Interisland movements of woodland caribou in Newfoundland

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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). Swimming for quadrupedal terrestrial mammals can be thought of as a set of trade-offs. Costs include high energy expenditure and risk of drowning. Specifically, even though caribou are adept swimmers, the energetic expenditure associated with swimming for quadrupedal mammals is significantly higher than walking or running (Fish 1993), whiledrowning 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).

Here, we describe the visual observation of an adult male caribou swimming between islands in the Fogo Island archipleago off the coast of Newfoundland, Canada. 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 query a large database of GPS radio-collared caribou. We identified 86 remotely sensed swimming events between XX islands from three individual caribou over a three-year period.

Caribou were introduced to Fogo Island (n = 26 animals introduced between 1964–67) and Change Island (n = 5 animals introduced in 1964) from the main Island of Newfoundland as part of a series of translocations and introductions throughout the province (Bergerud & Mercer 1989). While caribou populations are in decline throughout Canada (Festa-Bianchet et al. 2011), as well as in Newfoundland (Bastille-Rousseau et al. 2013), the Fogo Island herd has not declined to the same extent and currently consists of approximately 300 animals (Newfoundland and Labrador Wildlife Division, unpublished data). 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 XX 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 posit two potential mechanisms explaining the trade-offs associated with swimming in the North Atlantic Ocean: forage limitation and predator avoidance. For caribou living on small islands in the ocean, the same notions for why caribou swim in freshwater may also explain why caribou swim in the ocean (Leblond et al. 2016). Specifically, forage limitation (Miller 2002) and predator avoidance (Jeffery et al. 2007) have been proposed as potential explanations.

The Fogo Island archipelago is located in Newfoundland, Canada (49°N, 54°W), and comprises approximately ten islands. While Fogo Island is the largest island (237.71 km2), the archipelago includes at least three larger 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). All islands in the Fogo Island archipelago consist largely of coniferous and mixed forests of balsam fir (Abies balsamea), black spruce (Picea mariana), and white birch (Betula payrifera) as well as bogs, lakes, lichen and rocky barrens.

Forage limitation and over-grazing is a major issue for caribou populations (Schaefer et al. 2016; Zamin et al. 2017) and could explain movement between islands. Reduced access to foraging opportunities can result in higher conspecific competition for resources and lowered reproductive success for adult females (Schaefer et al. 2016). Forage scarcity has been proposed as a potential reason why caribou move 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 limit forage (Bergerud et al. 1990). Without sea ice, movement from the mainland to an island as well as between islands requires caribou to assess the trade-off associated with swimming.

The underlying mechanism driving forage limitation and the trade-off associated with swimming could be density-dependent habitat selection governed by the Ideal Free Distribution (Morris 1987; Bradbury et al. 2015). Ideal Free Distribution theory suggests that habitat selection is density-dependent and that variation in density between habitat patches leads to a fitness equilibrium (Bradbury et al. 2015). Fitness in a habitat patch depends on density where, ideally, the available resources on a habitat patch can sustain a specific number of individuals. In a hypothetical example, when density of a given habitat patch has exceeded the fitness equilibrium, animals are predicted to relocate and settle new habitat patches to reach equilibrium. Islands therefore represent distinct habitat patches with clear costs and benefits associated with swimming. For caribou in the Fogo Island archipelago, the role of forage limitation in animal habitat selection patterns and movement remains unknown, but it is possible that forage limitation and increased conspecific competition influences swimming between islands.

Predator avoidance could contribute to swimming behaviour of caribou (Miller 2002). Although caribou co-evolved with wolves (*Canis lupus*) throughout their range, wolves are extirpated from Newfoundland, including Fogo Island. Coyotes (*Canis latrans*) and black bears (*Ursus americanus*) are the primary predators of caribou in Newfoundland (Bastille-Rousseau et al. 2016). While predation by coyotes on adult female caribou does occur (ref?), it is relatively rare and the effect of predation on swimming behaviour is more likely the result of encounters which result in a flight response. For example, during calving, females may swim to small islands to give birth (Bergerud & Page 1987) or swim to islands in freshwater lakes with their calves to avoid predation.

Woodland caribou are also well known to disperse to remote locations, including islands, during calving (Bergerud & Page 1987; Cumming & Beange 1987). Moving to remote locations is a viable anti-predator strategy for caribou because it reduces detection and encounter rates by predators. For instance, the use of shoreline habitat in summer was deemed an effective anti-predator calving strategy because caribou avoided predators by using islands and peninsulas or swimming as a 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. Coyotes and black bears are responsible for the majority of mortalities for neonate caribou calves (Bastille-Rousseau et al. 2016), although predation can still occur after the calving period (Lewis & Mahoney 2014). However, on Fogo Island, coyotes are the only predator of caribou.

Caribou were introduced to Fogo Island in the 1960s and for several decades the 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 caribou began to occupy other islands in the archipelago. We surmise that, as density increased over time, competition among conspecifics and density-dependent habitat selection resulted in expansion of the population to nearby islands. Following density-dependent habitat selection theory, caribou should swim to new islands when the average fitness of individuals on the starting island exceeds the density-fitness equilibrium (Morris 1987). Animals would therefore be predicted to swim to new islands (i.e. settle new habitat patches) to reach a fitness equilibrium. 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 our suggestion that swimming among islands could be driven by density-dependent habitat selection (van Beest et al. 2014). For horses, selection for high quality habitat was highest when population density was low, but individuals tended to settle in lower quality habitats as population density increased, following Ideal Free Distribution theory (van Beest et al. 2014). Taken together, caribou may follow density-dependent habitat selection (Wittmer et al. 2007) and as population density increased, forage was depleted and competition increased.

Our observations add to the evidence that caribou can, and occaissionaly 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 unique 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 while predator avoidance is a 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.

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## Literature Cited

Bergerud, A. T. 1985. “Antipredator Strategies of Caribou: Dispersion Along Shorelines.” *Canadian Journal of Zoology* 63 (6). Canadian Science Publishing: 1324–9. <https://doi.org/10.1139/z85-199>.