (49°42′–51°00′N, 71°10′–72°09′W) and Portneuf Lake in the south (48°21′–49°45′N, 69°51′–71°12′W), two regions that are distinguished by their dominant forest cover. The southern part of the study area is dominated by black spruce (*Picea mariana*) with balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and jackpine (*Pinus banksiana*) while the northern region is dominated by old-growth coniferous forest and open forest with black spruce, balsam fir and jackpine stands. Weather conditions throughout the study area are comparable, with mean annual temperatures between −2.5 and 0.0 °C (extremes ranging from −38 to 33 °C) and mean annual precipitation between 1000 and 1300 mm, of which 30–35% falls as snow (Robitaille and Saucier, 1998). Moose, gray wolf and black bear compose the other large mammal species found in the study area. Forest harvesting is the main anthropogenic disturbance, with a logging history of ~40 years for the southern and ~15 years for the northern regions. Prior to data collection, the southern and northern regions were disturbed by anthropogenic features on ~35% and ~4% of their surface, respectively (Fig. 1). Being significantly less impacted by harvesting, the disturbance dynamic in the northern region is mainly driven by natural disturbances (i.e., major fires, windthrows and insect outbreaks).