Interisland movements and oceanic swimming of woodland caribou in Newfoundland

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

1Cognitive and Behavioural Ecology Interdisciplinary Program, Memorial University of Newfoundland 2Department of Biology, Memorial University of Newfoundland, Canada

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, and drowning is also possible (Miller and Gunn 1985). Despite the abundance of coastal and island caribou herds, only a handful of examples have documented caribou swimming in the ocean (e.g. Miller 1995, 2002, Jeffery et al. 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 distance 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). Using R version 3.6.1 (R Core Team 2019), we identified swimming events as two consecutive GPS locations (2-hour relocation rates) 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 - December 31) and we identified 12 adult female caribou that collectively had 127 swimming events over three years (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 occasions.

In total, 127 swimming events occurred throughout the ice-free season, with peaks in May and November. On average, caribou swam approximately 11 (range = 2-34) times per year and remained on each island for approximately 30 (range = 0-724) days before swimming again. Caribou may swim between islands in the ocean for similar reasons they swim in freshwater (Leblond et al. 2016). We propose that one such explanation, the forage limitation hypothesis, is a likely explanation for oceanic swimming for caribou that live on islands in the Fogo Island archipelago.

Forage limitation and over-grazing is a major concern for caribou populations: it can reduce female reproductive success (Schaefer et al. 2016) and thus could lead to movement between islands. 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). Caribou were introduced to Fogo Island (n = 26 animals between 1964–67) and Change Island (n = 5 animals in 1964) from Newfoundland as part of a series of translocations and introductions throughout the province (Bergerud & Mercer 1989). It is unknown when caribou began colonizing nearby islands, but given that some are small, over-grazing by newly arrived caribou may rapidly deplete forage on an annual cycle (Bergerud et al. 1990). Although unconfirmed, it is also possible that Fogo Island has experienced forage depletion since the introduction of caribou in the 1960s. More likely, however, is that fine-scale competition for foraging resources drives caribou to swim to new islands.

Movement 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 habitat selection patterns remains unknown, but swimming between islands may be at least partially governed by density-dependent habitat selection.

In total, 12 of 29 collared female caribou swam between islands in the Fogo Island archipelago. Only 3 of these 12 individuals had more than 10 swimming events, suggesting that for ~10% of collared individuals swim relatively frequently, on average occurring approximately every 15 days during ice-free seasons. We did not detect any swimming events for the remaining 17 individuals. It remains unclear whether these individuals do not swim, or whether swimming is rare, and thus undetected, for the majority of individuals. Overall, there appears to be three groups of individuals: those that swam often (n = 3, every ~15 days), those that swam occasionally (n = 9, every ~ 42 days), and those that never swam (n = 17). It is therefore possible that individuals vary in their tendency to swim. We are also unable to draw conclusions about the prevalence of swimming in the ocean by male caribou: our initial visual observation was of an adult male, but our GPS data only included adult females.

Oceanic swimming is relatively common among a minority of marked caribou. Of the three collared individuals that swam the most, two were collared on Western Indian Island and the third was collared on Fogo Island. Inter-island distances between Western and Eastern Indian Islands, and the smaller islands around them, are shorter than those between Fogo Island and others (Figure 2). It is possible that caribou display natal philopatry (e.g. Larue et al. 2018) to some of the smaller islands and thus are more likely to swim between them more frequently than animals that were born, or spend most of their time, on Fogo Island. The forage limitation hypothesis is 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 to be less costly or perceived competition or predation more acutely than their conspecifics.

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 it is unknown when caribou began to occupy other islands, although anecdotal evidence suggests it was during the 1990s. 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, our data suggest caribou only remain on smaller islands for a few days at a time, so the fitness equilibrium remains a theoretical construct. More likely, however, is that fine-scale competition, density-dependent habitat selection, and forage depletion drives individuals to periodically swim between islands. Given the presumed low density of coyotes on Fogo Island and the minimal risk they pose, predation risk does not appear to be a major driver of swimming.

Our observations add to the evidence that caribou can, and occasionally do, swim in the ocean (e.g. Miller 1995, 2002, Jeffery et al. 2007, Ricca et al. 2012). We suggest that swimming is likely more common than previously thought for caribou living on oceanic islands, and that forage limitation and the associated density-dependent habitat selection is an ultimate explanation for this phenomenon. Although our inference is limited to observations, islands appear to represent discrete foraging patches for terrestrial animals that can influence fitness via increased foraging opportunities. We also posit that individuals can vary in their evaluation of costs and benefits of movement between these habitat patches.

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

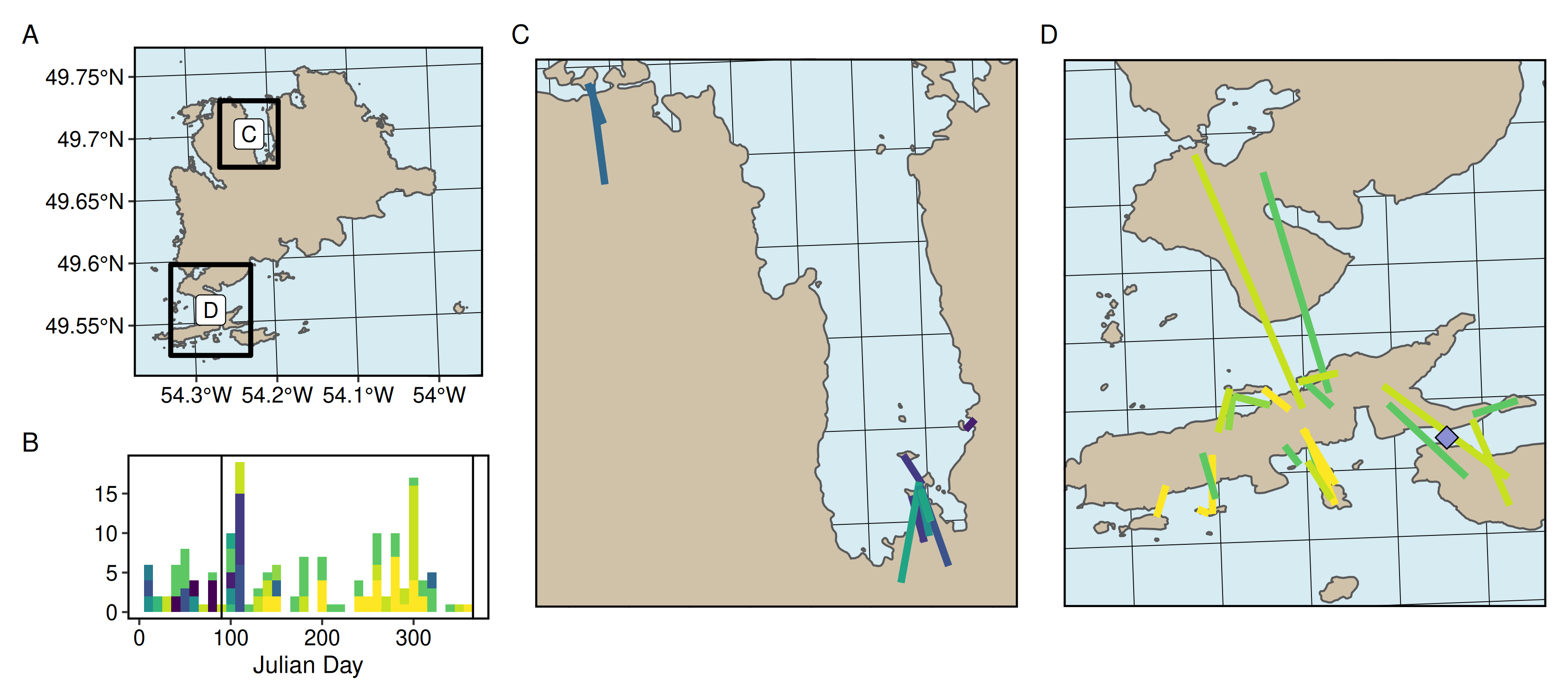


Figure 2: A) Map of the Fogo Island archipelago with swimming events between islands. B) Histogram displaying the distribution of swimming events throughout the year. Note, colours correspond to individual caribou. C) Inset of swimming events between small islands on the northern coast of Fogo island. D) Inset of swimming events between islands on the southern coast of Fogo island. Note, the grey diamond represents the location we observed an adult male caribou swimming (see Figure 1).

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