

RESEARCH ARTICLE

Ice cover and partner removal increase movements of invasive mesopredator in the coastal island mosaic

Pyry Toivonen^{1,2}  | Mikko Toivola^{3,4} | Vesa Selonen¹ ¹Department of Biology, University of Turku, Turku, Finland²Natural Resources Institute Finland, Turku, Finland³Finnish Wildlife Agency, Turku, Finland⁴Metsähallitus, Turku, Finland**Correspondence**

Pyry Toivonen

Email: pntoiv@utu.fi**Funding information**

Research Council of Finland, Grant/Award Number: 357199; Ministry of Agriculture and Forestry of Finland, Grant/Award Number: Sotka-project

Handling Editor: Kilian Murphy**Abstract**

1. The invasion of new areas is influenced by landscape structure, seasonal conditions and social interactions. Coastal and lake landscapes pose unique challenges for land animals due to water barriers, while the ice cover in northern latitudes can facilitate movement. For invasive alien species, information on movement capabilities provides data for management.
2. This study examines the movement patterns of an invasive mesopredator, raccoon dog, in a fragmented coastal environment in southwestern Finland to better understand its movement capabilities and potential expansion. Using GPS tracking, we investigated individual movements between islands, considering the role of ice cover, island connectivity and social interactions (partner removal by management).
3. The raccoon dog has low winter activity levels, but our findings demonstrate that the individuals remain active during the cold season and use ice cover to reach islands perhaps otherwise unreachable. The number and connectivity of islands also play a crucial role in movement distances. Moreover, the partner removal increases movement between islands during the summer. We conclude that the raccoon dog is highly mobile in the coastal landscape, with ice cover facilitating movements between islands.
4. *Practical implication.* To effectively manage this invasive species, creating single individuals should be avoided before avian breeding season. This strategy can help prevent solitary raccoon dogs from wandering and potentially colonizing new areas. Melting ice due to climate change is often mentioned as a benefit to invasive species, but our results provide an example of where the ice cover potentially enhances movement of an invasive species and thus requires consideration.

KEYWORDS

coast, dispersal, inter-island movement, invasive species, mesopredator, overwater movement, raccoon dog

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Ecological Solutions and Evidence* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

For invasive alien species, like for all species, the invasion potential depends on movement abilities of individuals. Whether or not new areas can be colonized depends also on landscape structure, that is, whether the movement between potential living sites is possible (Clobert et al., 2012). For example, in the coastal and lake landscapes, the movement between islands or over bays and fjords, may be problematic for land animals due to the hostile water matrix. In the northern latitudes, however, the ice cover aids movement of mammalian species that are active during the winter (Banfield, 1954; Lameris et al., 2021; Leblond et al., 2016; Seidler et al., 2015).

In general, climate change is expected to benefit invasive species by increasing primary production and decreasing ice cover in cold-adapted ecosystems (Callaghan et al., 2004; Parmesan, 2006; Walther et al., 2002). These factors are projected to become the primary driver of biodiversity change in boreal and Arctic ecosystems (Sala et al., 2000), especially by strengthening top-down species interactions, that is, predation pressure and interference between predators (Legagneux et al., 2014; Post et al., 2009; Stoessel et al., 2019). Reduced ice cover not only affects the ecology and demography of ice-dependent species (Kunnasranta et al., 2021; Øigård et al., 2014) but also decreases the period that land animals can use the ice for movement (Lameris et al., 2021; Leblond et al., 2016). These factors are often linked to negative effects on native species (e.g. Lee et al., 2017) but may also affect some invasive species.

Invasive mammalian mesopredators are concluded to be particularly harmful to many native species (Doherty et al., 2016; Pitt & Witmer, 2007). The decline of ground-nesting bird species is a Europe-wide phenomenon linked to predation by generalist mesopredators (McMahon et al., 2020). Two invasive mammalian predators currently inhabit the coastal region of Finland: the raccoon dog (*Nyctereutes procyonoides*) and the American mink (*Neovison vison*). Both have been believed to wreak havoc in the breeding bird populations. The raccoon dog benefits from climate change as it can better survive and increase activity during the winter months (Melis et al., 2007; Selonen, Toivonen, et al., 2024). Indeed, the raccoon dog has experienced a recent increase in northern Finland near the Arctic regions, suggesting a potential for further range expansion under climate change (Selonen, Toivonen, et al., 2024). Despite this, the threat that raccoon dogs pose to vulnerable prey populations is suggested to be highest in Finland in the coastal regions where raccoon dogs have invaded islands (Kauhala & Kowalczyk, 2011). There, the sea likely forms a barrier for movements, although the presence of the raccoon dog on islands demonstrates that it can reach these areas either by swimming or by utilizing ice cover. Whether or not the raccoon dog utilizes the ice cover for movement depends on its winter activity levels. The species clearly decreases activity in winter, using periodical sleep to survive over the cold months (Mustonen & Nieminen, 2018). Inactivity during ice cover would render movement between remote islands more difficult.

The potential threat of raccoon dogs to ground-nesting water birds is supported by the spatiotemporal habitat selection of raccoon dogs (Toivonen et al., 2024), their high population densities

(Selonen, Brommer, et al., 2024) and the results of artificial nest predation studies (e.g. Dahl & Åhlén, 2010; Holopainen et al., 2021; Nummi et al., 2019; Selonen et al., 2022) including one study with natural nests in the coastal region in Sweden (Dahl & Åhlén, 2010). Extensive resources have been invested in the removal of raccoon dogs from the Archipelago Sea (Toivola, 2022). Nevertheless, little is known about either the behaviour of raccoon dogs in the coastal area or the impact of the management procedures on this behaviour. It is possible that the removal of partners from individuals of this pair-bond forming species (Kauhala & Kowalczyk, 2011) may increase their movement levels (Herfindal et al., 2016). To better allocate resources and understand the threat raccoon dogs pose, more information about the movement behaviour of the species is required, which is why we study how the raccoon dog utilizes islands and what influences how far the raccoon dogs can move in the coastal landscape.

For raccoon dogs on these islands, our aims are to (1) investigate what factors influence the movement between islands in highly fragmented coastal landscape; (2) compare movement between islands during ice-free and ice-cover periods; and (3) improve our knowledge on how raccoon dogs can be managed and how the management (possible partner removal) influences their movements. We hypothesize that increase in the ice cover, the connectivity between islands and the partner removal all increase the movement distances between islands for raccoon dogs.

2 | METHODS

2.1 | Study species and study area

The raccoon dog is an omnivorous and monogamous species and can produce litters of up to nine offspring each year around May, starting at the age of 1 year (Kauhala, 1993). Raccoon dogs invaded Finland from the Soviet Union in the 1950s, and its current range covers most of the country except for the northern parts of Lapland (Kauhala & Kowalczyk, 2011). The raccoon dog's European range is expanding, mainly consisting of Eastern and Northern Europe, Germany and Denmark (Kauhala & Kowalczyk, 2011). Individuals introduced to Europe originated from the subspecies that can tolerate the cold climates of the native range in southeast Siberia by using winter sleep (Kauhala & Kowalczyk, 2011).

The study area is located in the southern hemiboreal zone, approx. 60.2° N, 22.0° W on the southwestern coast of Finland (Figure 1). This area, called the Archipelago Sea within the Baltic Sea, is home to many bird species. The whole area consists of 37,217 islands of various sizes (mean 0.65 km² ± 30.36 SD).

2.2 | GPS tracking and data

Thirty raccoon dogs were tracked using GPS collars from Followit AB between 2019 and 2024 (Table 1). Only two individuals were

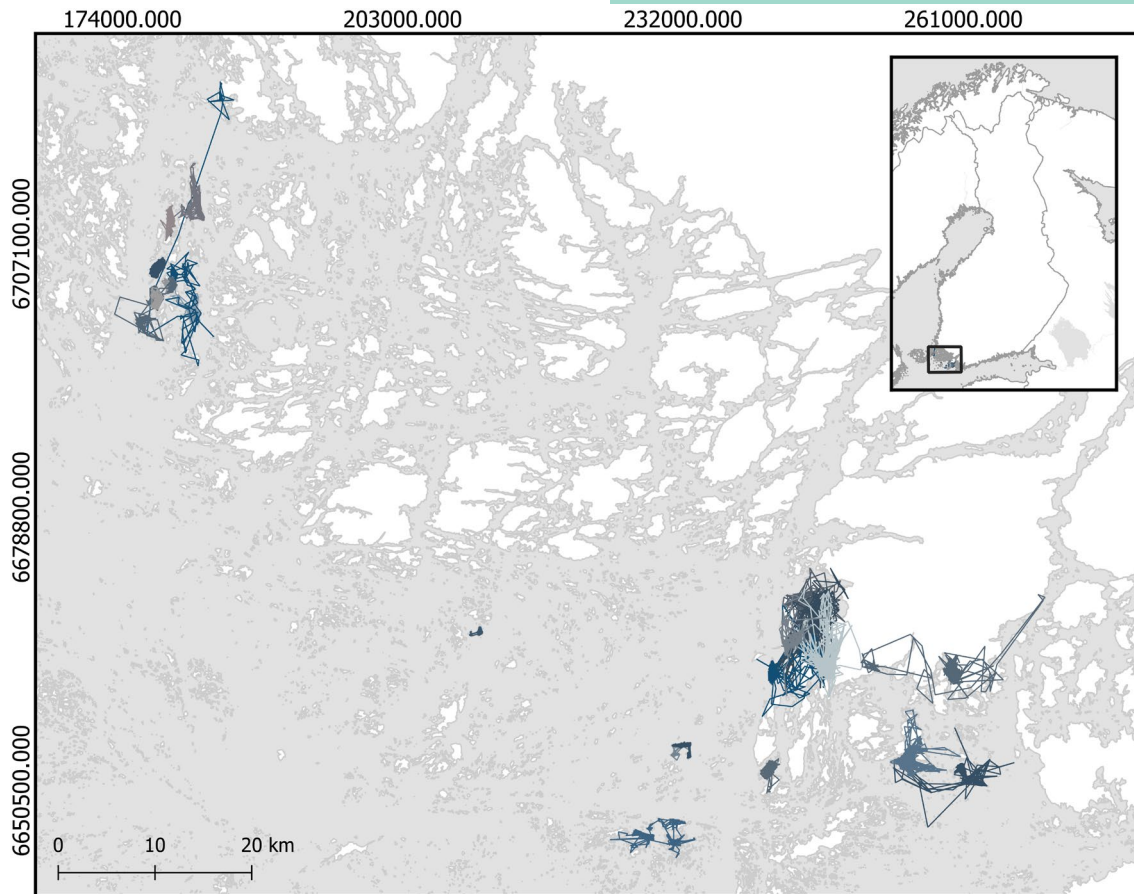


FIGURE 1 The study area and movement paths of the raccoon dogs used in the model. Each colour represents a unique individual, and in light grey is the sea. The study area is located on the southwestern coast of Finland, the Archipelago Sea. See [Figure S1](#) for individuals removed from the study.

followed for more than one annual cycle, but they remained on the same islands ([Table 1](#)). Ten individuals were followed with more than one collar during the tracking period. Three individuals had collars using iridium satellite system and 27 using GSM network. The average individual was tracked for 197 days (± 23 SE). Tracking was designed and executed by SLHSY (a coastal conservation and management NGO) in collaboration with Metsähallitus and the Finnish Wildlife Agency as part of their projects in eradicating invasive species in the coastal region. Individuals were tracked mostly for the purpose of finding their nests, cubs and partners. Because of this specific tracking purpose, raccoon dogs experienced partner removals that are one of the research interests in this study. Collaring (tagging) and killing of the animals did not require authorisation or permits by the Project Authorisation Board, or any research permits by The Finnish Wildlife Agency as these data were a by-product of invasive species eradication projects governed by governmental agencies according to the Finnish law.

We began data preparation by filtering out the first day of the designated tracking period to minimize the immediate human influence. We then inspected the data individually for outliers using both net squared displacement (NSD, see model-application in e.g. Bunnefeld et al., [2011](#)) and X-Y coordinate plots, and removed all

the clear outlier locations from the data. Examples of such cases were individual locations above NSD value of 200 when all the rest were below 100, indicating a failure in GPS location, or locations on a house where the collar was maintained.

We moved forward with data from 18,392 GPS fixes for 30 individuals. The mean location interval was 7.5h. For step length analysis, we limited the data to only include location intervals of 2 and 4h. In this data subset, we had 8415 steps with a mean step length of 512m (SD: ± 641 m) and a median of 307m. We compared steps associated with movements between islands (defined as hop events, see below) to steps within islands or mainland. For this, we did a Gaussian model, where step length (log-transformed) was explained with fixed effects hop event status (yes vs. no), month and step duration (2 or 4h). Individual ID was modelled as a random effect with Generalized Estimating Equations (GEE) in SAS Glimmix 9.4.

2.3 | Hop events between islands and least cost paths

To identify *hop events* (movement between islands), we joined the GPS data spatially with island polygons (buffered by 5m) from the

TABLE 1 Information about the raccoon dog individuals used in the study.

ID	Sex	Start date	End date	Partner removal month	GPS locs	Hops	Islands (hopped)	Mean dist (km, \pm SD)
R1	Female	2022-04-23	2022-08-13		386	7	7 (4)	0.07 \pm 0.08
R10	Male	2021-04-03	2021-06-05		191	4	4 (3)	0.30 \pm 0.18
R11	Male	2022-01-17	2022-07-14	January	588	2	3 (2)	0.12 \pm 0.00
R12	Male	2022-01-17	2022-08-20	January	721	3	6 (3)	0.07 \pm 0.05
R14	Male	2022-10-25	2023-02-17		328	2	4 (2)	0.07 \pm 0.00
R15	Male	2021-10-23	2021-12-30		288	8	4 (3)	0.13 \pm 0.11
R18	Female	2023-04-20	2023-08-04		305	4	5 (2)	0.05 \pm 0.00
R2	Male	2022-08-26	2023-03-22	August	665	43	20 (15)	0.29 \pm 0.35
R22	Male	2022-09-16	2023-09-15		1011	104	40 (33)	0.23 \pm 0.34
R23	Male	2021-01-09	2021-10-07	April	968	116	28 (23)	0.33 \pm 0.62
R24	Female	2019-08-02	2020-06-30		1124	34	13 (10)	0.28 \pm 0.19
R25	Male	2023-09-08	2024-02-24		505	129	45 (42)	0.62 \pm 1.07
R26	Male	2023-11-07	2024-01-23	September	350	34	8 (6)	0.28 \pm 0.33
R27	Female	2019-08-30	2020-07-03		699	74	7 (5)	0.13 \pm 0.07
R28	Male	2023-09-07	2024-03-08		547	67	24 (21)	0.75 \pm 0.73
R29	Female	2020-02-14	2020-08-19		704	34	11 (8)	0.30 \pm 0.33
R3	Female	2020-09-18	2021-04-04	October, January	606	129	40 (39)	0.90 \pm 1.10
R30	Male	2023-04-19	2023-09-12		409	66	4 (3)	0.05 \pm 0.00
R31	Male	2024-04-11	2024-06-24		276	13	9 (8)	0.19 \pm 0.26
R32	Male	2023-11-06	2024-02-28	September	355	38	10 (9)	0.21 \pm 0.37
R5	Male	2022-01-17	2022-05-09	January	381	2	6 (2)	0.03 \pm 0.00
R6	Male	2020-09-28	2021-07-15	November	850	2	5 (2)	0.38 \pm 0.00
R8	Male	2020-12-13	2021-11-11	January, September	1019	21	13 (9)	0.83 \pm 0.91
R13*	Male	2020-10-30	2022-07-31	March, August	1670	0	2 (0)	
R16*	Female	2021-10-30	2022-04-05		298	0	1 (0)	
R17*	Male	2021-10-30	2022-12-27	April	1157	0	1 (0)	
R34*	Female	2024-03-09	2024-06-22		395	0	2 (0)	
R4*	Male	2020-09-18	2021-02-11	December	478	82	26 (24)	
R7*	Female	2021-04-11	2021-09-10		681	0	2 (0)	
R9*	Female	2020-11-07	2021-03-28	March	437	0	3 (0)	

Note: Start date is the first date of the tracking period and end date the last. Partner removal month is the month on which the individuals' partner was killed. GPS locs is the number of GPS locations during the tracking period. Hops is the number of events where the individual has moved from one island to another for more than two consecutive steps. Islands is the number of unique islands the individual has visited during the tracking period and in parentheses are the number of unique hop event islands. Mean dist is the mean distance between the two islands of hop events in the units of kilometres. Individuals marked with an asterisk (*) were removed from the analysis.

study area. We classified consecutive movements between two islands where the individual did not go back to the original island in two steps as island hop events. Movements between islands where the individual came back the next step after leaving were not classified as hop events. This kind of small-scale movement was common in the dataset between islands very close to each other. We calculated the shortest edge to edge Euclidean distance between the start and end islands forming a hop event (note that other islands could have located between these two islands). We removed an individual that had a collared partner to avoid pseudoreplication by removing the one with least GPS locations. After

data preparation, we had 23 individuals (13,276 GPS fixes) with 917 observed island hop events (Table 1).

We defined a *hop-landscape* by first calculating the bounding box between the two locations forming a hop event and then extending it by 1 km to all sides. Within it we then calculated the number of islands and estimated the mean ice cover for the date of the event from a raster file provided by Finnish Meteorological Institute (see Data Availability Statement). Ice cover was mainly limited to the months of January–March and varied in time and space (Figure 2).

We then used a least-cost path model (see e.g. Ludwig, 2020) to estimate the number of islands needed to minimize overwater

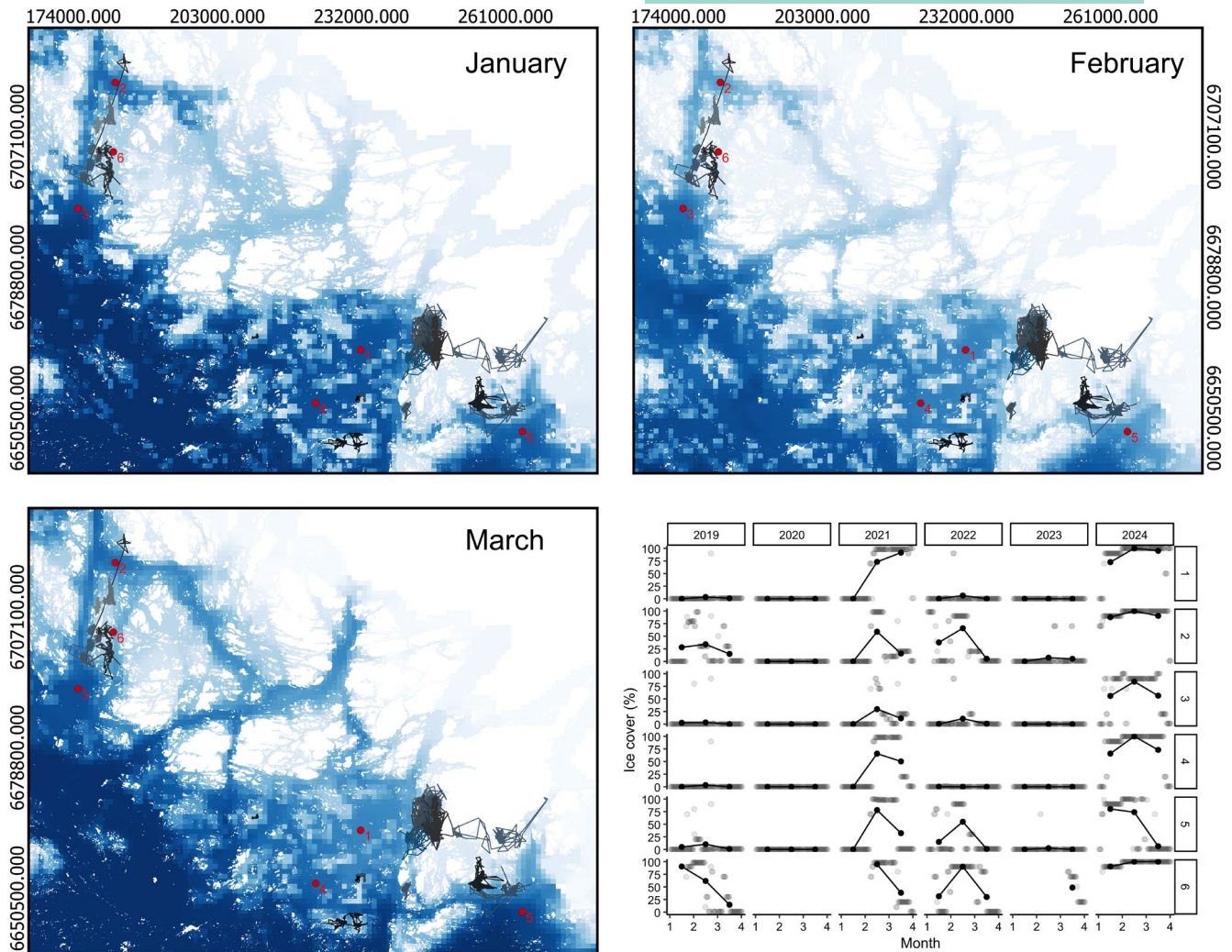


FIGURE 2 Average ice cover during January, February and March in the study area. In the lower right pane is the monthly averages (points connected with lines) and daily ice cover (transparent points) for select coordinates (red points). Missing values are interpreted as zeros in the analyses.

travel (hereafter referred to as 'stepping stones') within the hop landscape. To estimate least cost paths, we rasterized the island polygons to 5×5 m rasters. Least cost paths were then estimated from these rasters with 16 directions (setting in the R package) and land was given five times bigger conductance value than the sea (frozen or not). This way land is five times more conductive (less costly) than the sea. According to a sensitivity analysis, these settings minimized overwater travel without considerably increasing the total path lengths. The number of stepping stones derived from the least cost path indicate how well overwater travel can be minimized between the islands within the hop-landscape. We calculated distances between the stepping stone islands to estimate required overwater distances.

Because of the partner removal of the tracked individuals, each individual was given status according to the closest past partner removal date (Table 1). Status was classified as 'after' if the individual had experienced partner removal and 'before' if it had not experienced partner removal yet or never in the data.

Data preparations were done in R (v. 4.4.1, R Core Team, 2024) using the 'tidyverse' (v. 2.0.0, Wickham et al., 2019) and 'sf' (v. 1.0-16, Pebesma, 2018) packages. Least cost paths were modelled with 'leastcostpath' package (v. 2.0.12, Lewis, 2023). In addition, 'shiny' (v. 1.8.1.1, Chang et al., 2024) and 'plotly' (v. 4.10.4, Sievert, 2020) packages were used in the visual inspection of the data.

2.4 | Modelling hop event distance

We fitted a log-normal generalized additive model for location and scale (GAMLS) with the hop event distance as the response variable (edge to edge Euclidean distance between start and end islands; unit kilometres). The predictor variables for the location parameter (mean) were the mean ice cover within the hop-landscape (%), the number of islands within the hop-landscape, the number of stepping stones, the month of the hop event and

the partner removal status of the individual. The month was fitted by the partner removal status (interaction). In addition to the fixed effects, we fitted the model with individual ID as a random effect to account for individual variation. In the first rounds of model fitting, we also tested the effect of island area at the start and the end of the hop events and sex, but they were not significant, they decreased the model fit and/or had identifiability issues. Different combinations of variables were assessed by comparing concurvity (collinearity), deviance and Akaike Information Criterion (AIC) values.

The model reported above performed the best, but the stepping stones variable had heteroscedasticity, which was addressed by allowing the scale parameter (standard deviation) to vary with stepping stones by including the variable in the sigma formula of the model. We also removed one outlier observation from individual R23 because of its clearly outlying residual while having a hop distance of only 6 m. The model was fitted in R using smooth functions from the 'mgcv' package (v. 1.9-1, Wood, 2011) but implemented as GAMLS using the 'gamls' package (v. 5.4-22, Rigby & Stasinopoulos, 2005) and 'ga' function in the 'gamls.add' package (v. 5.1-13, Stasinopoulos & Rigby, 2024).

Ice cover and partner removal status (dummy variable) were fitted as standard linear terms while all the other predictors were fitted as smooth terms (month with cyclic cubic regression splines and rest with thin plate regression splines). This is because partner removal was a dummy variable and the expected effects were linear for ice cover (and smooth term for ice cover converged to linear term); for the other variables, smooth terms fitted better. In addition, we fitted two simple ANOVA models comparing hop event (Euclidean) distances and least cost path overwater distances between frozen and unfrozen sea using the built-in stats package in R.

3 | RESULTS

The GPS tracked raccoon dogs ($n=23$) frequently moved between islands and visited or occupied 249 separate islands during the tracking. About 6% of GPS locations were classified as hop events (movement between islands; Table 1). Moved step lengths were clearly longer for hop events (model fitted average, 95% CI: 927 m, 716–1174 m) than for steps within land areas (220 m, 169–285 m; $F_{1,21}=349.2$, $p<0.0001$). Mean observed hop event distance (Euclidean edge to edge distance between start and end islands; Table 2) in the raw data was 0.42 ± 0.74 km (maximum around 6 km and minimum around 6 m; Figure 3).

The number of stepping stones, identified with the least cost path model, and within the hop landscape, increased the hop event distance (Figure 4; smooth effects in Table 2). The second stepping stone approximately doubled the hop distance, and after the fourth stepping stone, the effect evened out with increasing uncertainty (Figure 4). Average total overseas distance was $0.29\text{ km}\pm 0.48$ SD between the stepping stones, and on average, each path included 1.33 ± 1.94 SD stepping stones.

Ice cover increased hop-event distances (Table 2): for every unit increase in ice cover, the natural logarithm of hop-event distance increases by 0.0056 units (95% CI: 0.0046, 0.0066). That is, 100% ice cover increased the hop-event distances by approximately 75% compared to 0% ice cover (Figure 4). In the raw data, the difference was clearer, hop-event distance being $0.91\text{ km}\pm 0.06$ SE and $0.22\text{ km}\pm 0.01$ SE with a >25% and <25% ice cover, respectively. Longest hop event during ice-free period was 3.38 km, but this hop event would have required only 0.22 km of overwater travel between stepping stones (Figure 3d). The overseas distance between stepping stones also clearly increased when the sea was frozen (Figure 5, $F_{1,910}=342.5$, $p<0.0001$, $n_{\text{ice}}=280$, $n_{\text{water}}=632$).

TABLE 2 Summary table of the generalized additive model for location and scale ($n=916$ hop events for 23 individuals) explaining hop-event distances between islands in a coastal area in Finland. Estimates, test statistics and parameters for linear terms are reported first and then the parameters and test statistics for smooth terms. Results are given for location (μ , mean) and scale (σ , standard deviation) parameters. EDFs are the efficient degrees of freedom for smooth terms and Ref DFs are the reference degrees of freedom in the absence of penalization of wiggleness. Significant p -values are bolded.

Parameter	Linear effects	Estimate \pm SE	t-Statistic	p
μ	Intercept	-1.9314 ± 0.0334	-57.766	<0.0001.
	Ice cover	0.0056 ± 0.0005	11.274	<0.0001
	Partner removal (after)	0.0034 ± 0.0484	0.071	0.943
σ	Intercept	-0.2915 ± 0.0236	-12.48	<0.0001
	Smooth effects	EDF (Ref DF)	F-statistic	p
μ	Islands in hop-landscape	3.780 (3.969)	44.01	<0.0001
	Stepping stones	4.662 (5.661)	188.63	<0.0001
	Month: Partner removal (before)	7.101 (8.000)	9.15	<0.0001
	Month: Partner removal (after)	0.000 (8.000)	0.00	0.47
σ	Stepping stones	3.351 (2.924)	30.73	<0.0001

Note: For partial effects, see Figure S3. All reported estimates and effects are in log-scale. Model DF: 38.21, Residual DF: 877.79. Mean squared error: 0.16 km, Root mean squared error: 0.40 km, Mean absolute error: 0.19 km.

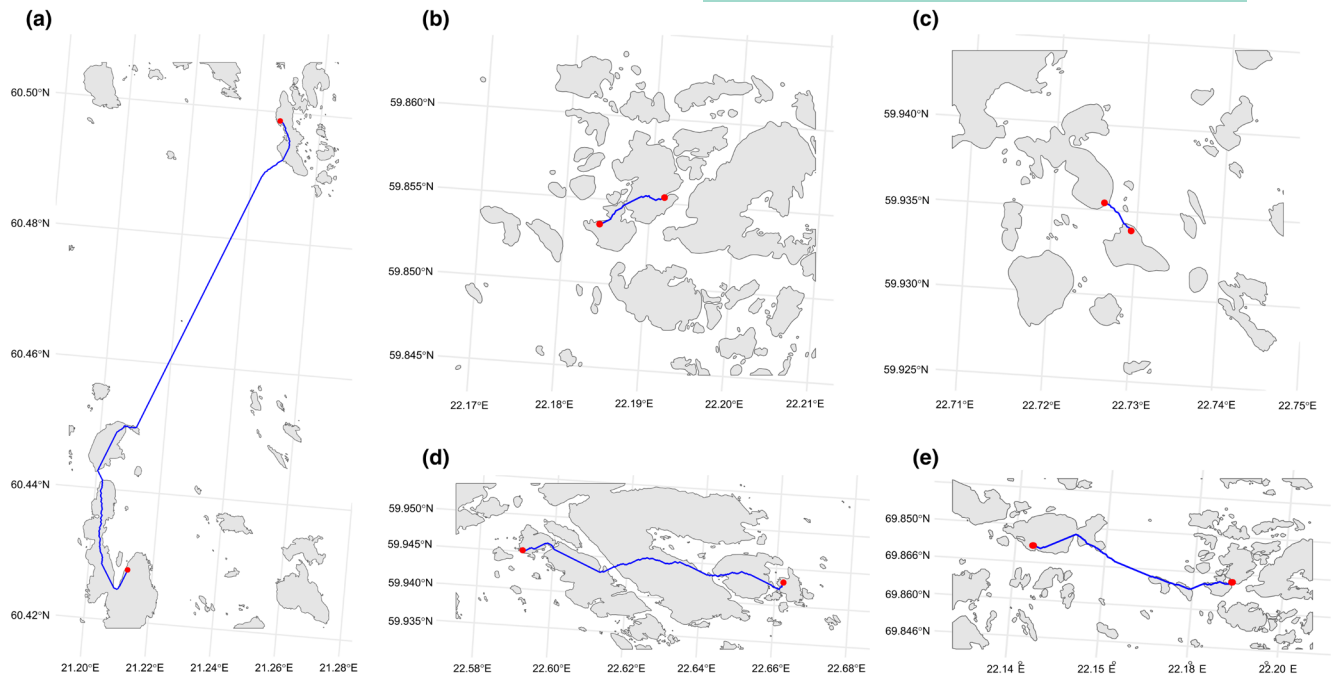


FIGURE 3 Least cost paths and hop-event landscapes estimated for (a) hop event with the longest Euclidean distance (6.15 km) between islands (100% ice cover), (b) hop event with the shortest Euclidean distance (0.006 km) between islands, (c) event with median Euclidean distance (0.15 km) between islands, (d) hop event with the longest Euclidean distance (3.38 km) between islands during ice-free period and (e) hop event with the longest overwater distance (0.98 km) during an ice-free month (August). Red dots are the start and end points of least cost path, blue lines are the estimated least cost paths and grey polygons are islands within the hop-landscape.

Month had an interactive effect with the partner removal on hop event distance (smooth effects in Table 2). In other words, partner removal increased the distances raccoon dogs moved during the summer (Figure 4). For full model statistics and diagnostics, see Table 2 and Figure S2. The model was a good fit especially at smaller distances but became less accurate towards the longest distances, still maintaining a reasonably good fit (Figure S2).

4 | DISCUSSION

We observed that raccoon dogs actively move between islands in the coastal study area in Finland. The individuals remained active during winter months and the ice cover increased the distances moved between islands. The connectivity of the landscape in the form of an increased number of stepping stone islands and the number of islands in the nearby sea landscape increased movement distance. Finally, the removal of partners increased movement between islands but only during the summer.

Melting ice due to climate change is often mentioned to benefit invasive species (e.g. Lee et al., 2017), but our results provide an opposite example where ice cover potentially enhances invasion in a similar fashion as it benefits the movement of native land mammals in the boreal and arctic regions (Banfield, 1954; Lameris et al., 2021; Leblond et al., 2016; Seidler et al., 2015). The raccoon dog is most active during other seasons than winter (Selonen, Toivonen, et al., 2024), but our results demonstrate that the individuals

remained active during the cold season and used ice cover to reach islands that might have otherwise been unreachable. Thus, our results fit with studies showing that the species does not use very long periods of winter sleep in the boreal region of Finland (Mustonen & Nieminen, 2018; Selonen, Toivonen, et al., 2024). It is, however, expected that the warming winter weather would benefit raccoon dog invasion through increased over-winter survival (Melis et al., 2007). Thus, climate change can influence raccoon dogs in an interesting way: The disappearance of ice cover would decrease the reach of raccoon dogs in coastal areas but on the other hand helps them to survive over the winter. Increased survival and lowered dispersal ability could increase densities within the islands, creating increasing pressure for local prey populations and competition among raccoon dog individuals.

Regardless, ice cover was not the most important factor increasing the movements between islands even though being significant part of it. Stepping stones and number of islands in the vicinity (connectivity) had the biggest effect on the movement distances. However, our model failed to precisely explain the very longest distances. We assume that the raccoon dog density or existence of other raccoon dog couples on the island are one of the reasons together with habitat quality that might explain dispersal decisions behind the longest observed movement distances. However, this was not tested in this current study due to the lack of data. Habitat quality can be defined in many ways, but according to previous research, raccoon dogs are generalist in the coastal region but do prefer more open and wet habitats than forests (Toivonen et al., 2024).

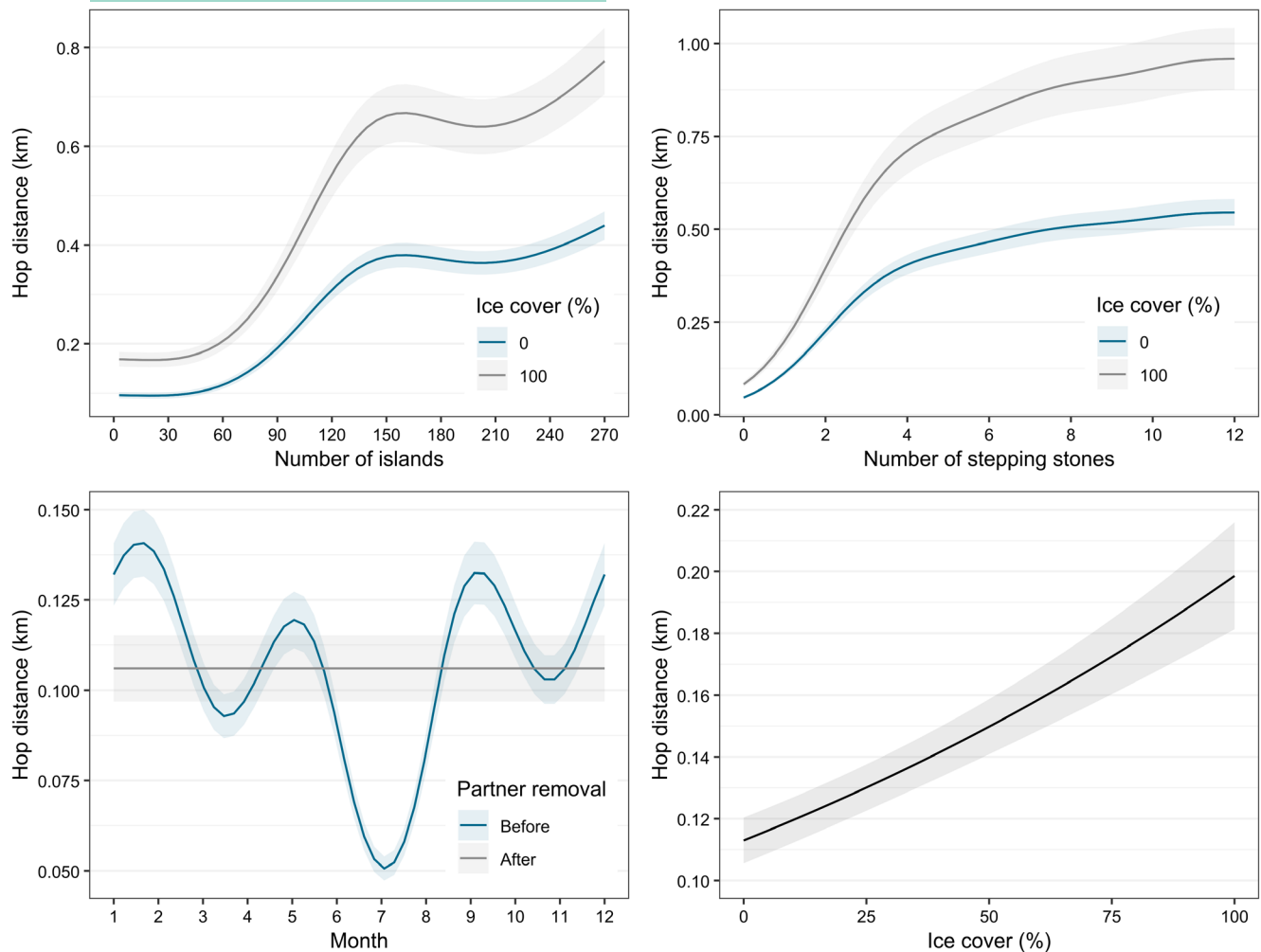


FIGURE 4 The conditional predictions of number of islands within the experienced “hop-landscape” (upper left pane), stepping stones (upper right pane), interaction of partner removal and month (lower left pane) and ice cover (lower right pane) on the distance between consequently visited islands (hop event distance). Non-focal variables have been set to their mean (continuous) or mode (factor).

Stepping stones reduce the distance required to travel overwater and more islands within the landscape allows more connected travel routes and more plausible end points. More connected landscape promoting longer movement is an expected result (e.g. Taylor et al., 1993). Raccoon dogs seem to not have problems moving between islands 200m apart (mean distance without ice cover). Thus, inter-island movement seems to be part of their normal habitat use and the movement often was back and forth between the same islands (Table 1). In addition, small islands are often in the vicinity of larger islands and may become part of regular home ranges of individuals, leading to lots of small hop event distances observed in our study. Earlier, Dueser et al. (2013) studied the inter-island movements of raccoons (*Procyon lotor*) on the Virginia barrier islands in the United States and found them to be infrequent events (only 1.3% of individuals moved between islands, see also Porter et al., 2015). In our case with the raccoon dogs, 93.3% of collared individuals moved between islands and visited on average 12 islands.

The frequent movement between islands might explain the large home ranges observed in Toivonen et al. (2024) for the raccoon

dogs inhabiting coastal area. Previously, Dahl and Åhlén (2010) found raccoon dogs to move between islands frequently and reported 1.2km to be the longest swimming distance observed. Dahl and Åhlén (2010) did not follow raccoon dogs during periods of ice cover. Our longest estimated swimming distances were comparable to those by Dahl and Åhlén (2010) being 0.98km from August (Figure 3e) and 1.96 and 1.85km from March. However, in the latter cases, the raccoon dog could have made a detour using ice visible in satellite images (Figure S4) but not detected by our ice cover raster. Despite these two events possibly overestimating the swimming capabilities, removal of them would not have increased the modelled effect of the ice cover and would have decreased the mean overwater distance during ice-free period only by 5.6m. No other individuals were at the border of frozen and unfrozen sea, which could have produced this kind of uncertainty. It has to be also noted that the longest swimming distances observed in the current study and also in Dahl and Åhlén (2010) were done in the archipelago with no partners. In our case, the longest certain swim (0.98km) took place in an area of active campaign that had removed other raccoon dogs

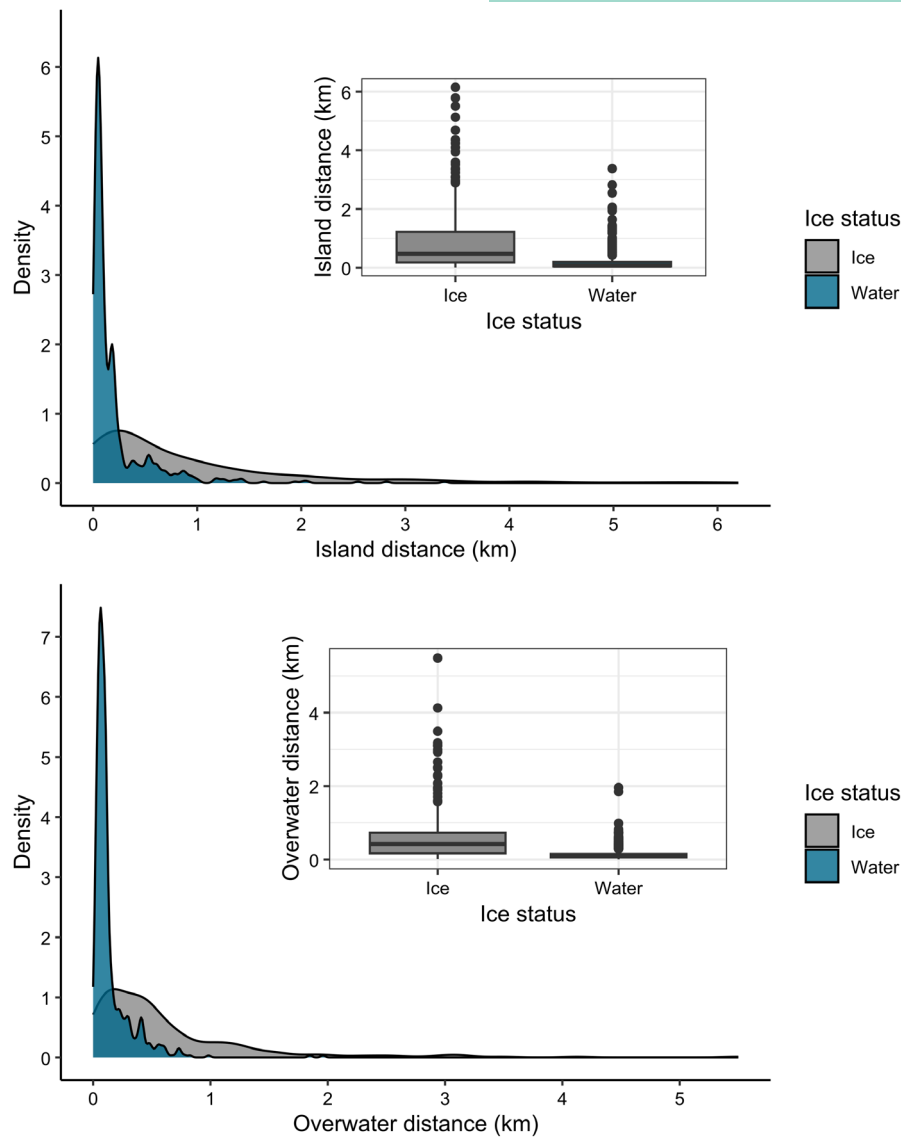


FIGURE 5 Distributions of distance between consecutively visited islands (hop event; upper pane) and overwater distance according to least cost paths (lower pane) during when the sea is frozen (ice) and unfrozen (water). In smaller panes are box plots of the same data.

(Metsähallitus, 2024). In Dahl and Åhlén (2010) the individuals were relocated to Swedish archipelago where no raccoon dogs are present. Shortage of partners in addition with ample food resources during summer months may have induced higher will to swim. The individuals without partners may actually, at least partly, resemble dispersing juveniles. Natal dispersers have higher movement activity in mammals compared to resident individuals within home range (Clobert et al., 2012). We lack data on natal dispersers (Drygala et al., 2010), but it is known that adult raccoon dogs may travel long distances when lacking a partner (Herfindal et al., 2016). Thus, we believe that the movement patterns observed here robustly reflect the invasion potential of the species in the coastal landscape.

Partner removal increased the movement distances of raccoon dogs, but mainly during June–August, well after the breeding season of the species (Kauhala & Kowalczyk, 2011). During

December–February, individuals that had experienced partner removals had decreased movement distances. That is, during winter, partner removal did not induce longer movements between islands, although in general ice cover was observed to increase movement. Apparently, partner seeking was not a priority for raccoon dogs in winter, although the mating season starts already late winter/early spring (peaking in March) and lack of a partner at that time may prevent reproduction from the given year. Young raccoon dogs born in the spring become adults in July, and at that time, partner removal had the largest observed effect on hop events. Perhaps individuals that had lost partners aimed to locate a new partner during summer and autumn before next year's mating season. July–September are the preferred months for dispersal, at least in young raccoon dogs (Drygala et al., 2010), and new pairs seem to be typically formed in the autumn (Mulder, 2012).

4.1 | Implications for management practices

Our results indicate that if a monogamous predator is prosecuted incorrectly, eradication may lead to unwanted effects. Removal of an individual from a pair may lead to dispersal of the solitary individual and expansion of the population. Currently, there are ongoing projects, which target long-term eradication of raccoon dogs from important nesting areas of archipelago birds (Toivola, 2022), but in practice, the hunting in most cases removes only single individuals. Based on our results, the remaining raccoon dog from a pair is more active in summer and has increased reach between islands during the breeding season of birds. This might have negative consequences for birds breeding in the nearby islands and facilitate colonization of new islands. The wandering individual may also be very difficult to catch and end up reproducing in a totally new area. We therefore recommend that hunting should always result in the removal of both the female and the male, which prevents both reproduction and solitary individuals with increased movement activity. However, the effect of partner removal was season-specific, and apparently, the individuals were unwilling to start searching for new territories during the cold season.

Active and long-reaching movement of solitary raccoon dogs in the archipelago during summer can be especially harmful for late-nesting waterbirds such as velvet scoter (*Melanitta fusca*) which is nationally (Lehikoinen et al., 2019) and internationally (BirdLife International, 2020) threatened species. Raccoon dogs are known to prey on artificial and natural nests in the archipelago (Dahl & Åhlén, 2010), and according to artificial nest predation studies done at the lakeshores, are among the most common predators preying on them (Holopainen et al., 2021; Selonen et al., 2022). In these areas, the American mink is another invasive predator threatening ground-nesting birds (Banks et al., 2008; Nordström et al., 2002; Salo et al., 2007). These two invasive species are likely to have conjoining effects on local bird populations (Jaatinen et al., 2022). Taking into account the strong effects alien carnivores more generally have on their prey (Salo et al., 2007), better knowledge on the combined effect of the raccoon dog and the American mink on their prey species is needed.

The information about the possible reach (swim and travel distances) can be used to estimate the range which individuals of an invasive species can colonize. This helps in evaluating island-specific likelihoods for colonization and reduces the costs required for managing the spread of the species. Exceptionally cold winters with increased ice cover may aid the colonization of isolated islands. If followed by a period of several warmer winters, the individuals may get isolated and these islands end up densely populated. This may increase the local predation pressure. That is, the loss of ice cover may also drive up the densities in isolated islands. Currently, there are examples of such possibly problematic islands for raccoon dogs (Tunnhamn, Nötö, Bolax and Jungfruskär within our study area). Tunnhamn, at worst, had observed spring densities of 9.4 individuals per km² (see Table S1) and Jungfruskär 6.1 ind./km² (Table S2) while the estimated maximum spring densities by Kauhala et al. (2006)

were 0.77 ind./km² in the mainland and on average 3.7 ind./km² near wetlands by Selonen, Brommer, et al. (2024). On the other hand, if raccoon dogs are successfully removed it is likely that these areas remain free of raccoon dogs if there is no ice cover in winter.

5 | CONCLUSIONS

The northern regions are increasingly vulnerable to invasive species, with climate change significantly altering the dispersal and survival of the species living in these areas (Lameris et al., 2021; Leblond et al., 2016). Ice cover, a critical feature of northern ecosystems, plays an important role in the movement of various species, both native and invasive. Our study demonstrates that ice can act as a facilitator for the dispersal of invasive species, exemplified by the raccoon dog in coastal landscapes, where ice cover and stepping stone islands enable longer movement distances. Similar to the raccoon dog, other species, such as red foxes, may experience altered dispersal patterns due to changing ice conditions. Consequently, the loss of ice due to warmer winters could potentially create a barrier for some invasive species, while simultaneously improving overwinter survival rates. The management strategies need to consider these contrasting effects. The successful management of invasive species also requires a comprehensive understanding of their life history traits, including mating systems. Monogamy, exhibited by the raccoon dog, is a significant factor that can influence dispersal patterns and management strategies. To effectively manage raccoon dogs and protect ground-nesting birds, creating single individuals should be avoided before the avian breeding season. This strategy can help prevent solitary raccoon dogs from wandering and potentially colonising new areas.

AUTHOR CONTRIBUTIONS

Pyy Toivonen, Mikko Toivola and Vesa Selonen conceived the idea. Mikko Toivola produced and provided the GPS data. Pyy Toivonen prepared and analysed the data and produced figures. Pyy Toivonen led the writing of the manuscript. Mikko Toivola and Vesa Selonen contributed to writing and gave final approval for the publication.

ACKNOWLEDGEMENTS

This study would not have been possible without the input of SLHSY ry in collaring and removing the raccoon dogs. We would especially like to thank Tommy Arfman for his input in the field work.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70068>.

DATA AVAILABILITY STATEMENT

GPS-data is archived, with the permission of Saarioluonnon hoito- ja suojeluyhdistys SLHSY ry, in the MoveBank Data Repository, <https://doi.org/10.5441/001/1.659> (Toivonen et al., 2025a). Other data and code are archived in <https://doi.org/10.5281/zenodo.15273657> (Toivonen et al., 2025b). This study has been conducted using E.U. Copernicus Marine Service Information: <https://doi.org/10.48670/moi-00132> (Karvonen & Simila, 2007). The island dataset was constructed using sea and island information from Finnish Environment Institute.

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: [Coast](#), [dispersal](#), [invasive species](#).

ORCID

Pyry Toivonen  <https://orcid.org/0009-0004-4689-2574>

Vesa Selonen  <https://orcid.org/0000-0002-3126-5357>

REFERENCES

- Banfield, A. W. F. (1954). The role of ice in the distribution of mammals. *Journal of Mammalogy*, 35, 104–107. <https://doi.org/10.2307/1376080>
- Banks, P. B., Nordström, M., Ahola, M., Salo, P., Fey, K., & Korpimäki, E. (2008). Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: Review of a long-term experimental study. *Boreal Environment Research*, 13, 3.
- BirdLife International. (2020). *Melanitta fusca*. The IUCN Red List of Threatened Species 2020: e.T22724836A183801134.
- Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C. M., Dettki, H., Solberg, E. J., & Ericsson, G. (2011). A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. *The Journal of Animal Ecology*, 80, 466–476. <https://doi.org/10.1111/j.1365-2656.2010.01776.x>
- Callaghan, T. V., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., Ims, R. A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E., & Zöckler, C. (2004). Biodiversity, distributions and adaptations of arctic species in the context of environmental change. *Ambio*, 33, 404–417. <https://doi.org/10.1579/0044-7447-33.7.404>
- Chang, W., Cheng, J., Allaire, J., Sievert, C., Schloerke, B., Xie, Y., Allen, J., McPherson, J., Dipert, A., & Borges, B. (2024). *shiny: Web application framework for R*. R package Version 1.8.1.1. <https://CRAN.R-project.org/package=shiny>
- Clobert, J., Baguette, M., Benton, T., & Bullock, J. M. (2012). *Dispersal ecology and evolution*. Oxford University Press.
- Dahl, F., & Åhlén, P. A. (2010). Nest predation by raccoon dog *Nyctereutes procyonoides* in the archipelago of northern Sweden. *Biological Invasions*, 21, 743–755. <https://doi.org/10.1007/s10530-018-1855-4>
- Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 11261–11265.
- Drygala, F., Zoller, H., Stier, N., & Roth, M. (2010). Dispersal of the raccoon dog *Nyctereutes procyonoides* into a newly invaded area in Central Europe. *Wildlife Biology*, 16, 150–161. <https://doi.org/10.2981/08-076>
- Dueser, R., Moncrief, N., Keišs, O., Martin, J., Porter, J., & Truitt, B. (2013). Overwater movement of raccoons (*Procyon lotor*) in a naturally fragmented coastal landscape. *Northeastern Naturalist*, 20, 511–528. <https://doi.org/10.1656/045.020.0315>
- Herfindal, I., Melis, C., Åhlén, P.-A., & Dahl, F. (2016). Lack of sex-specific movement patterns in an alien species at its invasion front—Consequences for invasion speed. *Ecology and Evolution*, 6, 5570–5584. <https://doi.org/10.1002/ece3.2300>
- Holopainen, S., Väänänen, V. M., Vehkaoja, M., & Fox, A. D. (2021). Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. *Biological Invasions*, 23, 3795–3807. <https://doi.org/10.1007/s10530-021-02608-2>
- Jaatinen, K., Hermansson, I., Mohring, B., Steele, B. B., & Öst, M. (2022). Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure. *Oecologia*, 198, 543–552. <https://doi.org/10.1007/s00442-021-05101-8>
- Karvonen, J., & Simila, M. (2007). SAR-based estimation of the baltic sea ice motion. *Proc. of the international geoscience and remote sensing symposium 2007 (IGARSS 07)* (pp. 2605–2608).
- Kauhala, K. (1993). Growth, size, and fat reserves of the raccoon dog in Finland. *Acta Theriologica*, 38, 139–150. <https://doi.org/10.4098/AT.arch.93-12>
- Kauhala, K., Holmala, K., Lammers, W., & Schregel, L. (2006). Home ranges and densities of medium-sized carnivores in south-east Finland, with special reference to rabies spread. *Acta Theriologica*, 51, 1–13. <https://doi.org/10.1007/BF03192650>
- Kauhala, K., & Kowalczyk, R. (2011). Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: History of colonization, features behind its success, and threats to native fauna. *Current Zoology*, 57, 584–598. <https://doi.org/10.1093/czoolo/57.5.584>
- Kunnastranta, M., Niemi, M., Auttila, M., Valtonen, M., Kammonen, J., & Nyman, T. (2021). Sealed in a lake—Biology and conservation of the endangered Saimaa ringed seal: A review. *Biological Conservation*, 253, 108908. <https://doi.org/10.1016/j.biocon.2020.108908>
- Lameris, T., Hoekendijk, J., Aarts, G., Aarts, A., Allen, A., Bienfait, L., Bijleveld, A., Bongers, M., Brasseur, S., Chan, Y., Lameris, T. K., Allen, A. M., Bijleveld, A. I., Bongers, M. F., Chan, Y.-C., de Ferrante, F., Gelr, J., Derksen, H., Dijkgraaf, L., ... van Langevelde, F. (2021). Migratory vertebrates shift migration timing and distributions in a warming Arctic. *Animal Migration*, 8, 110–131. <https://doi.org/10.1515/ami-2020-0112>
- Leblond, M., St-Laurent, M. H., & Côté, S. D. (2016). Caribou, water, and ice—Fine-scale movements of a migratory arctic ungulate in the context of climate change. *Movement Ecology*, 4, 14. <https://doi.org/10.1186/s40462-016-0079-4>
- Lee, J., Raymond, B., Bracegirdle, T., Chadès, I., Fuller, R. A., Shaw, J. D., & Terauds, A. (2017). Climate change drives expansion of Antarctic ice-free habitat. *Nature*, 547, 49–54. <https://doi.org/10.1038/nature22996>
- Legagneux, P., Gauthier, G., Lecomte, N., Schmidt, N. M., Reid, D. G., Cadieux, M.-C., Berteaux, D., Bêty, J., Krebs, C. J., Ims, R. A., Reid, D., Yoccoz, N. G., Morrison, R. I. G., Leroux, S. J., Loreau, M., & Gravel, D. (2014). Arctic ecosystem structure and functioning shaped by climate and herbivore body size. *Nature Climate Change*, 4, 379–383. <https://doi.org/10.1038/NCLIMATE2168>
- Lehikoinen, A., Jukarainen, A., Mikkola-Roos, M., Below, A., Lehtiniemi, T., Pessa, J., Rajasärkkä, A., Rintala, R., Rusanen, P., Sirkiä, P., Tiainen, J., & Valkama, J. (2019). Birds. In E. Hyvärinen, A. Juslén, E. Kempainen, A. Uddström, & U.-M. Liukko (Eds.), *The 2019 Red List of Finnish species* (pp. 560–570). Ministry of the Environment & Finnish Environment Institute.
- Lewis, J. (2023). *leastcostpath: Modelling pathways and movement potential within a landscape*. R package Version 2.0.12. <https://CRAN.R-project.org/package=leastcostpath>

- Ludwig, B. (2020). Reconstructing the ancient route network in Pergamon's surroundings. *Land*, 9, 241. <https://doi.org/10.3390/land9080241>
- McMahon, B. J., Doyle, S., Gray, A., Kelly, S. B. A., & Redpath, S. M. (2020). European bird declines: Do we need to rethink approaches to the management of abundant generalist predators? *Journal of Applied Ecology*, 57, 1885–1890.
- Melis, C., Nordgård, H., Herfindal, I., Kauhala, K., Åhlén, P.-A., Strann, K.-B., & Andersen, R. (2007). Raccoon dogs in Norway—Potential expansion rate, distribution area and management implications. *Rapports Zoologiska Serien*, 3, 1–49.
- Metsähallitus. (2024). *Saariston pienpetopyynnin 2020–2023*. <https://julkaisut.metsa.fi/julkaisu/saariston-pienpetopyynnin/>
- Mulder, J. (2012). A review of the ecology of the raccoon dog (*Nyctereutes procyonoides*) in Europe. *Lutra*, 55, 101–127.
- Mustonen, A. M., & Nieminen, P. (2018). A review of the physiology of a survival expert of big freeze, deep snow, and an empty stomach: The boreal raccoon dog (*Nyctereutes procyonoides*). *Journal of Comparative Physiology. B*, 188, 15–25. <https://doi.org/10.1007/s00360-017-1114-5>
- Nordström, M., Högmänder, J., Nummelin, J., Laine, J., Laanetu, N., & Korpimäki, E. (2002). Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. *Ecography*, 25, 385–394. <https://doi.org/10.1034/j.1600-0587.2002.250401.x>
- Nummi, P., Väänänen, V.-M., Pekkarinen, A.-J., Eronen, V., Mikkola-Roos, M., Nurmi, J., Rautiainen, A., & Rusanen, P. (2019). Alien predation in wetlands—The raccoon dog and water birds' breeding success. *Baltic Journal of Forest Science*, 25, 228–237. <https://doi.org/10.46490/vol25iss2pp228>
- Øigård, T. A., Haug, T., & Nilssen, K. T. (2014). Current status of hooded seals in the Greenland Sea. Victims of climate change and predation? *Biological Conservation*, 172, 29–36. <https://doi.org/10.1016/j.biocon.2014.02.007>
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, 10, 439–446. <https://doi.org/10.32614/RJ-2018-009>
- Pitt, W. C., & Witmer, G. W. (2007). Invasive predators: A synthesis of the past, present, and future. In A. M. T. Elewa (Ed.), *Predation in organisms*. Springer.
- Porter, J. H., Dueser, R. D., & Moncrief, N. D. (2015). Cost-distance analysis of mesopredators as a tool for avian habitat restoration on a naturally fragmented landscape. *Journal of Wildlife Management*, 79, 220–234. <https://doi.org/10.1002/jwmg.829>
- Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S., Høye, T. T., Ims, R. A., Jeppesen, E., Klein, D. R., Madsen, J., McGuire, A. D., Rysgaard, S., Schindler, D. E., Stirling, I., Tamstorf, M. P., ... Aastrup, P. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325, 1355–1358. <https://doi.org/10.1126/science.1173113>
- R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rigby, R. A., & Stasinopoulos, D. M. (2005). Generalized additive models for location, scale and shape. *Journal of the Royal Statistical Society: Series C: Applied Statistics*, 54, 507–554. <https://doi.org/10.1111/j.1467-9876.2005.00510.x>
- Sala, O. E., Chapin, F. S., III, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287, 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>
- Salo, P., Korpimäki, E., Banks, P. B., Nordström, M., & Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B*, 274, 1237–1243.
- Seidler, R. G., Long, R. A., Berger, J., Bergen, S., & Beckmann, J. P. (2015). Identifying impediments to long-distance mammal migrations. *Conservation Biology*, 29, 99–109. <https://doi.org/10.1111/cobi.12376>
- Selonen, V., Banks, P. B., Tobajas, J., & Laaksonen, T. (2022). Protecting prey by deceiving predators: A field experiment testing chemical camouflage and conditioned food aversion. *Biological Conservation*, 275, 109749. <https://doi.org/10.1016/j.biocon.2022.109749>
- Selonen, V., Brommer, J. E., Klangwald, C., & Laaksonen, T. (2024). Successful invasion: Camera trap distance sampling reveals higher density for invasive raccoon dog compared to native mesopredators. *Biological Invasions*, 26, 1–10. <https://doi.org/10.1007/s10530-024-03323-4>
- Selonen, V., Toivonen, P., & Tuomikoski, E. (2024). Invasion in cold: Weather effects on winter activity of an alien mesopredator at its northern range. *European Journal of Wildlife Research*, 70, 74. <https://doi.org/10.1007/s10344-024-01824-0>
- Sievert, C. (2020). *Interactive web-based data visualization with R, plotly, and shiny*. Chapman and Hall/CRC.
- Stasinopoulos, M., & Rigby, R. (2024). *gamlss.add: Extra additive terms for generalized additive models for location scale and shape*. R package Version 5.1-13. <https://CRAN.R-project.org/package=gamlss.add>
- Stoessel, M., Elmhagen, B., Vinka, M., Hellström, P., & Angerbjörn, A. (2019). The fluctuating world of a tundra predator guild: Bottom-up constraints overrule top-down species interactions in winter. *Ecography*, 42, 488–499. <https://doi.org/10.1111/ecog.03984>
- Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68, 571–573. <https://doi.org/10.2307/3544927>
- Toivola, M. (2022). *Luonnonhoidollinen vieraspetopyynti saaristossa—Sotka-hankkeen tuloksia*. Metsähallituksen luonnonsuojelujulkaisuja, Sarja A 239. <https://julkaisut.metsa.fi/julkaisu/luonnonhoidollinen-vieraspetopyynti-saaristossa-sotka-hankkeen-tuloksia/>
- Toivonen, P., Laaksonen, T., Piironen, A., & Selonen, V. (2024). The habitat preferences of invasive raccoon dog imply elevated risks for wetland-associated prey species. *Oecologia*, 206, 73–85. <https://doi.org/10.1007/s00442-024-05614-y>
- Toivonen, P., Toivola, M., & Selonen, V. (2025a). Data from: Ice cover and partner removal increase movements of invasive mesopredator in the coastal island mosaic. *Movebank Data Repository*. <https://doi.org/10.5441/001/1.659>
- Toivonen, P. N., Toivola, M., & Selonen, V. (2025b). Data and code from: Ice cover and partner removal increase movements of invasive mesopredator in the coastal island mosaic. *Zenodo*. <https://doi.org/10.5281/zenodo.15273656>
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., BeeBee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. <https://doi.org/10.1038/416389a>
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4, 1686. <https://doi.org/10.21105/joss.01686>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B: Methodological*, 73, 3–36.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Locations of the individuals removed from the analyses.

Figure S2. Model diagnostics.

Figure S3. Partial effects of the model.

Figure S4. Hop event with the longest overwater distance estimated by least cost path minimizing overwater distance. In the background is ice cover raster (1 km² resolution) from the same date as the event and Sentinel satellite image (Sentinel-2 L2A) from 8 days later. According to the satellite image, the raccoon dog individual could have also utilized ice bridge to eliminate overwater travel completely. This ice bridge is not captured by the ice cover raster used.

Table S1. Individuals killed in Tunnhamn between June 2020 and October 2021. Date is the date of death. X and Y are the

coordinates of the kill event in EPSG:3067. N is the number of individuals killed.

Table S2. Individuals killed in Jungfruskär between October 2020 and April 2023. Date is the date of death. X and Y are the coordinates of the kill event in EPSG:3067. N is the number of individuals killed.

How to cite this article: Toivonen, P., Toivola, M., & Selonen, V. (2025). Ice cover and partner removal increase movements of invasive mesopredator in the coastal island mosaic. *Ecological Solutions and Evidence*, 6, e70068. <https://doi.org/10.1002/2688-8319.70068>