Arctic migratory raptor selects nesting area during the previous breeding season

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

IP developed the project idea. TC and IP analysed the data and wrote the manuscript. IP, OK, and MW prepared the database. KS provided valuable suggestions for data analyses. IP, OK, IF, MW, and TC conducted fieldwork. MW obtained funding. All authors took part in the preparation of the manuscript including logical interpretation and presentation of the results. All authors approved the final version of the manuscript for publication.

Keywords

habitat selection, Migration, Arctic Ecology, Rodent cycles, Rough-legged buzzard, movement ecology, prospecting movements

Abstract

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Migratory species travel large distances and thus have very little time after arrival for habitat selection. This is especially evident in arctic migrants, which are limited by a short breeding season and environmental conditions. This general time constraint is amplified in Rough-legged buzzards (Buteo lagopus) who, as many other arctic predators, rely on rodent (lemming) cycles during the breeding season, a 3-5 year period of waxing and waning local food abundance. It remains unclear how arctic predators, especially migrants, can find nesting areas where rodents peak when their selection time is so limited. Here we show that rough-legged buzzards already search for a nesting location during the previous breeding season in a post-breeding period. In the following year, individuals return to and attempt to breed in the area they inspected the year before. In the region with no rodents, buzzards prospected less and therefore showed a high level of philopatry. Therefore, as rodent cycles have been predicted to collapse in the warming Arctic, we can expect arctic predators to change their movement patterns in the future. This could potentially affect genetic diversity and cause populations to become more isolated. We anticipate our study provides a step forward towards understanding movement and settlement decisions in animals experiencing environmental conditions that strongly change between years.

Contribution to the field

The manuscript addresses how migratory animals can find a suitable breeding site in a concise time after arriving at the breeding area, especially how Arctic migrants could find the peaks of rodents, a highly unpredictable food resource. These questions have been puzzling scientists for many decades. This study found solid evidence that migrants can search and find breeding areas during the preceding breeding season. After breeding, they search for the appropriate area, and the following year, they return to this observed area for breeding. Future global warming is expected to stagnate the rodent cycles and thus shorten Arctic raptors' post-breeding movements, which could potentially affect genetic diversity and cause populations to become more isolated. This study describes the new type of habitat selection, one of the fundamental biological processes. This novel finding has general significance to biologists. It would be interesting for the specialists in organismal biology – how migratory species find nesting areas when their selection time is limited, and in population ecology – why delayed density dependence occurs among populations of migratory species. We anticipate that this strategy of deciding to inhabit a specific area much in advance will help scientists and conservationists understand the present and predict future animal movement and distribution patterns.

Ethics statements

Studies involving animal subjects

Generated Statement: Ethical review and approval was not required for the animal study because To carry out the work for this study, Pokrovsky Ivan applied for and obtained permit No. 77-18/0854/4388 from The General Radio Frequency Centre, permit No. RU/2018/406 from Federal Service for Supervision of Communications, Information Technology and Mass Media (Roskomnadzor), and permit No. RU0000045099 from Federal Security Service. No specific permissions were required from Federal Service for Supervision of Natural Resources (Rosprirodnadzor) according to §44 and §6 of the Federal Law of the Russian Federation No. 52 from 24.04.1995 (last update 24.04.2020) “On Wildlife”, and from Federal Service for Technical and Export Control (FSTEC/FSTEK) according to Russian Federation government decree No. 633 from 29.08.2001 and Letter from FSTEK No. 240/33/1373 from 06.04.2015. There were no Special Protected Natural Territories in our study area, and our activities did not include withdrawal of investigated species from nature. All our protocols met the ABS/ASAB guidelines for the ethical treatment of animals. In Nenetsky, the work was carried out in agreement with the Nenetsky Nature Reserve in a buffer zone..

Studies involving human subjects

Generated Statement: No human studies are presented in this manuscript.

Inclusion of identifiable human data

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Data availability statement

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Arctic migratory raptor selects nesting area during the previous breeding season

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Abstract

Migratory species travel large distances and thus have very little time after arrival for habitat selection. This is especially evident in arctic migrants, which are limited by a short breeding season and environmental conditions. This general time constraint is amplified in Rough-legged buzzards (*Buteo lagopus*) who, as many other arctic predators, rely on rodent (lemming) cycles during the breeding season, a 3-5 year period of waxing and waning local food abundance. It remains unclear how arctic predators, especially migrants, can find nesting areas where rodents peak when their selection time is so limited. Here we show that rough-legged buzzards already search for a nesting location during the previous breeding season in a post-breeding period. In the following year, individuals return to and attempt to breed in the area they inspected the year before. In the region with no rodents, buzzards prospected less and therefore showed a high level of philopatry. Therefore, as rodent cycles have been predicted to collapse in the warming Arctic, we can expect arctic predators to change their movement patterns in the future. This could potentially affect genetic diversity and cause populations to become more isolated. We anticipate our study provides a step forward towards understanding movement and settlement decisions in animals experiencing environmental conditions that strongly change between years.

Keywords: habitat selection - migration - Arctic ecology - rodent cycles - rough-legged buzzard - movement ecology - prospecting movements

Introduction

The decision of animals to inhabit a specific area is of significant importance for their reproduction success and survival [1]. Particularly so in migratory species that travel large distances and thus have very little time after their arrival to the breeding grounds to choose an appropriate location for reproduction. This lack of time is especially evident in arctic migrants, which are particularly limited by a short breeding season [2–4]. Another limitation for migratory arctic species is the timing of migration. Spring migration and the options for arrival to the breeding area are limited in time by the photoperiod [5] and extreme environmental conditions on the breeding grounds, such are low temperature, scarcity of food, and snow cover [6]. Another aspect to consider is the fluctuating environment of the Arctic during the reproductive season. Environmental conditions, including food resources, fluctuate highly, and arctic predators, which rely on lemmings and voles as their main food source, must efficiently track or predict this variable resource.

A key component of life in the tundra habitat is the rodent cycle (with the differences in amplitude of more than 100 fold) representing an abundant resource for numerous predators such as the stoat (*Mustela erminea*), arctic fox (*Vulpes lagopus*), long-tailed skua (*Stercorarius longicaudus*), snowy owl (*Bubo scandiacus*) and rough-legged buzzard (*Buteo lagopus*) every three to five years [7–10]. The cycle is defined by a period where lemming and vole abundance rises for a few years, reaches a peak and afterwards crashes [11, 12]. The rodent cycle, which appears as a pulsed resource, can be at the peak in one area while it might be at its lower point in another within the same season [13, 14]. While resident predator species staying year-round in the Arctic can track this pulsed and spatially heterogeneous resource [15, 16], it remains unclear how migratory species that spend only a limited time in the Arctic find the areas with rodents' peak during the concise settlement decision process. Moreover, due to climate warming, rodent cycles now appear to collapse and flatten in many Arctic regions [17–20]. Therefore, it rises a question of how these changes in rodent cycles will affect habitat selection by Arctic predators.

To tackle these questions, we used a migratory arctic breeder, the rough-legged buzzard as a model species. Rough-legged buzzard specialises in small rodents during the breeding season. However, it can breed in areas with no rodents and shift to alternative prey [21–24]. Yet, small rodents are the preferred food source for buzzards and feeding on rodents (at its peak) during the breeding season results in higher breeding success of individuals [8, 10]. Rough-legged buzzards in our study breed either in the areas with a cyclic density of rodents (Nenetsky, Vaigach and Yamal) or in areas with no rodents (Kolguev Island), where a variety of geese species breed in large numbers annually [25], providing a stable resource for the rough-legged buzzard [24]. Thus, areas with rodent cycles are for the purpose of this study classified as "variable resource" areas and areas with no rodents as "stable resources".

Here, we hypothesize that rough-legged buzzards select nesting areas during the previous breeding season. The typical shape of the rodent cycle consists of four years with about three years of increasing rodent numbers (from low to medium to peak abundance) followed by a rapid crash thereafter (from the peak to low abundance) [11, 12]. Thus, if arctic predators were to predict rodent abundance for their next breeding season, they would win in three and lose in one out of four cases. Therefore, if a breeding area is in the "variable resource" region, buzzards after the nesting season would search for a suitable future nesting area for the following year. After such a phase of prospecting movement, i.e., potential search for a nesting area, it would migrate to the wintering area, and after returning from spring migration, attempt to breed in a suitable nesting area that it had found in the previous summer. At the same time, if a breeding area is in the "stable resource" region (i.e., with no rodents), buzzards after breeding would have minimum or no prospecting movement. They would stay in their nesting area until the end of the breeding season, afterwards migrate South to overwinter, and return in spring to the same area for breeding. The hypothesis is illustrated on Figure 1.

Prospecting movements is a widespread phenomenon in bird ecology [26–29]. It was shown that birds could choose the future nesting habitat during the previous year [27] and that birds with bad breeding performance tend to change the nesting territory more often [30–32]. Therefore, failed breeders should prospect more than successful conspecifics. Thus, we could expect that rough-legged buzzards would stay in the Arctic during the whole breeding period regardless of their breeding success. At the same time, failed breeders will have extra time available during the breeding season to search for a suitable breeding area for the following year and, thus, will prospect more than successful breeders. Although the existing studies provide us with a good basis for assumptions of Arctic raptors behaviour, most of the studies on prospecting movements were on non-breeding birds [28, 29] or breeding passerine birds [27, 30, 33], which change their breeding site in a fairly limited space (5-10 sq km); and the main methods for these studies were ring recoveries and field observations. All of this together raises the question of whether this phenomenon can be relevant for species that change their breeding territory by hundreds or thousands of kilometres, such as rough-legged buzzards. And whether this phenomenon may thus explain the ability of arctic raptors to find regions with rodent peaks in the tundra. Nowadays, modern tracking technologies allow us to monitor the prospecting behaviour of the birds on a big scale with precise details and find out how raptors search for the rodent peaks and how they can adapt to the changes happening in the Arctic.

Our specific predictions are as follows: (i) buzzards, regardless of nesting success, will remain in the Arctic for the rest of the summer. Failed breeders will not migrate to the wintering grounds earlier. We expect no difference between successful and unsuccessful breeders but also for the non-breeding individuals in the timing of departure. (ii) Individuals who failed to breed will have extra time available during the breeding season to search for a suitable breeding area for the following year. Thus, failed breeders will prospect more (travel larger distances, cover larger areas and move further away from the nest) than the successful breeders. (iii) In areas with stable resources, buzzards will prospect less than in the areas with variable resources since food resources are stable and individuals do not need to travel far to find alternative suitable nesting areas. (iv) Individuals will return to the area they explored during the previous breeding season. Regardless of areas with stable or variable resources, buzzards would return to the exploration area, i.e., the potential nesting area they selected during the previous post-breeding period.

Note that throughout the text, we use the term "nesting area" for the area where rough-legged buzzards breed, "post-breeding period" for the period in the breeding season after a breeding attempt, "prospecting" for the potential search for a new nesting area during the post-breeding period, and "exploration area" for the area individuals prospected during the previous season and potentially return to in the following breeding season.

Materials and methods

Study area

Fieldwork was conducted in June-August 2013-2019 in NW Russia on four study sites (Figure 2): Kolguev Island in the Barents Sea (hereafter Kolguev, $69°16'N$, $48°87'E$) in years 2013, 2015, 2017-2019; Nenetsky Nature Reserve in the Pechora river lowlands (hereafter Nenetsky, $68°20'N$, $53°18'E$) in 2014; Vaigach Island (hereafter Vaigach $69°43'N$, $60°08'E$) in 2015; and 'Erkuta' tundra monitoring site in the southern part of Yamal peninsula (hereafter Yamal, $68°12'N$, $68°59'E$) in 2016. For the details on permits, see the ethical statement in the Suppl. material.

Data collection

Between 2013 and 2020, we tracked 43 adult rough-legged buzzards (35 females and 8 males). We caught birds with bow nets on the nests and equipped them with 45g solar GSM-GPS-ACC loggers (e-obs GmbH) and 15g solar GSM-GPS loggers (UKn - University of Konstanz, Model ”Lika”) using a Teflon harness. E-obs loggers were attached on 28 individuals, UKn loggers on 13 and two individuals were first equipped with UKn loggers that were later replaced with e-obs loggers. E-obs loggers recorded GPS locations and 3D body acceleration during 24 hours/day. GPS positions were recorded every hour (full battery) and every 5 hours (normal battery). Three-axial body acceleration was measured every 5 min for 3.8 s at 10.54 Hz (40 data points per axis and 120 data points per ACC burst). Data were stored and then downloaded via GSM mobile phone network using GPRS technology or via UHF radio link using handheld base stations. UKn loggers recorded GPS positions every hour (full battery) and every 12 hours (normal battery) 24 hours/day.

In addition to the GPS data, we also collected information on the nest locations of the breeding individuals and the nesting success for each year (n=87). We estimated nest location and nesting success for 40 annual trajectories of individuals (9 for males and 31 for females) using direct field observations. For 47 annual trajectories (all of them females), we estimated the location of the nest and inferred nesting success from the bio-logging data (GPS and accelerometer) in the following way: If the bird stayed in one place (the difference between coordinates was <3m) for more than one day (24 hourly positions), we considered it as the beginning of incubation and this position as the nest coordinates. We verified this assumption with information about the bird’s body’s position for birds for which we used loggers with accelerometers (28 bird-years). In all cases, the accelerometer showed that the birds at this time were in a horizontal position, which is possible if the bird is flying, or incubating a clutch or covering the nestlings. If the bird stayed on the nest for more than 50 days from the start of incubation, we considered it a successful nest. The threshold of 50 days was used because the incubation period in wild rough-legged buzzards is at least 31 days [34] and after hatching, a female stays at the nest more or less continuously until young are 17-22 days old [22]. If a bird stayed less than 50 days in a nest, we assumed that it failed to breed. We verified our distinction between the failed and successful breeders with the direct observations, and in all cases, we correctly predicted nesting and breeding status. Therefore, for 87 annual trajectories, we estimated breeding attempts, and if a bird tried to breed, we estimated the nest coordinates. For 70 annual trajectories, we estimated the nesting success (successful/failed) and nesting duration (number of days the bird was incubating and feeding nestlings).

Data analyses

After removing outliers and duplicated timestamps, the data set comprised 43 individuals, 133 annual trajectories and 268.977 positions (Figure 2).

First, we investigated the relationship between the departure day from the breeding grounds and nesting performance. For each individual trajectory (GPS locations of a bird during the specific year), we noted the date when it crossed the latitude of 64 degrees (the approximate southern border of the breeding area of the rough-legged buzzard in this region) during the autumn migration. If the difference in days between the first GPS position before and the first position after a bird crossed the 64 degrees latitude was less than ten days, we used the mean value as a departure location and its corresponding date as departure day. If the difference was more than or equal to ten days, we did not use the departure day for the analysis as the calculated mean location was not likely to represent the departure location and, thus, departure day reliably. In total, we had 71 departure days for 35 birds from 2013-2020. When individuals crossed a latitude of 64 degrees more than once, we recorded the first crossing as a departure/arrival location.

Second, we compared prospecting movement between the individuals that bred in an area with stable resources and those that bred in an area with variable resources (Figure 1). Furthermore, we compared prospecting movement after breeding attempt between the individuals who failed to breed and those who bred successfully. Prospecting movement was assessed for GPS locations between the nest location and the location corresponding to the date of 10 days before the departure location. The threshold of 10 days was selected based on visual inspection of a different set of locations included with different thresholds. By removing 10 days before departure, we made sure to include only locations that are a part of prospecting movement and avoided including locations that were already part of autumn migration. Prospecting movement was quantified by the cumulative distance (using ”move” R package [35]), area covered using the 95% MCP - Minimum Convex Polygon estimator (”adehabitatHR” R package [36]), and the distance from the nest to each GPS location (using ”raster” R package [37]). The three parameters were calculated by including the first five data points (GPS locations) and every step adding an additional data point (e.g. 95% MCP was estimated for the first five locations, then again for six locations, for seven locations, etc. until all locations were included). In total, we calculated the three parameters for 14 individuals that bred in an area with stable resources (5006 data points) and 13 individuals that bred in an area with variable resources (4686 data points).

Third, we assessed whether individuals that failed to breed the following breeding season returned to the same area they inspected the year before i.e. exploration area and attempted to breed (Figure 1B). To test whether individuals inspected the area they returned to the following year to breed, we calculated the minimum distance between each GPS location of an individual's annual trajectory to the nest location of the following year (using "sp" R package [38, 39]). We calculated these trajectory-to-nest distances for individuals that failed to breed and those that bred successfully for a total of 18 individuals (35 data points). To test if successful breeders return to the same area to breed and failed breeders to the different area, we calculated the distance between the nest locations of the current and the following year (20 individuals, 37 data points) and compared them between the failed and successful breeders.

Statistical analysis

We tested whether rough-legged buzzards stay in the Arctic until the end of the breeding season, regardless of the nesting success and duration. We ran a linear mixed model (LMM) with departure day as a response variable, nesting success as a fixed effect and bird ID as a random effect, and a linear model (LM) with departure day as a response variable and nesting duration as a predictor. To account for pseudoreplication in the LM, we ran ten models each with one year per individual included (years per individual included in each model were randomly selected) and performed model averaging. We additionally checked whether the sex of individuals or season (year) influence departure days. We used LMMs with departure days as a response variable, year as a fixed effect and bird ID as a random effect. We ran 10 LMs and performed model averaging as described above.

Next, we investigated if failed breeders prospected more during the post-breeding period than successful breeders and if this difference was more pronounced in individuals breeding in areas with variable than in areas with stable resources. Prospecting behaviour of individuals that bred successfully and those that failed to breed was investigated using LMMs with log cumulative distance, log MCP or log trajectory-to-nest distance included as a response variable, an interaction between the Julian day and nesting success as a predictor and annual trajectory identity as a random effect. We ran the three models separately for stable and variable resources and performed a model averaging of 10 models, so that in each model, only one bird ID per annual trajectory was included. The inclusion of annual trajectory in the models was randomly selected. To average the models, the sample sizes of data sets used for models had to be the same, thus we used an approximate minimum sample size of randomly selected rows per annual trajectory included (n = 1800 for stable resources and n = 2000 for variable resources).

Additionally, we compared prospecting behaviour between individuals in areas with variable vs. those in areas with stable resources. We used LMMs with log MCP or log trajectory-to-nest distance included as a response variable, prey variability as a predictor and bird ID as a random effect. In the case of log cumulative distance, the LMM did not converged so we ran ten models each with one year per individual included and performed model averaging as described above.

For all models, we first performed an overall test of full-null model comparison. We fitted the LMMs with a restricted maximum likelihood method using lmerTest [40]. Model averaging was performed using the "MuMIn" R package [41]. Assumptions of normally distributed and homogeneous residuals were fulfilled.

Results

Departure days

Rough-legged buzzards stayed in the Arctic during the post-breeding period, and the timing of departure from the breeding grounds was similar for the individuals that bred successfully (mean ± SE: 276.4 ± 1.9, n = 29) and those that failed to breed (mean ± SE: 278.8 ± 1.6, n = 27). Five individuals that did not attempt to breed departed from the breeding grounds at the similar time than the other two groups (mean ± SE, 272.0 ± 4.3, n = 5). The model results confirmed that failed and successful breeders departed from the breeding grounds at the approximately same time (full-null model comparison: $\chi^2 = 1.56$, df = 1, P = 0.21; Table S1; Figure 3). Also, nesting duration of individuals that failed to breed did not influence the timing of departure (Table S2; Figure 3). Note that no full-null comparison is provided for this model since we performed model averaging and used only one annual trajectory per individual (Sum of squares = 3.65, df = 1, P = 0.814).

Departure days significantly differed between the years (2013 - 2020) with the timing of departure becoming later every year (full-null model comparison: $\chi^2 = 34.45$, df = 7, P 0.001; Table S3; Figure S1). However, each year, we had a similar proportion of successful vs failed breeders (mean ± SE; failed: 4.6 ± 1.2, successful: 4.8 ± 1.0), meaning that our results were not year-dependent.

Prospecting behaviour

All three parameters measuring prospecting behaviour during the post-breeding period, cumulative distance, MCP and trajectory-to-nest distance, had higher values for failed than successful breeders.

Cumulative distance measured for birds breeding in stable resources increased with Julian day significantly more for individuals that failed to breed than for individuals that bred successfully (full-null model comparison: $\chi^2 = 2287.8$, df = 3, $P < 0.001$; Table S4; Figure 4A). For birds breeding in variable resources, the cumulative distance also increased with Julian day and was influenced by the nesting success (full-null model comparison: $\chi^2 = 2772.6$, df = 3, $P < 0.001$; Table S5; Figure 4B).

MCP increased with the Julian date and was significantly larger for individuals that failed to breed than for individuals that bred successfully. This effect was seen in individuals that bred in stable resources (full-null model comparison: $\chi^2 = 841.1$, df = 3, $P < 0.001$; Table S6; Figure 4C) as also for individuals that bred in variable resources (full-null model comparison: $\chi^2 = 1225.9$, df = 3, P = 0.002; Table S7; Figure 4D).

Trajectory-to-nest distance increased with the Julian day and it was significantly larger for failed breeders than for successful breeders. This was the case for individuals breeding in stable resources (full-null model comparison: $\chi^2 = 139.7$, df = 3, $P < 0.001$; Table S8; Figure 4E) and also for individuals breeding in variable resources (full-null model comparison: $\chi^2 = 1035.8$, df = 3, $P < 0.001$; Table S9; Figure 4F).

Furthermore, individuals breeding in areas with variable resources explored larger areas and travelled more and further from the nest than those breeding in areas with stable resources (Table S10-S12; Figure 5). Full-null model comparison showed significant results for cummulative distance (Sum of Squares = 0.0, Res. Df = 27, $P < 0.001$), MCP ($\chi^2 = 5.8$, df = 1, P = 0.016) and trajectory-to-nest distance ($\chi^2 = 8.7$, df = 1, P = 0.003).

Return to the explored area

Both successful and failed breeders returned to the area they explored during the previous breeding season. The minimum distance measured between an individual´s annual trajectory and nest location of the following year was comparable between individuals in stable and those in areas with variable prey (Figure 6). The mean (± SE) distance for stable resources was 5.2 ± 4.8km (range: 0.0m - 115.4km, n = 24) and for variable prey was 8.7 ± 7.2km (range: 1.5m - 80.5km, n

= 11). When removing outliers of 115.4km and 80.5km, the mean ± SE is 0.4 ± 0.1km (range: 0.3m - 2.2km) for stable and 0.4 ± 0.1km (range: 1.5m - 6.9km) for variable prey. These are the two cases where individuals upon spring migration flew in the direction of the nest location of the previous year but decided to settle before reaching that location (Figure S2).

The distance between the nest locations of the current and the following year was smaller for stable then for variable prey (Figure 7). The mean (± SE) distance for stable prey was 2.2 ± 0.7km (range: 2m - 17.2km, n = 24) and for variable prey was 63.6 ± 27.9km (range: 0.2km - 341.4km, n = 13). When removing outlier of 341.4km the mean ± SE is 40.5 ± 17.0km (range: 0.2 - 139.0).

Discussion

We hypothesised that rough-legged buzzards select nesting areas during the previous breeding season, and we found evidence for this behaviour from our data. We clearly showed that rough-legged buzzards return and attempt to breed in the exploration area, i.e. the area they inspected the year before.

First, we showed that the departure date from the breeding grounds did not differ between the individuals that failed to breed, bred successfully or those that did not attempt to breed. Meaning, that also after nesting failure, individuals stayed in the Arctic. The reason for staying could be extra time available that they could use to search a nesting area for the following year.

Second, both failed and successful breeders prospected during the post-breeding period. Failed breeders prospected more than successful breeders, likely because they had more time to explore the area after the failed breeding attempt. However, this result could also suggest that failed breeders are more eager than successful breeders to find a suitable nesting area for the following year. The difference in prospecting between the failed and successful breeders was especially evident in areas with variable resources, while the difference in areas with stable resources was smaller. A likely explanation is that Kolguyev Island provides stable resource-rich habitat [25], so individuals do not need to search for an area far away from their initial breeding site. During the entire study, not a single bird has left the island during the prospecting movement. This behaviour indicates that the main reason for the prospecting movement in the post-breeding period is the search for the territory with a high density of preys.

Third, Rough-legged buzzards that failed to breed as well as those that bred successfully returned to the area they explored the year before. Breeding success did not determine if individuals will return to the same nesting area. In some cases, failed breeders could search for a nest location but still return to the same area to breed since they did not find a more suitable location. In contrast, successful breeders could find a more suitable nesting area during their prospecting movement and return to that area for breeding in the following year. However, regardless of the breeding success or how much they prospected, rough-legged buzzards bred in the area they have previously surveyed. We had only two exceptions to this rule.

Two individuals which bred successfully, in the following year during the spring migration were moving towards their nest location of the previous year but stopped before the coast (Figure S2, Figure 5). The reason could be that they found a suitable nesting area on the way and decided to settle, or at the time of arrival to the coast, the wind conditions were not suitable for crossing, so they decided to settle on the mainland. Wind conditions are indeed an important factor when deciding to cross water bodies [42]. Yet, in the following years, individuals returned to the same area for breeding (Figure S4). This behaviour suggests that rough-legged buzzards could have mixed two-phase habitat selection. They select the future breeding territory during the post-breeding period and may refine their choice during the following year. In the second phase, they may either find a better territory en route to a previously selected area (Figure S2, Figure 5) or decide not to breed if breeding conditions in the designated location have turned out to be poor.

Described two-step habitat selection could explain the asynchrony encountered in the density dynamic of arctic raptors and their prey. While the density of rough-legged buzzards is usually highest in the years with a peak of rodents [8, 10], sometimes it could be highest in the year after the rodent peak [23]. The latter type of predator-prey density dependence is well known and explained by a series of time-delayed numerical responses. However, it is characteristic of sedentary resident specialist predators [43], and there was no clear explanation of this dynamic for migratory species. Migratory raptors were assumed to find the territory with a high density of prey during habitat selection. However, if habitat selection occurs a year before, as we showed in this study, their density should be highest year after year with the highest prey density. At the same time, predators who arrived on the territory with a low prey density could decide not to nest in that season. Thus, as a result, for rough-legged buzzards, we could meet both types of predator-prey density dynamic – either delayed or direct density dependency.

With the global change, rodent peaks are predicted to become less regular [18, 19]. In several areas across the Arctic, the rodent cycles already started to stagnate [20]. We do not have precise information on rodent cycles for our entire study area, but in the areas close to our study sites, the cycles are still evident [20]. Yet, in the future, we can expect that with less evident lemming cycles, rough-legged buzzards will likely switch to alternative prey and thus change their movement patterns. We speculate that prospecting movement during the breeding season in failed breeders would become less evident with shorter distances and smaller areas covered. This could potentially affect genetic diversity and cause populations to become more isolated, as was the case for peregrine falcons (*Falco peregrinus*) [44].

In summary, we showed that the prospecting movement during the post-breeding period plays an important role in finding a nesting area for the following year. Such a way of dealing with a lack of time and extreme arctic environment suggests that rough-legged buzzards have highly developed spatial memory due to memory-demanding ecological conditions, maybe more than it was previously thought [45]. We expect that this strategy is used by many migratory species, both non-breeders [28,46] as well as breeders [27,33,47] but especially Arctic birds or other animals that face limited time for breeding, fluctuating resources, and harsh environmental conditions. This type of habitat selection shed light on the questions of autecology - how migratory species find nesting areas when their selection time is limited, and synecology – why there is delayed density dependence among migratory species. This study is a step forward in understanding movement and settlement decisions in animals experiencing changing environmental conditions and help us to predict future changes caused by climate warming in the Arctic.

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Author contributions

IP developed the project idea. TC and IP analysed the data and wrote the manuscript. IP, OK, and MW prepared the database. KS provided valuable suggestions for data analyses. IP, OK, IF, MW, and TC conducted fieldwork. MW obtained funding. All authors took part in the preparation of the manuscript including logical interpretation and presentation of the results. All authors approved the final version of the manuscript for publication.

Data availability

The data is a part of the Arctic Animal Movement Archive. We also intend to archive the data on Movebank data repository.

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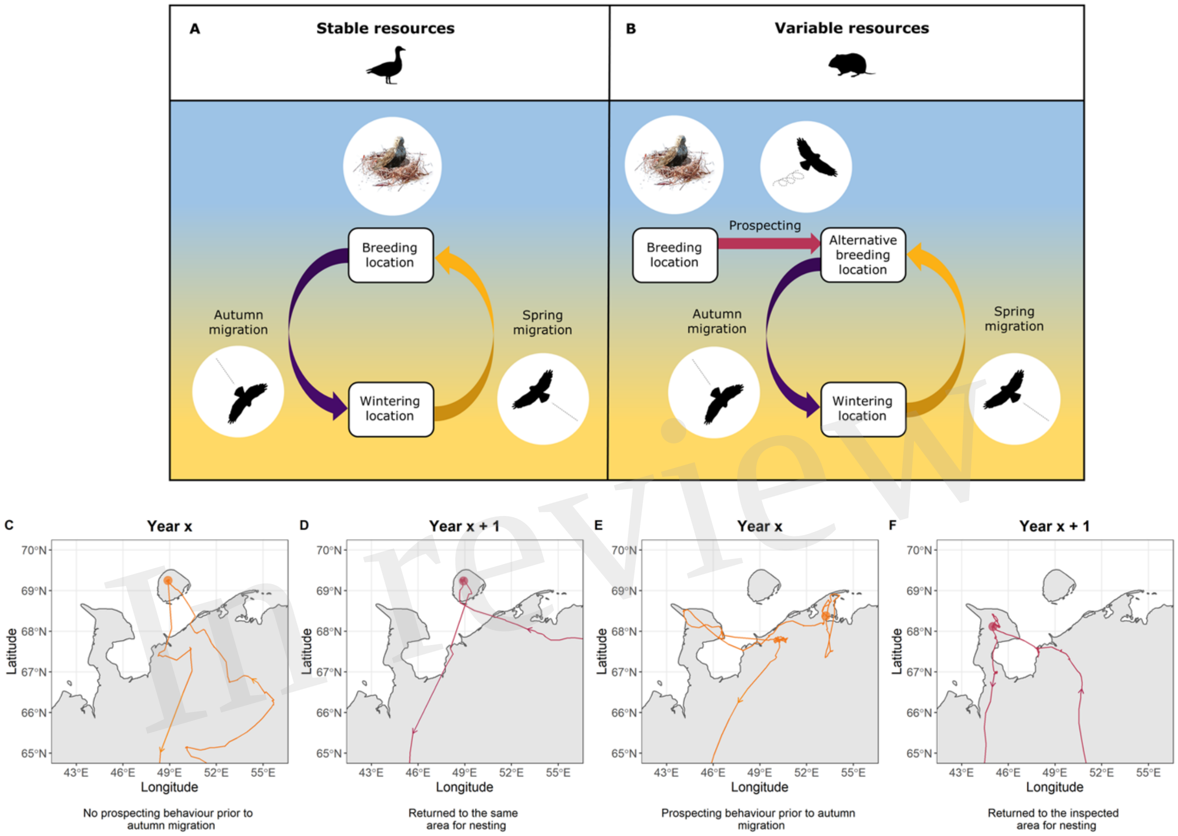

No prospecting behaviour prior to autumn migration

Returned to the same area for nesting

Prospecting behaviour prior to autumn migration

Returned to the inspected area for nesting

Figure 1: The overall scheme of the hypothesis. (A) If an individual breeds in areas with stable resources, it stays within the nesting area until the end of the breeding season, afterwards migrates to the south to overwinter and in spring returns to the same area for breeding. (B) If an individual breeds in areas with variable resources, it leaves the nesting area and searches for a suitable nesting area for the following year. After this phase of prospecting movement, it migrates to the wintering area and after spring migration, it attempts to breed in the suitable nesting area that it found in the previous summer. (C-F) Exemplary trajectories for two consecutive years of (C, D) individual that breeds in areas with stable resources and (E, F) individual that breeds in areas with variable resources. Nest locations are marked with dots and arrows represent movement direction.

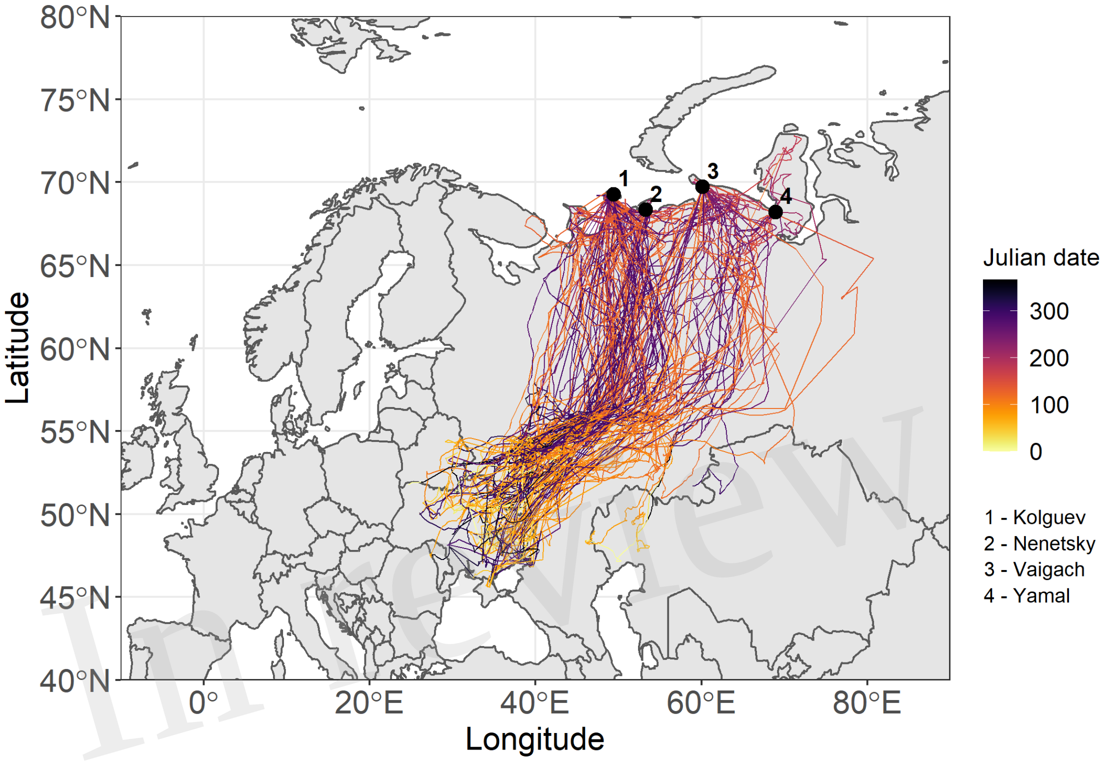

Figure 2: GPS trajectories of 43 rough-legged buzzards (133 annual tracks). The colour gradient represents Julian date. Locations of the study sites are marked with black dots.

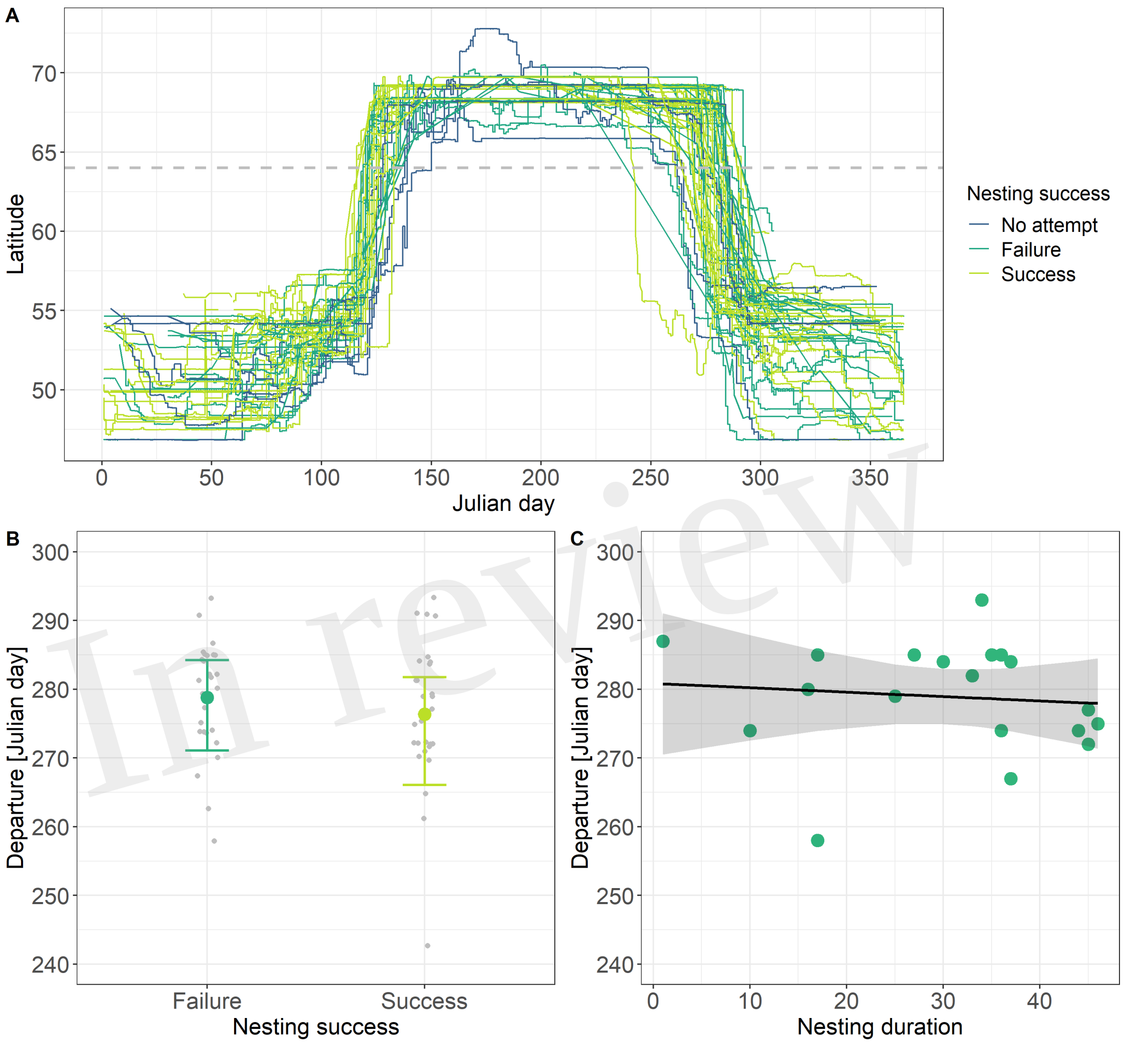

Figure 3: Relationship between the nesting success and departure days in rough-legged buzzards. (A) Latitude change during the annual life-cycle. (B) Departure day as a response of nesting success (predicted 95% CIs from LMM using the bootstrapping method and 500 simulations in "ciTools" R package [48] with lower limit representing minimum CI and upper limit representing maximum CI; grey dots represent raw data). (C) Departure day as a response of nesting duration of individuals that failed to breed (predicted CIs from LM with only one year of data per individual included; blue dots represent raw data).

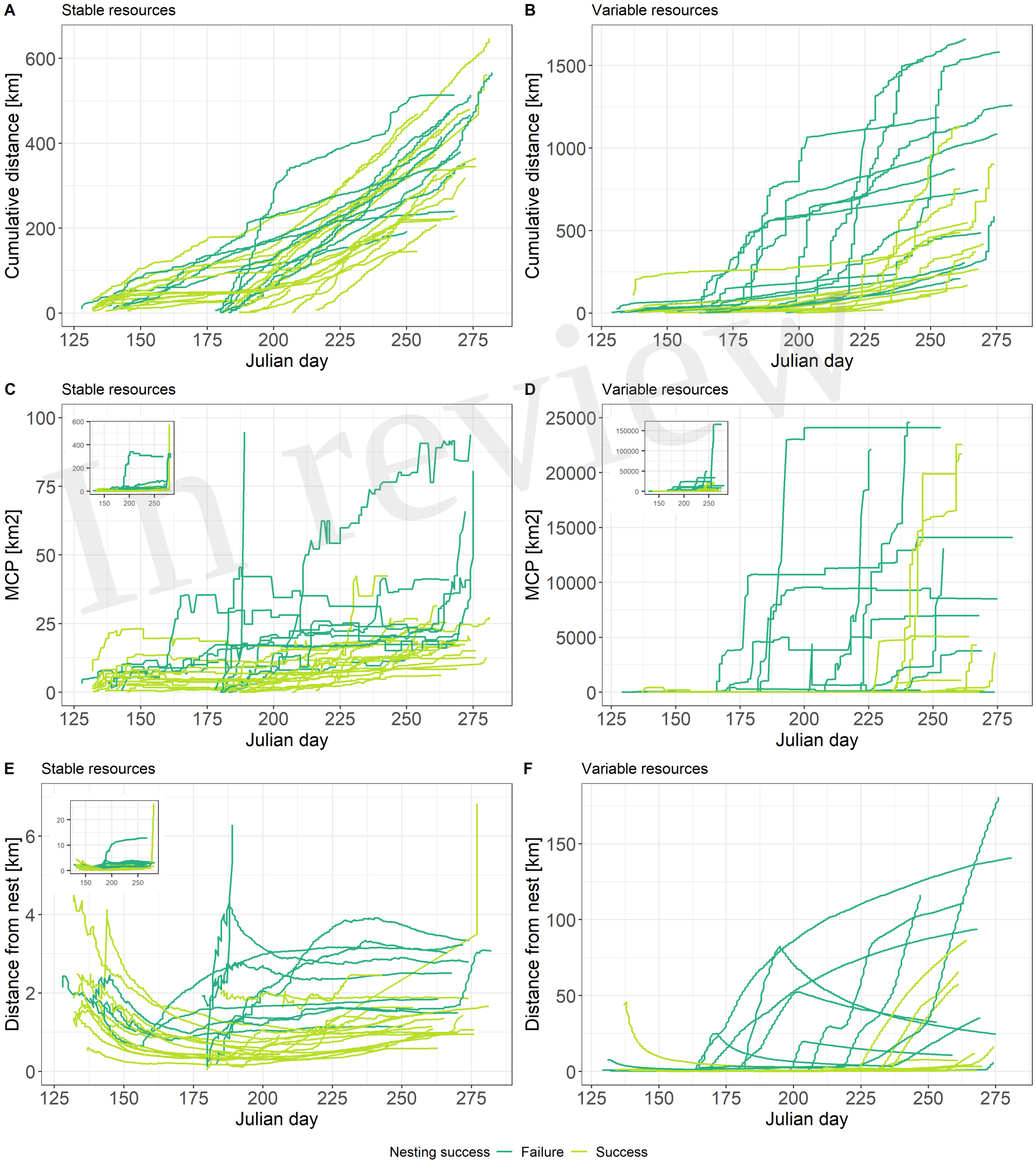

Figure 4: (A) Cummulative distance as a function of julian date for stable resources. (C) Cummulative distance as a function of julian day for variable resources. (C) MCP as a function of julian day for stable resources. (D) MCP as a function of julian day for variable resources. (E) Nest distance as a function of julian day for stable resources. (F) Nest distance as a function of julian day for variable resources.

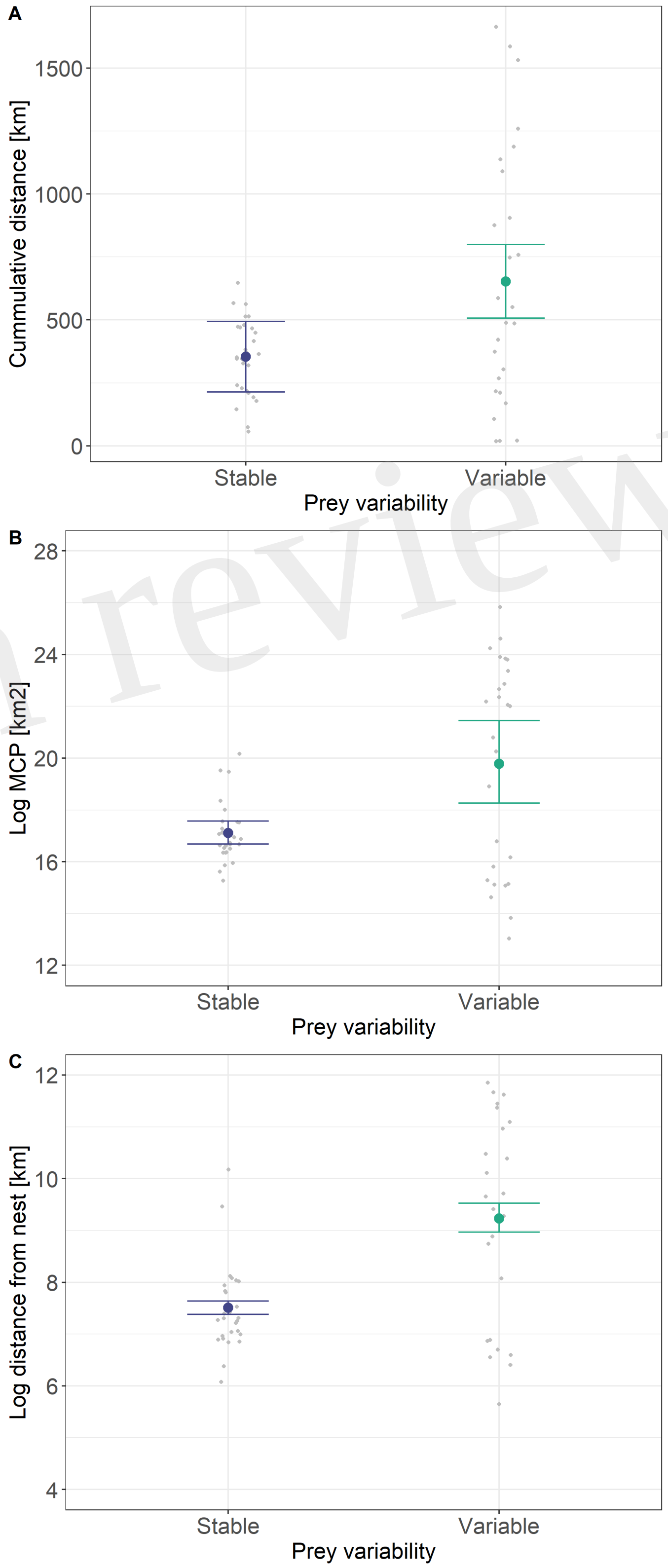

Figure 5: (A) Cummulative distance (B) MCP and (C) distance from nest as a function of prey variability (stable vs variable).

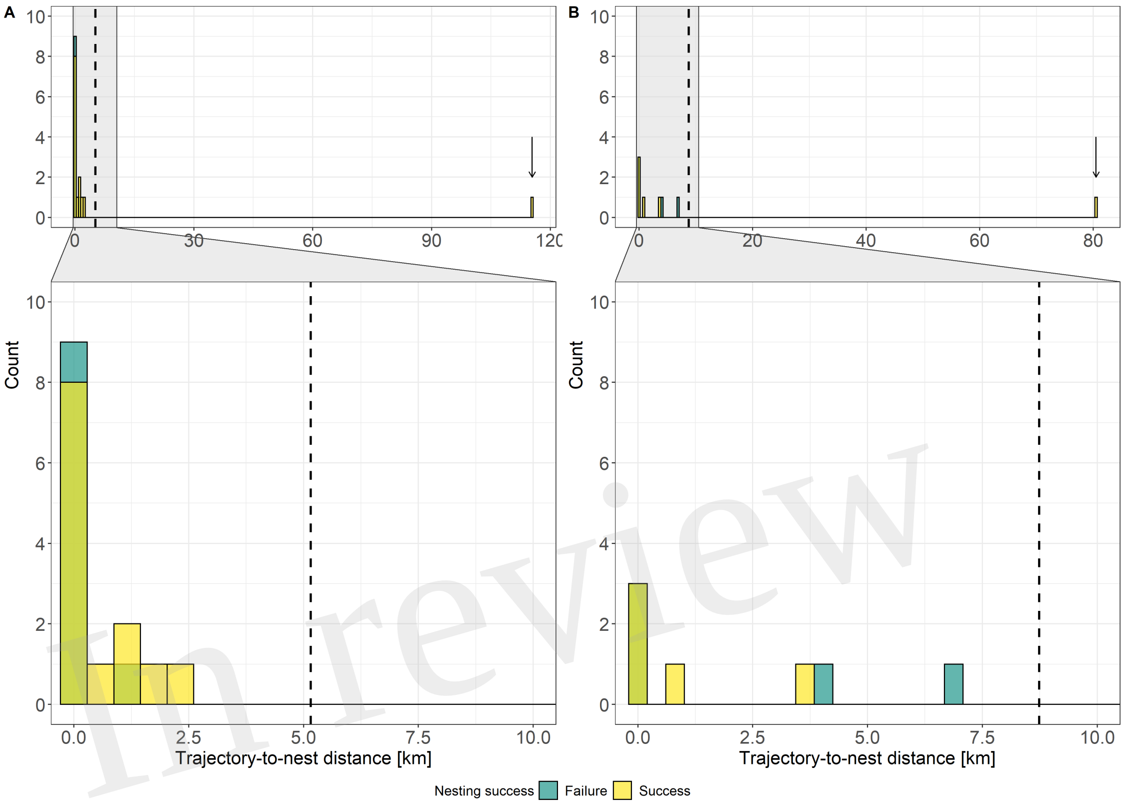

Figure 6: Histogram of the minimum distance between the trajectory of the current year and nest location of the following year (trajectory-to-nest distance) for (A) stable and (B) variable resources. Dashed line represents the mean value.

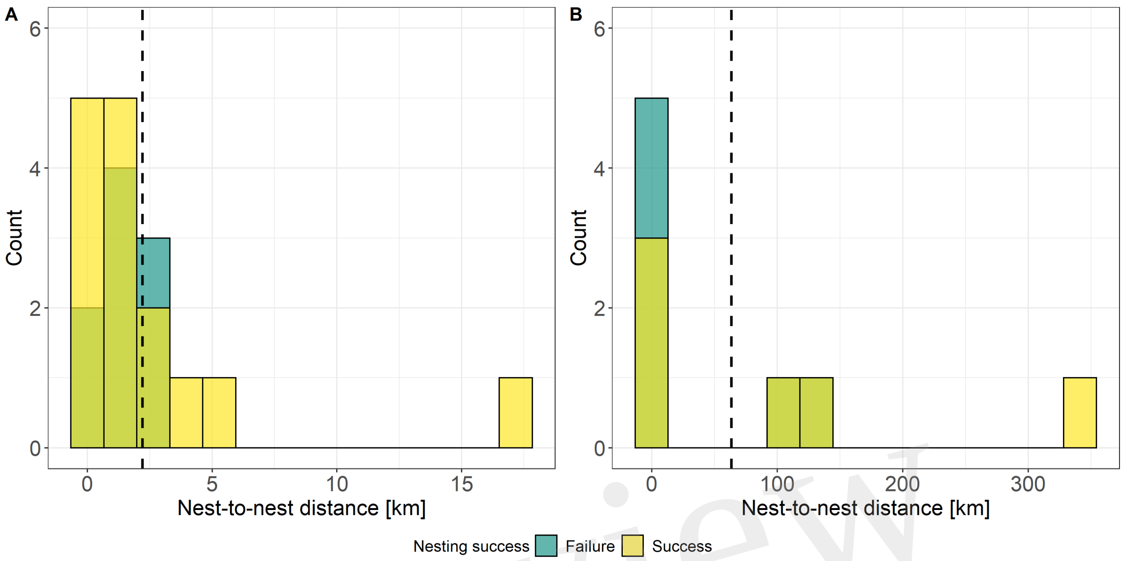

Figure 7: Histogram of the distance between the nests of the current and the following year (nest-to-nest distance) for (A) stable and (B) variable resources. Dashed line represents the mean value.

Figure 1.TIFF

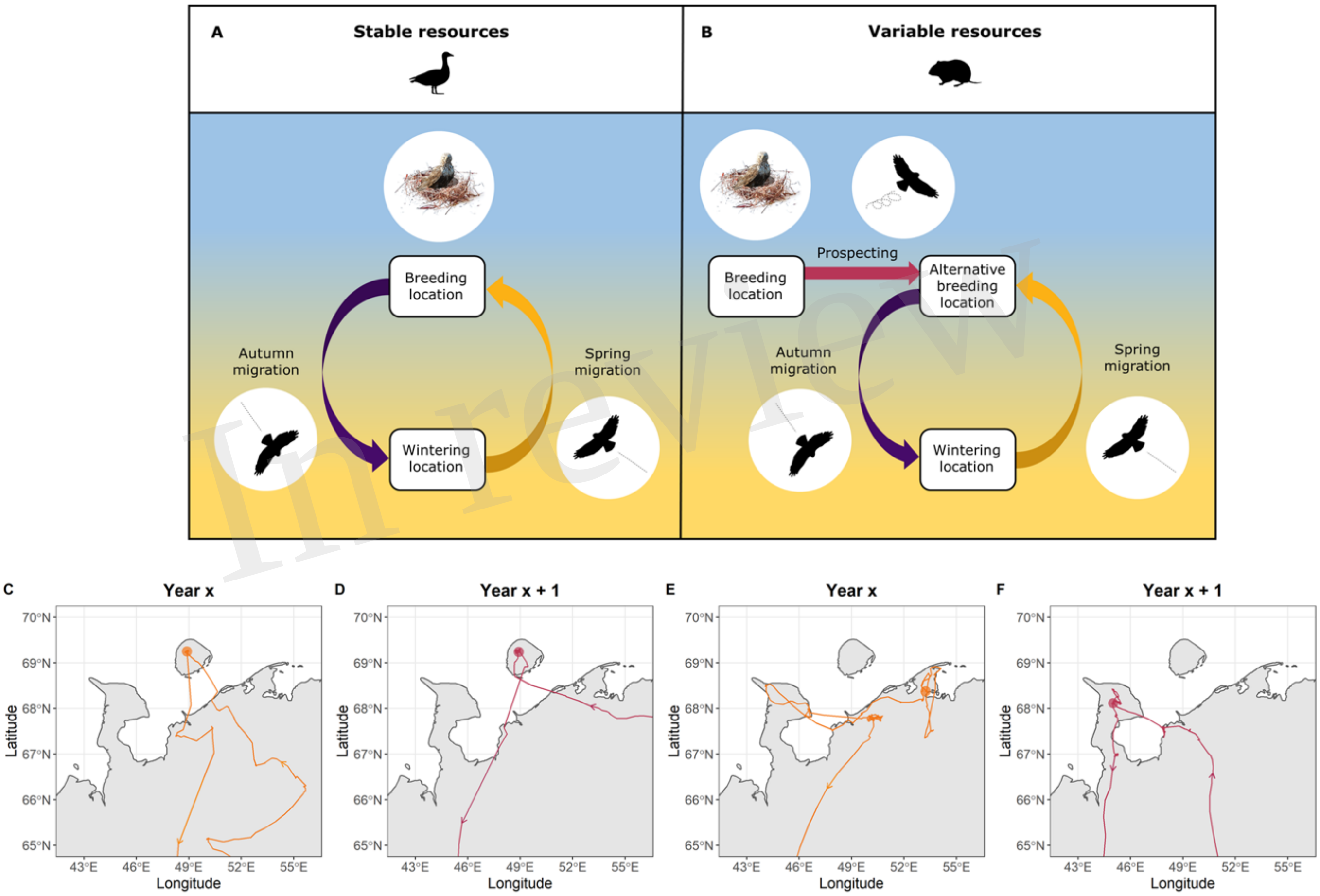

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Figure 2.TIFF

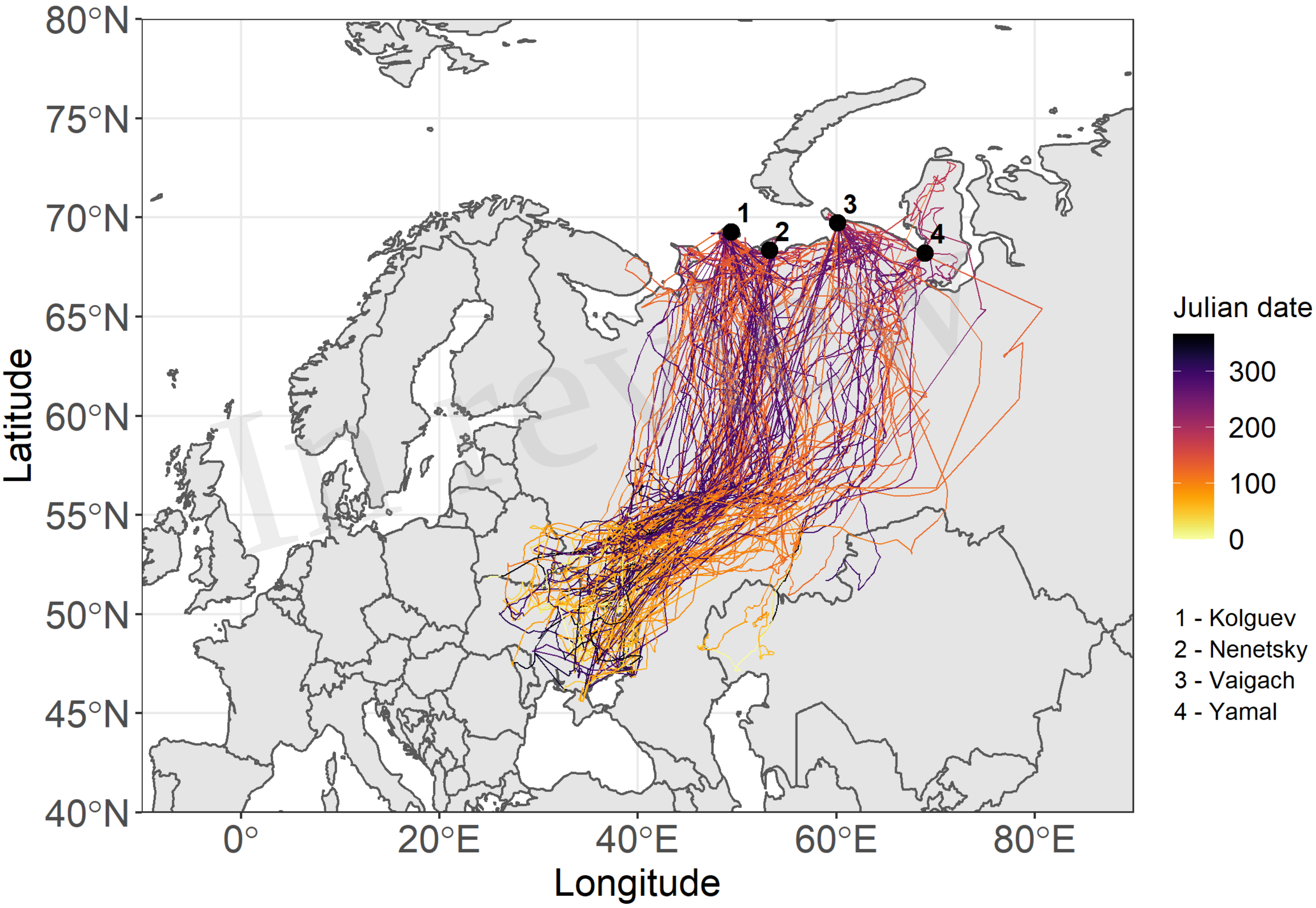
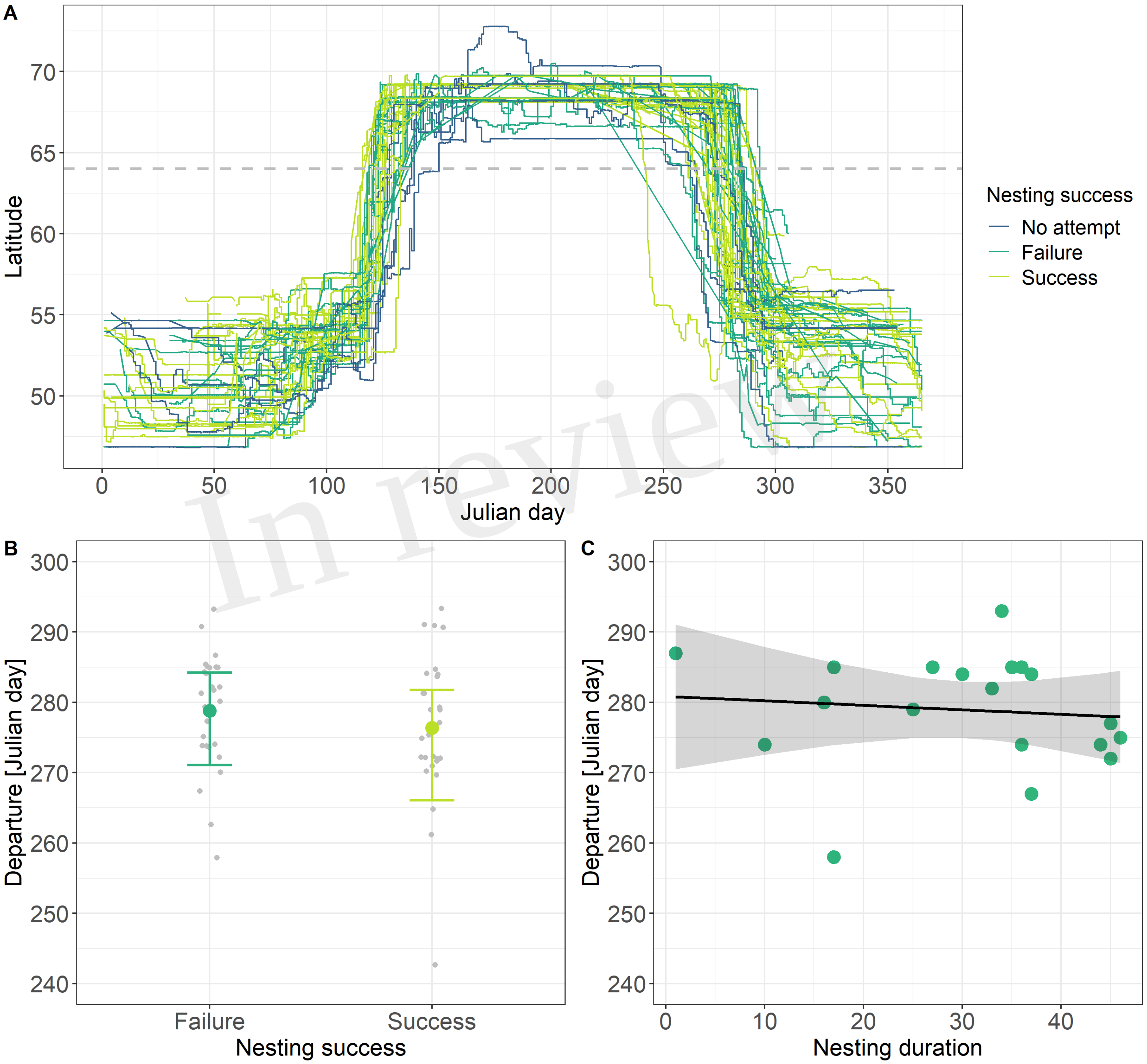


Figure 3.TIFF



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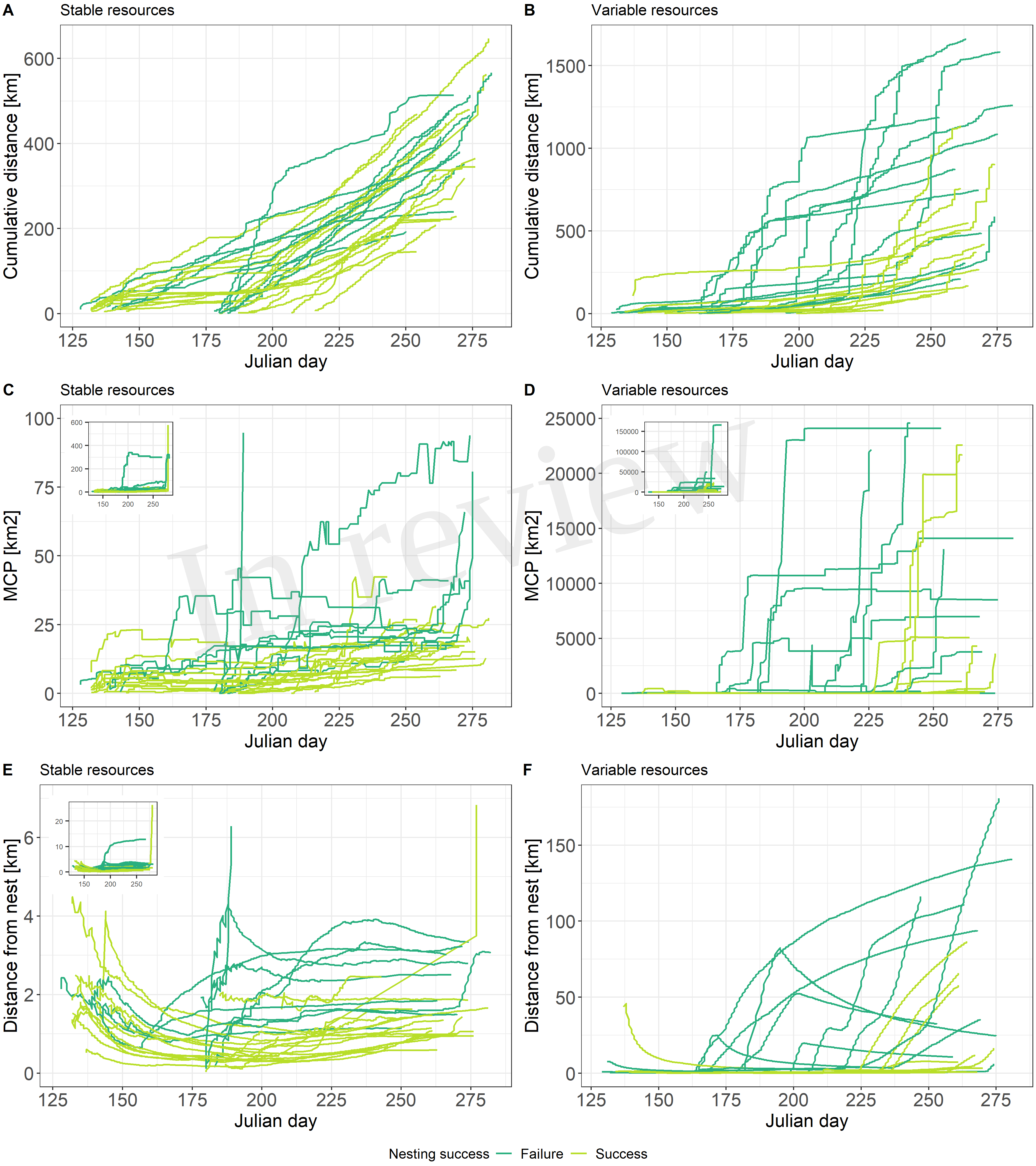

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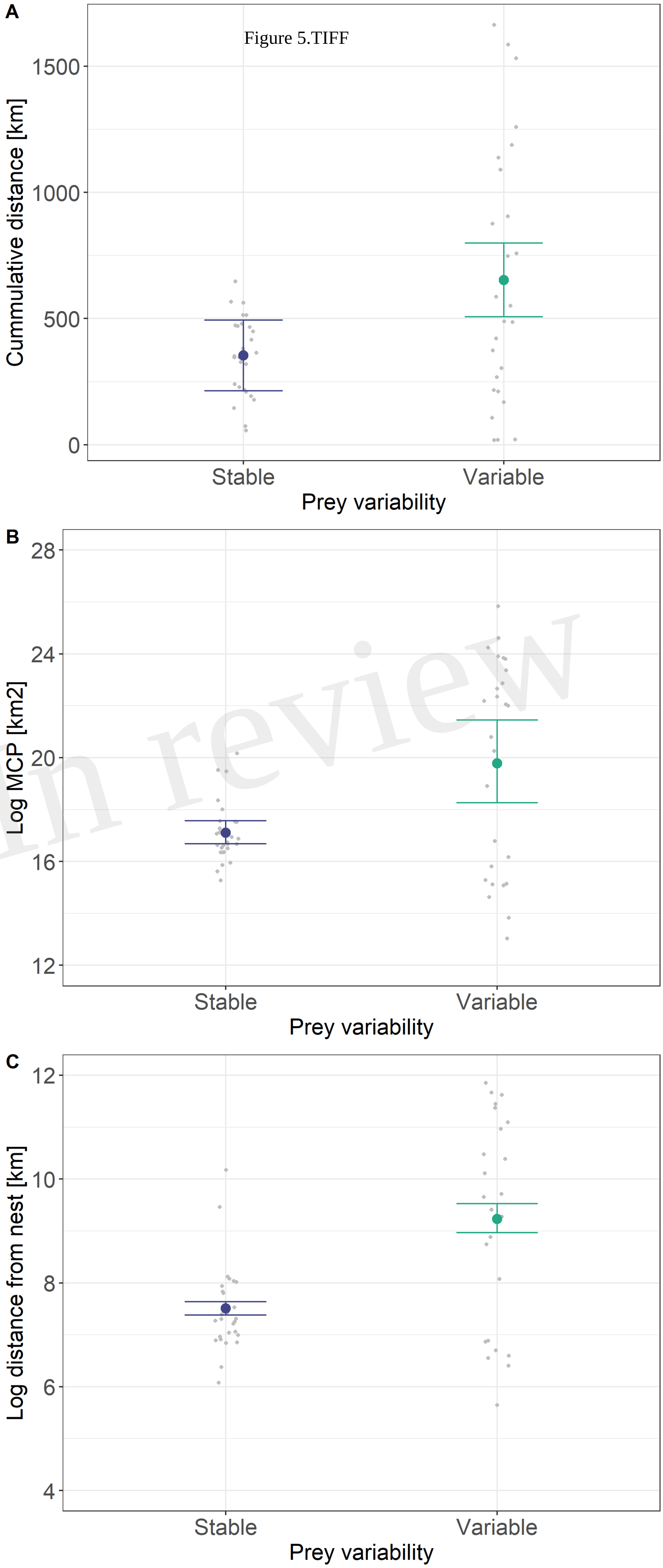

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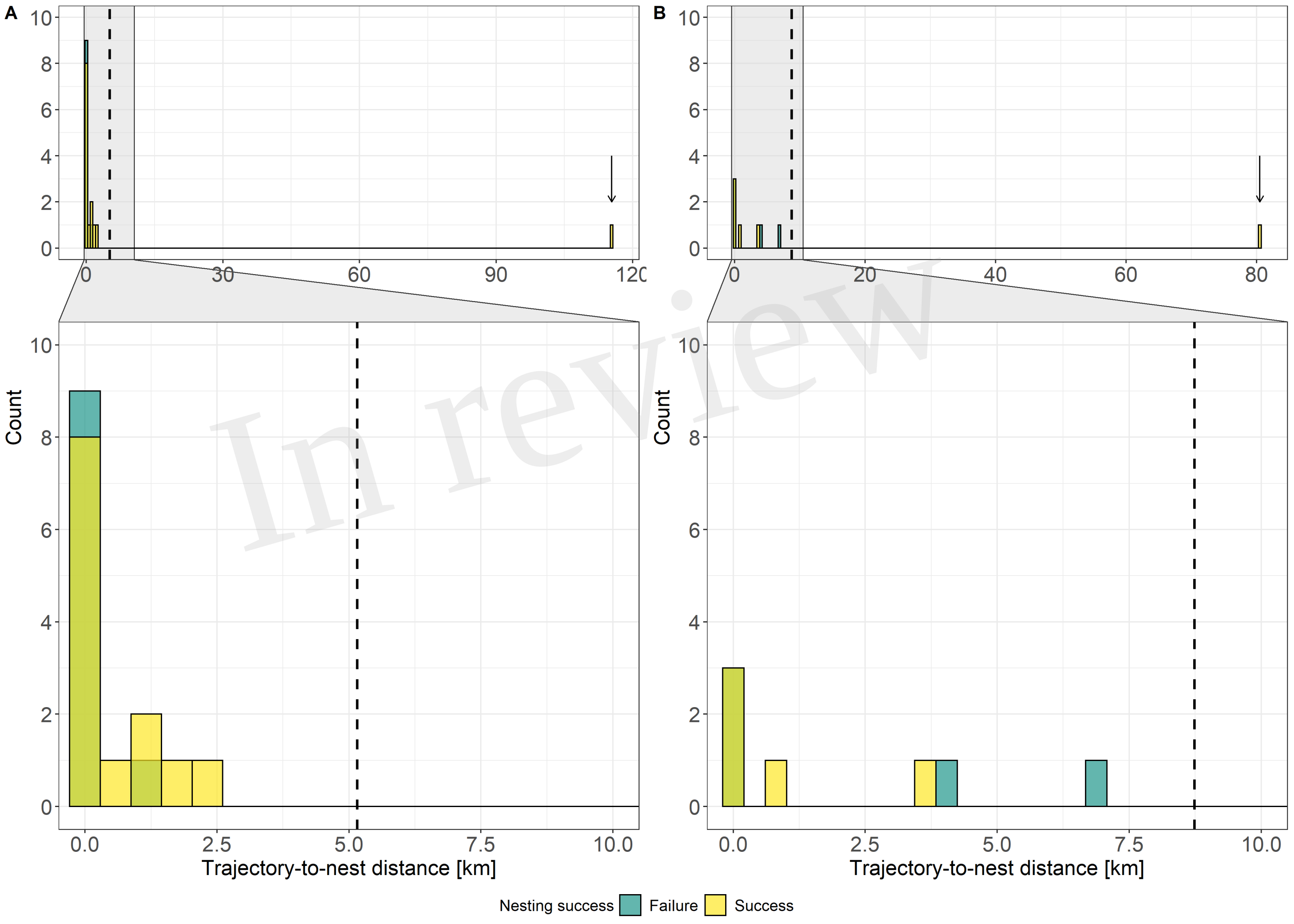

Figure 7.TIFF