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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 and 1967 (Bergerud and Mercer 1989). During fieldwork on 30 May 2017, we observed an unmarked adult male caribou swim between two smaller islands (Fig. 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 refers to the constraints on food availability associated with changes in abundance

(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 a patch and island size as a proxy for energy intake in a patch (Fig. 2).

Forage limitation and over-grazing can reduce reproductive success of female caribou (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. Because there are no wolves on the Island of Newfoundland, coyotes (*Canis latrans*) and black bears (*Ursus*

Fig. 1. Photograph of swimming unmarked adult male caribou (*Rangifer tarandus*) from Western Perry Island to Eastern Perry Island, Newfoundland, Canada taken on 30 May 2017.
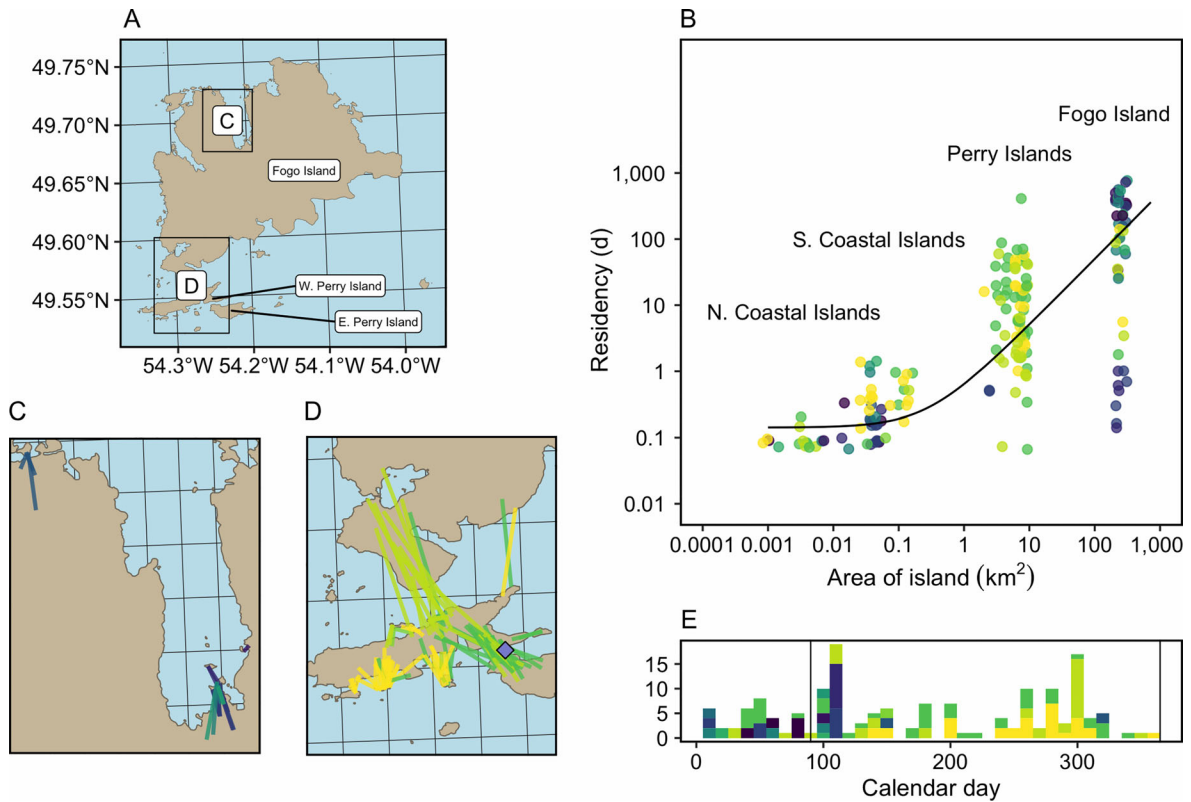
FIG. 2. (A) Map of the Fogo Island archipelago with swimming events from 13 caribou between islands. (B) Correlation between area of an island (km²) and the residency in days an individual caribou spent on that island (linear mixed effects regression with identity as a random effect: β = 1.08, SE = 0.06; t = 17.5, df = 177, P < 0.001). (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. The gray diamond represents the location we observed an adult male caribou swimming (see Fig. 1). (E) Histogram displaying the frequency of swimming events throughout the year (with 1 = 1 January). Colors correspond to individual caribou, which are consistent in all panels, and vertical black bars delineate the ice-free season (1 April to 31 December).

americanus) are the major predators of caribou (Lewis and Mahoney 2014). Within the Fogo Island archipelago there are no black bears; the density of coyotes is low (Huang et al. 2021) and the probability of coyote 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 behavior for caribou elsewhere in their range (e.g., Jeffery et al. 2007).

We identified swimming events as two consecutive GPS locations (2-h relocation rates) on different islands (*n* = 29, for collaring details see Peignier et al. 2019). 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-h 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 above approximately 0.1 km²; (2) caribou know the 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.

We identified 127 swimming events over three years (Fig. 2). In total, 13 of 29 collared female caribou swam among islands (Fig. 2). These 13 caribou swam on average approximately 3 (range = 2–34) times per year and remained on each island for a median of 3 d (mean = 30 d, range = 0–724 d) before swimming again. We found that caribou residency increased proportionally with the size of the island for islands larger than approximately

0.1 km^2, such that caribou spent less time on smaller islands and more time on larger islands, providing preliminary evidence for links between swimming, forage limitation, and the marginal value theorem (Fig. 2B). In many cases, the smaller islands in the archipelago are forage limited and the larger islands provide greater opportunities to forage.

The increase in residency with island size and hence forage abundance 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 behavior. For example, caribou primarily rely on their sense of hearing and smell, and 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 that is driven by aspects of social cognition (Seyfarth and Cheney 2015). Meanwhile, once an individual has visited an island, the island may become part of the cognitive map used to navigate within their home range (e.g., African elephants *Loxondonta africana*; Presotto et al. 2019).

From our natural history observations and proximal movement data on caribou swimming, characteristics of destination islands, and residency on the islands, we have presented some evidence for the marginal value of resources that may serve as evidence of forage limitation for caribou swimming between islands. Further investigation into the nuance of forage profitability, local density, and the role of both social and spatial cognition is needed. Here, we have proposed a thought exercise that integrates the marginal value theorem with novel natural history observations to explain swimming behavior for terrestrial animals and opens the door for future studies of caribou in our system and other island archipelagos inhabited by caribou.

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