On the marginal value of swimming in woodland caribou

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Movement is costly. Even for adept swimmers like caribou (*Rangifer tarandus*), which have hollow hair shafts that aid in flotation, the energetic expenditure of swimming for terrestrial mammals is markedly higher than walking or running (Miller and Gunn 1985). The drivers that promote the decision to swim for terrestrial mammals, like caribou, are often related to the profitability of forage (Miller et al. 1977) and the risks of predation (Jeffery et al. 2007, Jordan et al. 2010). The Fogo Island archipelago, off the coast of Newfoundland, Canada, is home to approximately 300 woodland caribou, descendants of 26 individuals introduced from the Island of Newfoundland to Fogo Island between 1964–67 (Bergerud and Mercer 1989). During fieldwork on May 30, 2017, we observed an unmarked adult male caribou swim between two smaller islands (Figure 1) a distance of 470 m which took approximately 9 minutes. Given that swimming is energetically expensive, we ask how often do caribou swim between islands, how long do they occupy islands, and ultimately what motivates swimming? Here, we frame swimming and island residency as a model of patch use as described by the marginal value theorem (Charnov 1976) within the context of the forage limitation hypothesis. For caribou, the forage limitation hypothesis is the constraints on food availability associated with changes in abundance through time (Klein 1991, Schaefer et al. 2016). Here, we integrate our understanding of forage limitation in caribou populations by using island residency as a proxy for time in patch and island size as a proxy for energy intake in a patch (Figure 2).

Forage limitation and over-grazing is a concern for caribou populations and can lead to reduced female reproductive success (Klein 1991, 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). We submit that testing the marginal value theorem could improve our understanding of forage limitation. The marginal value theorem posits that animals will forage optimally by depleting the resources in a given patch (i.e. island) before moving to a new patch (Charnov 1976). Depletion of resources on small islands could therefore mirror patterns of over-grazing and forage limitation that occur for caribou herds at higher densities in Newfoundland (Schaefer et al. 2016) and elsewhere in their range (Klein 1991).

Our focus on forage is due to the limited presence of predators in our system. Throughout their range, wolves (*Canis lupus*) are the primary predator of caribou, although there are no wolves on the Island of Newfoundland, predation on adult caribou by coyotes (*Canis latrans*) does occur (Lewis and Mahoney 2014). Within the Fogo Island archipelago, coyotes exist at low density (Huang et al. 2021) and the probability of occurrence decreases on the smaller islands. The low density of predators throughout the archipelago is therefore an unlikely driver of swimming in our system, though predation may still influence swimming behaviour for caribou elsewhere in their range (e.g. Jeffery et al. 2007).

We identified swimming events as two consecutive GPS locations (2-hour relocation rates) on different islands. Newfoundland typically experiences pack ice in late winter and caribou may travel between islands by walking over the ice. We restricted our dataset between April 1 and December 31 to distinguish swimming from walking on ice. We calculated island residency as the duration of time, measured on 2-hour relocation rates, an individual caribou was observed on an island. Residency was therefore a proxy for when the benefits of foraging no longer exceeded the costs of swimming between islands. Our test of the marginal value theorem for the case of oceanic swimming by caribou is based on three assumptions: (1) resources are proportional to the size of each island; (2) caribou know approximate value of the resources on an island before they swim to and from that island; and (3) the cost of swimming to and from an island is less than the value of resources on that island when the caribou departs. Should these assumptions hold, we would predict a positive relationship where caribou depart smaller islands sooner than larger islands.

Swimming behavior was common among GPS radio-collared caribou in the population (n = 29, for collaring details see Peignier et al. 2019). We identified 127 swimming events over three years (Figure 2). In total, 13 of 29 collared female caribou swam among islands (Figure 2). Of the caribou that swam, caribou swam on average approximately 3 (range = 2-neventidMax) times per year and remained on each island for a median of 30 (range = 0-724) days before swimming again. We found that caribou residency increased proportionally with the size of the island, such that caribou spent less time on smaller islands and more time on larger islands, providing preliminary evidence for links between forage limitation and the marginal value theorem (Figure 2B).

The apparent relationship between island size and residency creates a framework to test our assumptions about the marginal value of resource use by caribou. We extend this framework to test prospective mechanisms that drive movement by caribou more generally, and swimming specifically. For example: 1) If caribou assess the relative value of resources in a patch, or on an island, we predict that residency should increase as the value of resources elsewhere becomes depressed. Longer relative residency might be an indicator of forage limitation and variation in residency could be a predictor of fitness costs and reduced reproductive success. 2) Density-dependent habitat selection (Fretwell and Lucas 1969, Morris 2003) could be invoked to explain what drives caribou to swim and expand their ranges to include smaller islands. As caribou density increases on larger islands, competition for resources increases such that animals may have similar fitness benefits by selecting islands that at lower density would not be as profitable. At high local density, individual residency may decrease, thus, increasing the frequency of swimming. As such, density-dependent habitat selection may represent an ultimate explanation for why caribou swim between islands. 3) Cognition is an important proximate mechanism that drives swimming behaviour. For example, caribou primarily rely on their sense of hearing and smell thus may not see or perceive an island when they enter the water to swim to it. How then do caribou know about the presence, and subsequently the value, of an island? Social and spatial cognition are almost certainly involved and tests of the role of cognition could help elucidate why caribou swim. For example, a novice individual may trust an experienced individual to lead them to a new island, a result which is driven by aspects of social cognition (Seyfarth and Cheney 2015). Meanwhile, once an individual has visited an island, it may become part of the cognitive map used to navigate within their home range (e.g. African elephants Loxondonta africana Presotto et al. 2019).

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 to access islands during calving (Bergerud et al. 1990). Even for adept swimmers like caribou, which have hollow hair shafts that aid in flotation, 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 few studies have documented caribou swimming in the ocean, and most of these lack observation, but rather deduce swimming based on presence of caribou on a previously uninhabitated island (e.g. Miller 1995, 2002, Jeffery et al. 2007, Ricca et al. 2012). Caribou may swim between islands in the ocean for similar reasons they swim in freshwater (Leblond et al. 2016), mainly concerning predator avoidance or to access new habitats and foraging opportunities. We propose that one such explanation, the forage limitation hypothesis, is the most likely explanation for oceanic swimming for caribou that live on islands in the Fogo Island archipelago.

Caribou were introduced to Fogo Island between 1964–67 as part of a series of translocations throughout the province (Bergerud and Mercer 1989). Typical caribou predators such as black bears (*Ursus americanus*) and wolves (*Canis lupus*) are absent from Fogo Island; the dominant predator is coyote (*Canis latrans*), which predate calves but it remains unclear what threat they pose, if any, to adult caribou (Rayl et al. 2014). Given the minimal risk of predation to adults and low density of coyote on Fogo Island, we propose that forage limitation is more likely to drive movement between islands than predator avoidance. 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 caribou were first seen on nearby islands during this same period. Increased competition for resources on Fogo Island due to this increase in density could have precipitated movement to other islands.

Forage limitation and over-grazing is a major concern for caribou populations and can lead to reduced female reproductive success (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 the Fogo Island population, as the population grew and predation pressure was insufficient to maintain population density, forage depletion could lead caribou to make similar, but riskier and more costly, movements between islands during the ice-free season. Given the small size of other islands near Fogo (Figure 2), over-grazing by newly arrived caribou could rapidly deplete forage on an annual cycle (Bergerud et al. 1990), leading to more frequent movements back and forth between islands rather than permanent relocation.

The trade-off associated with swimming between islands can be understood as density-dependent habitat selection governed by the Ideal Free Distribution (Morris 1987). 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 (Morris 1987). 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.

Forage limitation may be the ultimate explanation for caribou swimming between oceanic islands, but a number of proximate mechanisms remain untested. Our observations of caribou swimming in the ocean lead to five questions for future research:

1. How do energetic costs and risks of swimming differ from walking on sea ice? Walking over ice is less energetically expensive than swimming, but may pose a greater risk of mortality from falling through the ice. Although the presence and extent of sea ice varies annually, we deduce that although the majority of inter-island movements occur between April 1 and December 31, some inter-island movements appear to be caribou walking on sea ice between islands (Figure 2B). Our aim for future research on the trade-offs of these types of movement considers how the costs, e.g. energy expenditure or mortality, and benefits, e.g. novel foraging opportunities, may vary seasonally.
2. If swimming is a function of density-dependent habitat selection, what are the costs of movement between patches? IFD assumes zero-cost movement, but could the risk and energetic costs associated with oceanic swimming be estimated using the potential fitness deficit that caribou are willing to tolerate before swimming to a new island?
3. In relation to questions 1 and 2: how do individuals vary in their propensity to swim and their assessment of the costs and benefits of swimming between islands? We observed some individuals that regularly engaged in swimming events, while others were never observed swimming in the ocean? Our existing research on individual behavioural variation in caribou movement ecology ]Webber et al. (2020)] provides a basis to investigate the role of inherent individual differences in swimming behaviour. Specifically, the forage limitation hypothesis applies uniformly across populations, but individuals could evaluate the costs and benefits of swimming differently.

We surmise that for Fogo Island, 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. Our focal 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 present several hypotheses related to the nuances and further variation within the idea that density-dependent habitat selection governs swimming behaviour, and posit that above and beyond these additional factors, 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.

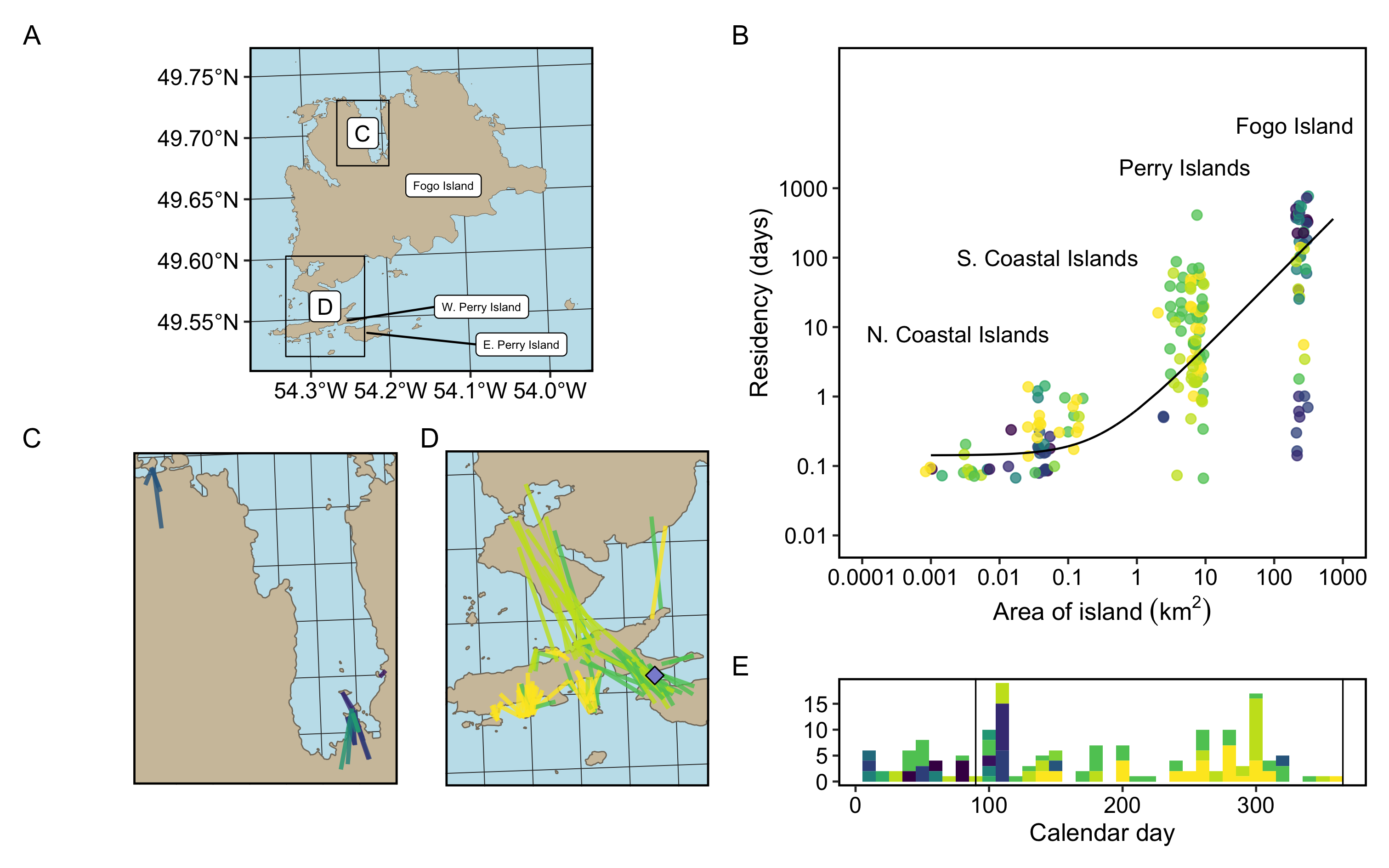


Figure 2: A) Map of the Fogo Island archipelago with swimming events between islands. B) Histogram displaying the frequency of swimming events throughout the year. Note, colours correspond to individual caribou and vertical black bars delineate the ice-free season (April 1 to December 31). C) Inset of 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).

Table 1:

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Moves to | Moves away | Proportion lichen | Estimated density (caribou per km2) | Average group size (95% CI) | Calf:cow ratio between June and August |
| Fogo Island | 31 | 32 | 0.12 | 0.9803922 | 3.05 (2.7, 3.4) | 0.34, (0.28, 0.39) (n = 283 groups) |
| Western Perry Island | 53 | 54 | 0.03 | 6.6666667 | 2.95 (1.89, 4.02) | 0.22, (0.05, 0.39) (n = 23 groups) |
| Eastern Perry Island | 18 | 18 | 0.12 | 5.2631579 | 3.71 (1.97, 5.46) | 0.67, (0.23, 1.00) (n = 7 groups) |

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