



Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate

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ARTICLE INFO

Article history:

Received 10 July 2017

Initial acceptance 4 September 2017

Final acceptance 19 February 2018

MS. number: A17-00554R

Keywords:

fission dynamics
landscape heterogeneity
landscape knowledge
Rangifer
social bonds

Collective movement decisions are often based on personal and conspecific knowledge. In fission–fusion animal societies, individuals rarely have the same level of information about their environment, with knowledge being a reflection of past individual and collective decisions. Knowledge of the environment is particularly essential in heterogeneous landscapes, where resources may vary in space and time. Indeed, landscape heterogeneity, a product of the quantity and configuration of resources as well as predators and competitors, is the basis of both individual and collective movement decisions. We assessed individual movement decisions of an alpine ungulate as a function of landscape knowledge and landscape heterogeneity. We hypothesized that individuals would base their decisions on previous information in areas they know well, especially in highly heterogeneous landscapes. These individual decisions would have consequences for the collective movement decisions of groups. To test this hypothesis, we used GPS collars to monitor the movements of ~45% of the individuals ($N = 28$) of a small population of woodland caribou, *Rangifer tarandus caribou*, between 2013 and 2016. We assessed the fission probability of caribou dyads ($N = 3681$, from 172 dyad combinations) in relation to landscape knowledge, landscape heterogeneity and social bonds between dyad members. The probability of group fission was influenced by the interaction between the variables describing landscape knowledge of dyadic members and social bonds. The probability of group fission and the influence of habitat or social bonds on fission probability increased with landscape knowledge. In familiar landscapes, individuals were more likely to stay with conspecifics if they shared a strong social bond or if they were in preferential habitat. Such fine adjustments in movement and social decisions demonstrated the importance of the information held by conspecifics when occupying unfamiliar areas. By staying with conspecifics, individuals could gain access to high-quality resources without the energetic cost of locating such resources.

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Living in a group can confer advantages, as communication among conspecifics lowers predation risk (Roberts, 1996) and increases the efficiency of resource detection and acquisition (Creel & Creel, 1995). However, group living also incurs costs to the individual animal, such as transmission of diseases and parasites (Côté & Poulinb, 1995; but see Mooring & Hart, 1992), reduced reproductive opportunities and increased competition for resources (Lian, Zhang, Cao, Su, & Thirgood, 2007; Molvar & Bowyer, 1994). These costs include aggression that leads to reduced fitness,

morbidity or mortality (Beauchamp, 2014; Krause & Ruxton, 2002; Ward & Webster, 2016). The advantages and disadvantages of group living can also be dynamic. Grouping with conspecifics may benefit the individual only during certain seasons or under specific environmental conditions or interspecific challenges, such as the presence of predators or when searching for resources across highly heterogeneous landscapes (Creel & Winnie, 2005; Fortin et al., 2009).

The ecological variability in the benefits and costs of staying in a group drives fission–fusion dynamics (Kerth, Ebert, & Schmidtke, 2006; Merkle, Sigaud, & Fortin, 2015). Each individual builds its own decision-making rules based on its intrinsic characteristics (e.g. landscape knowledge, habitat preference, nutritional state and reproductive demand), often creating groups of similar individuals

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(e.g. age class, sex and family bond) (Conradt, 1998; Ruckstuhl, 1998, 1999; Sueur et al., 2011). Consequently, similar individuals have stronger social bonds (Bercovitch & Berry, 2013; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Djaković et al., 2012) and are more likely to maintain group structure (Carter et al., 2013; Merkle et al., 2015).

Groups composed of familiar individuals are more stable, with group behaviour offering numerous advantages: cooperative anti-predator behaviour (Chivers, Brown, & Smith, 1995), reduction in competition (Utne-Palm & Hart, 2000) and greater reproductive opportunity (Höjesjö, Johnsson, Petersson, & Järvi, 1998). Familiar individuals also learn more easily from each other (Figueroa, Solà-Oriol, Manteca, & Pérez, 2013; Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996). In domestic pigs, *Sus domestica*, for example, individuals show less neophobia towards a new food item if a familiar individual recently experienced the same item (Figueroa et al., 2013). This social learning from familiar individuals could be advantageous in heterogeneous landscapes.

Landscape heterogeneity is closely linked to the distribution of resources and predators and is known to have direct and indirect effects on the decision making of species exhibiting fission–fusion dynamics (Fortin et al., 2009; Kelley, Morrell, Inskip, Krause, & Croft, 2011; Smith, Kolowski, Graham, Dawes, & Holekamp, 2008). In a relatively homogeneous landscape, there are fewer reasons for interindividual variation in decision making. Thus, Sueur et al. (2011) hypothesized that groups should be more cohesive in such landscapes. Alternatively, in a very heterogeneous landscape, interindividual variation in decision making should be common (Sueur et al., 2011).

When minimizing predation risk and maximizing nutritional gain, animals will often base their decisions on past experiences (Merkle, Fortin, & Morales, 2014; Valeix et al., 2009). Beyond leadership and dominance level, individual and conspecific information are both known to have important impacts on collective decisions (Couzin et al., 2011; Merkle et al., 2015). For group dynamics of bison, *Bison bison*, Merkle et al. (2015) found that landscape knowledge, whether or not the area was visited by the individual in the last year, had great influence on the decision to follow the group or not. Greater knowledge of the landscape induced a higher probability of leaving the group. Uninformed individuals tend to increase group stability by reaching a consensus more easily (Couzin et al., 2011). Individuals, however, are rarely completely informed or uninformed of location, quantity and quality of resources available locally. It is currently unclear how group dynamics change from very unfamiliar places to frequently used patches, especially in heterogeneous landscapes.

Our objective was to assess how familiarity among conspecifics, landscape heterogeneity and landscape knowledge of woodland caribou, *Rangifer tarandus caribou*, as measured by the intensity of use of an area by an individual in the past, influenced the fission rate of groups of animals. In our study, group fission was defined as the splitting of dyads composed of two collared caribou. We hypothesized that individuals transiting areas they know well should find high-quality resource patches without relying on conspecific information. This knowledge of local resources should allow individuals to make their own choices in regards to habitat and group membership. As the availability of conspecific information is closely linked to the number of individuals in a group, the importance of landscape knowledge could also be influenced by group size. Increasing landscape heterogeneity should increase the fission rate, at least at a low or medium level of heterogeneity, as conflicts of interests between dyadic members is positively correlated to landscape heterogeneity. We also hypothesized that fission probability was influenced by familiarity among conspecifics, with groups of familiar individuals having a lower fission probability.

We used the Atlantic-Gaspésie caribou population as a biological model to test our hypothesis. *Rangifer* are social animals that are known to demonstrate fission–fusion group dynamics (Body, Weladji, Holand, & Nieminen, 2015). This population is small, allowing for the monitoring of a high proportion of the individuals with GPS telemetry devices (Lesmerises, Johnson, & St-Laurent, 2017). Furthermore, this population is found across a relatively heterogeneous landscape composed of forest and alpine ecosystems.

METHODS

Study Area

The study area covered the eastern part of the range of the Gaspésie caribou population, corresponding approximately to the limit of the Gaspésie National Park (48°50'N, 66°00'W). Much of the distribution of caribou is across high-elevation alpine habitats, which are dominated by Mount Jacques-Cartier (1268 m). Three ecological zones span the elevational gradient of the study area. The highest elevation zone (>1050 m) is composed of alpine tundra, a mat of lichens, mosses and graminoids along bare rocks and ericaceous shrubs. The subalpine forest (900–1050 m) is a transition zone where tree height decreases with elevation, forming a krummholz belt before becoming alpine tundra. Finally, at the lowest elevations, the montane zone consists of closed forest composed of balsam fir, *Abies balsamea*, white spruce, *Picea glauca*, black spruce, *Picea mariana*, and birch, *Betula* sp.

Caribou are found between 200 and 1260 m, but typically occur above 700 m (Mosnier, Ouellet, Sirois, & Fournier, 2003; Ouellet, Ferron, & Sirois, 1996). Gaspésie caribou are subdivided into three subpopulations, namely Albert ($N = \sim 20$ individuals), McGerrigle ($N = \sim 40$ individuals) and Logan ($N = \sim 15$ individuals) (Morin, 2017). Moose, *Alces americanus*, black bears, *Ursus americanus*, coyotes, *Canis latrans*, and a few white-tailed deer, *Odocoileus virginianus*, are also found within Gaspésie National Park. Wolf, *Canis lupus*, was extirpated from the south shore of the St Lawrence River since the mid-1800s.

Caribou Locations

We used GPS locations of Gaspésie caribou collected via a telemetry monitoring programme that took place between 2013 and 2016. In total, 43 adult caribou ($N = 17$ males, 26 females), proportionally distributed among the three subpopulations (i.e. $N = 28$ in the McGerrigle, $N = 6$ in the Albert, $N = 9$ in the Logan subpopulations), were captured, fitted with GPS-Argos collars and followed for 2.5 years (see Lesmerises et al., 2017, for more details). For the subsequent analyses, we kept only location data from the 28 individuals from the McGerrigle subpopulation as the number of individuals monitored in the two other subpopulations was insufficient to assess group dynamics.

Collars were programmed to acquire locations every 2 h (model TGW-4680-3, Telonics Inc., Mesa, AZ, U.S.A.) or every 3 h (model TGW-4680, Telonics Inc.) and to transfer relocations from the past week via an Argos link every 4 days. To limit the potential negative impacts of helicopter activity, and as recommended by the Animal Welfare Committee (Université du Québec à Rimouski (UQAR) certificate no. CPA-52-13-112; Ministère des Forêts, de la Faune et des Parcs (hereafter MFFP) certificate no. CPA FAUNE 13-08), captures were divided into two sessions of 22 and 21 animals each, conducted in early winter 2013 and 2014, respectively. Each collar had a drop-off mechanism (CR-2A, Telonics Inc.) programmed to release the collar on 1 June or 15 June 2016.

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