Interisland movements of woodland caribou in Newfoundland

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**Abstract**

**Introduction**

Caribou 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). Despite a large number of coastal and island caribou herds, limited evidence exists suggesting that caribou swim in the ocean as readily as they swim in freshwater (see Table 1). A key exception is Peary caribou swimming up to 2.6km between the Queen Elizabeth Islands (Miller, 1995; Miller, 2002). 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.

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). Additionally, drowning is also possible (Miller & Gunn, 1985) although the proportion of caribou that die from drowning is unknown. Swimming between islands or from the mainland to nearby islands can be beneficial. Among the most important benefits include avoiding predators and seeking under-foraged areas.

Forage limitation could explain movement between islands. 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.

Woodland caribou are well known to disperse to remote locations, including islands, during calving (Bergerud and Page 1987; Cumming and 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.

Here, we describe visual observation of a single swimming event by a caribou in the North Atlantic Ocean. This observation led us to investigate the prevalence of swimming of GPS radio-collared caribou in the Fogo Island archipelago in Newfoundland, Canada. We posit two potential mechanisms explaining the trade-offs associated with swimming in the North Atlantic Ocean: forage limitation and the associated density-dependent habitat selection and predator avoidance.

**Materials and methods**

**Study area**

Our study area was the Fogo Island, Newfoundland, Canada (49°N, 54°W). Fogo Island is a small (237.71 km2) island off the northeastern coast of Newfoundland and has humid climate with year-round precipitation. While Fogo Island is the largest island in the area, 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.

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 and 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).

In Newfoundland, wolves (*Canis lupus*) are extirpated, so coyotes (*Canis latrans*) and black bears (*Ursus americanus*) are the primary predators of caribou (Bastille-Rousseau, Schaefer, et al. 2016). Coyotes and black bears are responsible for the majority of mortalities for neonate caribou calves (Bastille-Rousseau, Schaefer, et al. 2016), although predation can still occur after the calving period (Lewis and Mahoney 2014). However, on Fogo Island, coyotes are the only predator of caribou.

**Caribou observation and swimming**

We fitted 29 (n = 15 in 2016; n = 14 in 2017) adult female caribou on Fogo Island (n = 25) and Western Indian Island (n = 4) with GPS collars (1240g, GPS 4400M; Lotek Wireless Inc., Newmarket, Ontario, Canada). Collars were deployed on individual caribou for two years and collars were redeployed on the same individuals for the duration of our study. Collars were programmed to collect relocation fixes every 2 hours. All animal capture and handling procedures were consistent with the American Society of Mammologists guidelines (Sikes and Gannon 2011) and were approved by Memorial University Animal Use Protocol No. 20152067.

During routine fieldwork on May 30, 2017, we observed an unmarked male caribou swim between Perry and Eastern Indian Islands; a swim of at least 470m, which took ~9 minutes (~52m/minute). To determine the prevalence of ocean swimming for the Fogo Island caribou herd, we queried nearly 200,000 GPS relocations from 26/29 collared adult female caribou between April 2016 and March 2019. We determined all instances of individual caribou moving between islands. We restricted the GPS dataset to the ice-free months of the year (beginning of April to end of November) and we assumed caribou swam in the ocean between islands when consecutive relocation fixes, i.e., 2 hour intervals, were located on different islands. For each swimming event, we identified the origin island, the terminal island, and the duration of time spent on the terminal island before swimming again.

**Statistical analysis**

We were interested in determining what factors might influence how long an individual remains on the terminus island. We therefore used linear regressions and regressed the duration of time spent on the terminal island as a function of the Julian date of arrival to the island, size of the terminal island, and the paired identity of islands (i.e., Fogo to Perry or Perry to Eastern Indian). All statistical analyses were conducted in R.

**Discussion**

We observed one swimming event in the field as well as 86 remotely sensed swimming events from three individual caribou over a three-year period. In general, caribou swam more frequently to larger islands. Fogo, Perry, and Eastern Indian islands are the largest, and the most commonly occupied. While caribou often swim across streams, rivers, and lakes (Leblond et al. 2016), few observations exist of caribou swimming in the ocean (see Table 1). Of the existing or inferred observations of caribou swimming in the ocean, none appear to be as prolific as the number and frequency of swimming events we observed. We surmise that for caribou living on small islands, the primary drivers of swimming are likely related to forage limitation and predator avoidance.

*Forage limitation and density-dependence*

Forage limitation and over-grazing is a major issue for caribou populations (Schaefer et al. 2016; Zamin et al. 2017). Reduced access to foraging opportunities can result in higher conspecific competition for resources and lowered reproductive success for adult females (Schaefer et al. 2016). 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.

Caribou were introduced to Fogo Island in the 1960s and for several decades the population did not exceed ~100 individuals (Bergerud and 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 and 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.

*Predator avoidance*

Predator avoidance could contribute to swimming behaviour of caribou in our system as well as others (Miller 2002). Unlike elsewhere in the range of caribou, wolves are extirpated from Newfoundland, including Fogo Island. In Newfoundland, coyotes are the primary predator of caribou (Bastille-Rousseau et al. 2016a). While predation by coyotes on adult female caribou is possible, it is relatively rare on Fogo Island (Webber and Vander Wal unpublished data). Therefore, any effect of predation on swimming behaviour is likely related to fine-scale encounters between coyotes and caribou which result in caribou swimming as a flight response. Alternatively, during calving, females may swim to small islands to give birth (Bergerud and Page 1987) or swim to islands with a calf at heel to avoid predation. Swimming with a calf at heel has been observed for caribou in freshwater lakes on Fogo Island (Webber and Vander Wal unpublished data), so we anticipate it may also be possible in the ocean. We suggest future studies assess encounter rates among caribou and coyotes to determine what proportion of encounters result in swimming behaviour.

Our observations represent the most frequent and numerous swimming events for caribou in the ocean (for comparison see 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 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, we suggest that because swimming behaviour is so common in our system, that density-dependent habitat selection and predation are plausible mechanisms explaining swimming behaviour in Fogo Island caribou.

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**Table 1:** Summary of studies where caribou were either observed visually or using GPS collar data, or assumed to have swam in the ocean to access one or more islands based on prior surveys indicating no animals on a given island. Our study is the first to present visual evidence of this phenomenon.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Region | Islands | Number of individuals observed swimming | Minimum distance | Study |
| Queen Elizabeth Islands | Vanier, Massey, and Marc Islands | At least 19 (2 collared) | 1.6km and 2.5km | Miller (1995) |
| Queen Elizabeth Islands | Vanier, Massey, Marc, Cameron, and Alexander Islands | 2 collared | 1.6km to 4.0km | Miller (2002) |
| Labrador | George Island | Unknown (but caribou were observed on George Island) | 9km | Jeffrey et al. (2007) |
| Aleutian Islands | Adak and Kagalaska Islands | Unknown (but caribou were observed on Kagalaska Island) | 0.4km | Ricca et al. (2012) |
| Fogo Island | Fogo, Western Indian, Eastern Indian, Blundon’s, Brother’s, Kate’s, North Long, and South Long Islands | 3 collared individuals (86 swimming events);  1 visual observation of an uncollared individual | ~0.1–1km | This study. |

**Table 2:** Summary of 86 inter-island movements for three individual caribou collared between 2016 and 2019.

|  |  |  |  |
| --- | --- | --- | --- |
|  | **Individual** | | |
| **Movement** | **FO2016011** | **FO2017001** | **FO2017013** |
| W. Indian → E. Indian | 9 | 4 | – |
| E. Indian → W. Indian | 10 | 3 | – |
| W. Indian → Brother’s | 1 | 1 | 3 |
| Brother’s → W. Indian | 1 | 1 | 3 |
| W. Indian → Blundon’s | 2 | – | – |
| Blundon’s → E. Indian | 2 | – | – |
| W. Indian → Fogo | 1 | 6 | – |
| Fogo → W. Indian | 1 | 5 | 1 |
| North Long → W. Indian | 1 | 4 | 1 |
| W. Indian → North Long | 1 | 4 | 1 |
| South Long → W. Indian | – | – | 8 |
| W. Indian → South Long | – | – | 8 |
| Kate’s → W. Indian | – | – | 2 |
| W. Indian → Kate’s | – | – | 2 |
| Number of inter-island movements | 29 | 28 | 29 |

**Fig. 1:** Image of swimming caribou (*Rangifer tarandus*) between Perry Island and Eastern Indian Island taken on 30 May 2017.

**Fig. 2:** Map of Fogo Island archipelago.