Interisland movements of woodland caribou in Newfoundland

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## Introduction

Caribou (*Rangifer tarandus*) are exceptional swimmers. Ample evidence exists that caribou swim in streams, rivers, and lakes during migration (Leblond et al. 2016) to avoid predators (Bergerud 1985) and access islands during calving (Bergerud et al. 1990). Even for adept swimmers like caribou, the energetic expenditure of swimming for quadrupedal mammals is significantly higher than walking or running (Fish 1993), while drowning is also possible (Miller & Gunn 1985). Despite a large number of coastal and island caribou herds, only a handful of examples have documented caribou swimming in the ocean (Table 1).

The Fogo Island archipelago, off the coast of Newfoundland, Canada (49°N, 54°W), is home to approximately 300 woodland caribou. During routine fieldwork on May 30, 2017, we observed an unmarked adult male caribou swim between Perry and Eastern Indian Islands (Figure 1), a swim of at least 470 m which took ~9 minutes (~52 m per minute). This observation prompted us to investigate the subset of GPS radio-collared caribou in the population (n = 29 adult females). Using these remotely sensed relocations, we determined that this observation was not unique and that several individuals engaged in this behaviour (details below).

Fogo Island is the largest island in the archipelago (237.71 km2), but there are at least three other large islands: Western Indian (77.6 km2), Eastern Indian (38.7 km2) and Change (XX km2) Islands, as well as numerous smaller islands, including Blundon’s (1.18 km2), North Long (1.01 km2), South Long (0.48 km2), Kate’s (1.64 km2), and Brother’s (1.59 km2) Islands (see Figure 1). Habitats are similar across the archipelago, consisting largely of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*) as well as bogs, lakes, lichen and rocky barrens.

Caribou were introduced to Fogo Island (n = 26 animals between 1964–67) and Change Island (n = 5 animals in 1964) from the main Island of Newfoundland as part of a series of translocations and introductions throughout the province (Bergerud & Mercer 1989). Since 2016 we have been studying the Fogo Island caribou herd (Bonar et al. 2017; Bonar et al. 2018; Peignier et al. 2019). To date, we have fitted 29 adult female caribou with GPS collars (1240g, GPS 4400M; Lotek Wireless Inc., Newmarket, Ontario, Canada), which were programmed to collect relocation fixes every 2 hours (see Bonar et al. 2018 for details). We used GPS locations from these individuals to investigate oceanic swimming events.

We identified swimming events as two consecutive GPS locations from an individual on different islands. This region typically experiences pack ice during the winter, so that caribou may be able to travel between islands by walking over the ice. We restricted our GPS data to the ice-free period of the year (April 1 - November 25) to avoid this possibility. Using these criteria, we identified three adult female caribou that collectively engaged in 86 swimming events (Fig 1??).

Caribou may swim between islands in the ocean for similar reasons that drive caribou swimming in freshwater (Leblond et al. 2016). We present two such explanations for these swimming events, forage limitation (Miller 2002) and predator avoidance (Jeffery et al. 2007), and discuss why these swimming events appear to be relatively commonplace for only a small subset of the population.

## Forage limitation

Forage limitation and over-grazing is a major concern for caribou populations (Schaefer et al. 2016; Zamin et al. 2017) and could explain movement between islands. Conspecific competition for resources driven by reduced foraging opportunities can decrease reproductive success of adult females (Schaefer et al. 2016). Forage scarcity has been proposed as a potential reason for caribou moving between arctic islands on the sea-ice in winter (Miller et al. 1977). For very small islands, over-grazing by newly arrived caribou may rapidly deplete forage (Bergerud et al. 1990). Without sea ice, movement from the mainland to an island, or between islands, requires caribou to assess the trade-off associated with swimming.

This trade-off can be understood as density-dependent habitat selection governed by the Ideal Free Distribution (Morris 1987; Bradbury et al. 2015). Ideal Free Distribution theory predicts a fitness equilibrium: when the density in a given habitat patch has exceeded the optimum for fitness within that patch, animals should relocate and settle new habitat patches, so that fitness is equal across all patches (Bradbury et al. 2015). Islands act as discrete habitat patches in this case, but the costs associated with swimming create a trade-off when moving between patches. For caribou in the Fogo Island archipelago, the role of forage limitation in animal habitat selection patterns and movement remains unknown, but swimming between islands may in part be explained by forage limitation and conspecific competition.

## Predator avoidance

Predator avoidance could also contribute to swimming behaviour of caribou (Miller 2002). During calving, female caribou are known to swim to small islands in freshwater lakes give birth, or with their calves after birth, to avoid predation (Bergerud & Page 1987). The use of shoreline habitat in summer is considered an effective anti-predator calving strategy by allowing for swimming to islands or peninsulas as a predation avoidance flight response (Bergerud et al. 1990). The use of water, and by association occasionally swimming, is therefore part of the fine-scale interactions between caribou and their predators and the use of islands appears to be an effective anti-predator strategy.

Historic predators of caribou such as wolves (*Canis lupus*) and black bears (*Ursus americanus*) are not present in the Fogo Island archipelago; coyotes (*Canis latrans*) are the top predator in this region. Predation by coyotes on adult caribou is relatively rare (ref?), so the potential predator effect on caribou swimming behaviour is likely to be a flight response to non-lethal encounters. Calves are susceptible to coyotes, particularly young calves, but the energetic costs to oceanic swimming are likely to be far greater for small calves.

## Individual variation

Three of 29 GPS-collared female caribou swam between islands in the Fogo archipelago. These swimming events were relatively frequent, on average occuring once every 24 days within our date range. However, we identified zero swimming events for the other 26 collared females. It remains unclear why this behaviour is seemingly common among 10% of our marked population, while 90% never engaged in it. Our initial direct observation of swimming was an adult male, but as we only have GPS data for females, we are unable to make conclusions on the prevalence of this behaviour among male caribou. It is theoretically possible that these other females moved rapidly back and forth between islands within the 2 hour fix rate of our GPS collars, which we would be unable to detect. We consider this highly unlikely given the range of residency times for caribou on any given island (min - max: XX - XX).

The two hypotheses presented above are generally thought to apply uniformly across populations, but individual caribou could evaluate the costs and benefits of swimming to another island differently. Potentially those three females, compared to the other 26, considered swimming less costly or perceived competition or predation to be of greater concern. The individual attributes that might influence how animals vary in their assessments of these trade-offs are unknown, and potential predictors such as age or personality traits are unknown for these caribou.

## Summary and conclusion

For several decades after their introduction to Fogo Island, the caribou population did not exceed ~100 individuals (Bergerud & Mercer 1989; Newfoundland and Labrador Wildlife Division, unpublished data). During the 1990s, population density reached 300 animals and anecdotal evidence suggests that [only then???] caribou began to occupy other islands in the archipelago. We surmise that as competition among conspecifics increased along with population size, density-dependent habitat selection resulted in expansion of the population to nearby islands. Following Ideal Free Distribution theory, caribou should swim to new islands when the average fitness of individuals on the starting island exceeds the density-fitness equilibrium (Morris 1987). While this is an ultimate explanation to a series of proximate observations, it is possible for density-dependent habitat selection to operate at such a fine-scale (Webber & Vander Wal 2018). Evidence from the Sable Island horse (Equus ferus caballus) system corroborates this hypothesis (van Beest et al. 2014). For horses, selection for high quality habitat was strongest at low population densities, but individuals tended to settle in lower quality habitats as population density increased, following Ideal Free Distribution theory (van Beest et al. 2014). Predator avoidance can also contribute to caribou swimming behaviour, but in this situation it seems a less likely explanation given predation is primarily a concern for young calves, which are the least likely to engage in this costly behaviour.

Our observations add to the evidence that caribou can, and occasionally do, swim in the ocean (Table 1). While past observations (e.g. Miller 1995, 2002; Jeffery et al. 2007; Ricca et al. 2012) have noted the exceptional nature of caribou swimming in the ocean, we suggest that this behaviour is likely more common than previously thought for caribou living on oceanic islands. We posit forage limitation and the associated density-dependent habitat selection is an ultimate explanation for why caribou swimming in the ocean, with predator avoidance as a potential proximate explanation. Although our inference is limited to observations, our observations suggest that islands represent discrete foraging patches for terrestrial animals that could influence fitness via increased foraging opportunities and safety from predators. We also suggest that individuals vary in their evaluation of costs and benefits of movement between these habitat patches.

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