Interisland movements and oceanic swimming of woodland caribou in Newfoundland

Quinn M.R. Webber1\*, Jack G. Hendrix1, Alec L. Robitaille2, Eric Vander Wal1,2

**Introduction**

Caribou (*Rangifer tarandus*) are exceptional swimmers. Ample evidence exists that caribou swim in streams, rivers, and lakes during migration (Leblond, St-Laurent, and Côté 2016), to avoid predators (Bergerud 1985), and access islands during calving (Bergerud, Ferguson, and Butler 1990). Even for adept swimmers like caribou, the energetic expenditure of swimming for quadrupedal mammals is significantly higher than walking or running , while drowning is also possible (Miller and Gunn 1985). Despite a large number of coastal and island caribou herds, only a handful of examples have documented caribou swimming in the ocean (e.g. Miller 1995, 2002; Jeffery, Otto, and Phillips 2007; Ricca et al. 2012).

The Fogo Island archipelago, off the coast of Newfoundland, Canada, is home to approximately 300 woodland caribou. During routine fieldwork on May 30, 2017, we observed an unmarked adult male caribou swim between Western 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 whether swimming behaviour was common among GPS radio-collared caribou in the population (n = 29 adult females; 1240g, GPS 4400M; Lotek Wireless Inc., Newmarket, Ontario, Canada). We identified swimming events as two consecutive GPS (2-hour relocation rates) locations from an individual occurred on different islands. Northeastern Newfoundland typically experiences pack ice during winter and caribou are known locally 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) and we identified three adult female caribou that collectively had 86 swimming events (Figure 2). In addition to our own visual and remotely sensed observations, residents of Fogo Island have also reported observing caribou swimming between islands on numerous occaisions.

In total, these 86 swimming events occured in month (n = Y), month (n = Y), and month (n = Y), while the remaining events were in month, month, and month (n = Y). On average, caribou swam between islands approximately ever 24 days, but some individuals swam up to XX times per week/month/whatever.

Caribou may swim between islands in the ocean for similar reasons that drive caribou swimming in freshwater (Leblond, St-Laurent, and Côté 2016). We present two explanations for these swimming events, forage limitation (Miller 2002) and predator avoidance (Jeffery, Otto, and Phillips 2007), and discuss why these swimming events appear to be relatively commonplace in the population.

**Forage limitation**

Forage limitation and over-grazing is a major concern for caribou populations (Schaefer et al. 2016) 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, Russell, and Gunn 1977). For very small islands, over-grazing by newly arrived caribou may rapidly deplete forage (Bergerud, Ferguson, and Butler 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, Vehrencamp, and Clifton 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, Vehrencamp, and Clifton 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 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 and give birth, or with their calves after birth, to avoid predation (Bergerud 1985). 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, Ferguson, and Butler 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, thus leaving coyotes (*Canis latrans*) as the top predator. Predation by coyotes on adult caribou is relatively rare (Bastille-Rousseau et al. 2016), so the potential effect of predators on caribou swimming behaviour is limited to non-consumptive effects associated with encounters and subsequent flight response. Adult females with calves at heel may be an exception because calves are highly susceptible to coyotes (Rayl et al. 2014), but the energetic costs for calves to swim in the ocean is likely far greater than adults. As one might expect, none of the 86 swimming events we observed occurred in the weeks after calves were born, suggesting swimming with in the ocean with a calf-at-heel is likely more risky than other predator avoidance behaviours.

**Individual variation**

In total, 3 of 29 collared female caribou swam between islands in the Fogo archipelago. These swimming events were relatively frequent, on average occuring once every 24 days during ice-free seasons. However, despite relatively frequent swimming events for these three individuals, we were unable to identify any swimming events for the other 26 collared females. It remains unclear why ocean swimming is relatively common among ~10% of our marked population, while the other 90% never swam. Of the three collared individuals, two were collared on Western Indian Island and the third was collared on Fogo Island. It is possible that individuals born on, or that live on, Eastern and Western Indian Island swim are more likely to swim between islands because inter-island distances are shorter than between Western Indian and Fogo Islands (Figure 2). Furthermore, it is unclear whether swimming is more common among males or females. Our initial observation was of an adult male, but our GPS data only includes females.

The forage limitation and predator avoidance hypotheses are generally thought to apply uniformly across populations, but individual caribou could evaluate the costs and benefits of swimming to another island differently. It is possible that some individuals, in our case ~10%, considered swimming less costly or that they perceived competition or predation more acutely than their conspecifics. Intrinsic life-history, physiological, or behavioural traits that might influence how animals vary in their assessments of swimming trade-offs remains unknown. Future work could assess the role of age, stress, or an individuals tendency to move potential predictors of swimming behaviour.

**Summary and conclusion**

For several decades after their introduction to Fogo Island, the caribou 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 [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, fine-scale density-dependent habitat selection is theoretically possible (Webber and Vander Wal 2018). Predator avoidance could also contribute to caribou swimming behaviour, but given the presumed low density of coyotes on Fogo Island and that predation primarily only affects young calves, we suspect predator risk is a possible, but less likely explanation for swimming.

Our observations add to the evidence that caribou can, and occasionally do, swim in the ocean (e.g. Miller 1995, 2002; Jeffery, Otto, and Phillips 2007; Ricca et al. 2012). Taken together, we suggest that swimming 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.

**Acknowledgements**

We thank M. Laforge, M. Bonar, C. Hart, and R. Huang for help in the field. Logistical support was provided by L. Bixby. We also thank members of the Newfoundland Wildlife Division including S. Moores, B. Adams, C. Doucet, W. Barney, and J. Neville for logistical support in the field as well as help with data data collection and management. We thank T. Bergerud and S. Mahoney for their vision in initiating much of the work on caribou in Newfoundland. Funding for this study was provided by the National Sciences and Engineering Research Council (QMRW, JGH, EVW). We respectfully acknowledge the territory in which data were collected and analyzed as the ancestral homelands of the Beothuk, and the island of Newfoundland as the ancestral homelands of the Mi’kmaq and Beothuk.



**Figure 1**: Image of swimming unmarled adult male caribou (*Rangifer tarandus*) from Western to Eastern Indian Island taken on 30 May 2017.

**Figure 2**: Map of the Fogo Island archipelago. 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. 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.

**Literature Cited**

Bastille-Rousseau, Guillaume, Nathaniel D Rayl, E Hance Ellington, James A Schaefer, Michael J L Peers, Matthew A Mumma, Shane P Mahoney, and Dennis L Murray. 2016. “Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey.” *Canadian Journal of Zoology* 94 (3): 191–98. <https://doi.org/10.1139/cjz-2015-0127>.

Bergerud, A. T. 1985. “Antipredator strategies of caribou: dispersion along shorelines.” *Canadian Journal of Zoology* 63 (6): 1324–9. <https://doi.org/10.1139/z85-199>.

Bergerud, A.T., R. Ferguson, and H.E. Butler. 1990. “Spring migration and dispersion of woodland caribou at calving.” *Animal Behaviour* 39: 360–68.

Bergerud, A.T., and W.E. Mercer. 1989. “Caribou Introductions in Eastern North America.” *Wildlife Society Bulletin* 17 (2): 111–20.

Bradbury, J.W., S.L. Vehrencamp, and K.E. Clifton. 2015. “The ideal free antelope: foraging dispersions.” *Behavioral Ecology* arv078: 1–11. <https://doi.org/10.1093/beheco/arv078>.

Jeffery, Rebecca A, Robert D Otto, and Frank R Phillips. 2007. “George’s Island, Labrador - A high-density predator-free refuge for a woodland caribou subpopulation?” *Rangifer*, no. 17: 51–56.

Leblond, Mathieu, Martin-Hugues St-Laurent, and Steeve D. Côté. 2016. “Caribou, water, and ice – fine-scale movements of a migratory arctic ungulate in the context of climate change.” *Movement Ecology*. Movement Ecology, 4:14. <https://doi.org/10.1186/s40462-016-0079-4>.

Miller, F.L. 1995. “Inter-island water crossings by peary caribou, south-central Queen Elizabeth Islands.” *Arctic* 48 (1): 8–12. <https://doi.org/10.14430/arctic1219>.

———. 2002. “Multi-Island Seasonal Home Range Use by Two Peary Caribou, Canadian High Arctic Islands, Nunavut, 1993-94.” *Arctic* 55 (2): 133–42.

Miller, F.L., and A. Gunn. 1985. “Observations of Barren-Ground Caribou Travelling on Thin Ice during Autumn Migration.” *Arctic* 39 (1): 85–88. <https://doi.org/10.14430/arctic2052>.

Miller, F.L., R.H. Russell, and A. Gunn. 1977. “Interisland movements of Peary caribou (<i>Rangifer tarandus pearyi</i>) on western Queen Elizabeth Islands, Arctic Canada.” *Canadian Journal of Zoology* 55 (6): 1029–37. <https://doi.org/10.1139/z77-131>.

Morris, D.W. 1987. “Tests of density-dependent habitat selection in a patchy environment.” *Ecological Monographs* 57 (4): 269–81.

Rayl, N.D., T.K. Fuller, J.F. Organ, J.E. McDonald, S.P. Mahoney, C. Soulliere, S.E. Gullage, et al. 2014. “Mapping the distribution of a prey resource: neonate caribou in Newfoundland.” *Journal of Mammalogy* 95 (2): 328–39. <https://doi.org/10.1644/13-MAMM-A-133.1>.

Ricca, Mark A., Floyd W. Weckerly, Adam Duarte, and Jeffrey C. Williams. 2012. “Range expansion of nonindigenous caribou in the Aleutian archipelago of Alaska.” *Biological Invasions* 14 (9): 1779–84. <https://doi.org/10.1007/s10530-012-0195-z>.

Schaefer, J.A., S.P. Mahoney, J.N. Weir, J.G. Luther, and C.E. Soulliere. 2016. “Decades of habitat use reveal food limitation of Newfoundland caribou.” *Journal of Mammalogy* 97 (2): 386–93. <https://doi.org/10.1093/jmammal/gyv184>.

Webber, Q.M.R., and E. Vander Wal. 2018. “An evolutionary framework outlining the integration of individual social and spatial ecology.” *Journal of Animal Ecology* 87: 113–27. <https://doi.org/10.1111/1365-2656.12773>.