Master's thesis

NTNU
Norwegian University of Science and Technology
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The effects of habitat size and distance to forest edge on the occupancy dynamics of rock ptarmigan (*Lagopus muta*) in Norway

Master's thesis in Biology
Supervisor: Vidar Grøtan, NTNU
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Abstract

Climate change induced warming have been particularly pronounced in high mountainous areas, showing rates nearly double the global trend. The alpine species occupying these areas are usually highly specialized, with narrow climatic niches, causing them to be at high risk of extinction. One consequence of climate change is an elevational shift of the treeline to higher altitudes, potentially exacerbating fragmentation and reducing suitable area for the species occupying these habitats. An alpine species, the rock ptarmigan (*Lagopus muta*), have declined in abundance in Norway the last decades and have as a result been placed on the Norwegian red list for species as near threatened (NT). This study applied eight years (2011-2018) of monitoring data, from 137 sites within rock ptarmigan habitat, to estimate the effects of habitat size and distance to forest edge on rock ptarmigan occupancy dynamics in Norway. Neither habitat size, nor distance to forest edge substantially explained the observed variation in occupancy between years. Additionally, occupancy did not vary more for sites in small patches than for sites in large patches and did not vary more for sites close to the forest edge than for sites located closer to the centre of the habitat. Latitude, on the other hand, had a strong effect on occupancy between years, affecting both colonization and local extinction probabilities positively. This study suggests that the site occupancy dynamics of rock ptarmigan in Norway are currently unaffected by the size of the habitat patch and the location of the site in relation to the treeline. However, an exploratory analysis indicates that habitat size might have greater influence on scales smaller than the observed scale of habitat sizes used in this study.

Sammendrag

Oppvarming som resultat av klimaendringer har hatt særskilt høy betydning i høyfjellsområder og viser oppvarmingsrater nærmere det dobbelte av den globale trenden. De alpine artene som oppholder seg i disse områdene er ofte svært spesialiserte, med smale klimatiske nisjer, som gjør dem ekstra sårbare for ekstinksjon. En konsekvens av klimaendringer er at tregrensen flytter seg høyere opp i fjellet, noe som kan forverre fragmentering og redusere tilgjengelig habitat for artene som benytter seg av disse høyfjellsområdene. En alpin art, fjellrype (*Lagopus muta*), har hatt en bestandsnedgang i Norge de siste tiår og har dermed blitt plassert på den Norske rødlisten for arter som nært truet (NT). Denne studien benyttet åtte år (2011-2018) med overvåkningsdata, fra 137 lokaliteter innenfor fjellrype habitat, for å estimere effekten av habitat størrelse og avstand til tregrensen på fjellrypens tilstedeværelsesdynamikk i Norge. Hverken habitat størrelse, eller avstand til tregrensen forklarte betydelige mengder av den observerte variasjonen i tilstedeværelse mellom år. I tillegg varierte ikke tilstedeværelse mer for lokaliteter i små områder enn for lokaliteter i store områder og varierte heller ikke mer for lokaliteter nær tregrensen enn for lokaliteter lenger unna tregrensen. Derimot hadde breddegrad en sterk effekt på tilstedeværelse mellom år og påvirket både kolonisering og lokal ekstinksjonssannsynlighet positivt. Denne studien antyder at tilstedeværelsesdynamikken til fjellryper i Norge foreløpig ikke er påvirket av størrelsen av området de benytter seg av og heller ikke av hvor lokaliteten befinner seg i forhold til tregrensen. Imidlertid indikerer en granskingsanalyse at størrelsen på habitatet kan ha større påvirkning på skalaer mindre enn den observerte skalaen for habitat størrelse benyttet i denne studien.

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Introduction

Alpine habitats are considered to be among the most vulnerable under the current climate change regime (Chamberlain et al., 2012; Gobiet et al., 2014; Nogués-Bravo, Araújo, Errea, & Martinez-Rica, 2007), and have showed an increase in temperature almost two times the global trend (Brunetti et al., 2009). One consequence of climate change is an elevational shift of the treeline to higher altitudes (Harsch, Hulme, McGlone, & Duncan, 2009), potentially exacerbating fragmentation and reducing suitable area for the species occupying these habitats (Chamberlain et al., 2012). Small habitat patches can only support small populations, and loss of habitat therefore increases the extinction probability of a population (Fahrig, 1997). Several studies have documented a northward and upward shift in the distributional ranges of both plants and animals (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Grabherr, Gottfried, & Pauli, 1994; Hickling, Roy, Hill, Fox, & Thomas, 2006) and predicted local extinction of alpine species (Guisan & Theurillat, 2000; Imperio, Bionda, Viterbi, & Provenzale, 2013). Additionally, many montane bird species already show negative population trends (Flousek, Telenský, Hanzelka, & Reif, 2015; Lehikoinen, Green, Husby, Kålås, & Lindström, 2014).

Climate change is expected to affect the availability of habitat for alpine dwelling species by reducing the size of large, contiguous habitat patches and fragmenting contiguous habitats into many smaller patches (Dirnböck, Essl, & Rabitsch, 2011). Beyond the effects of habitat loss, altering habitat configuration could have an additional effect on the population dynamics of alpine species in the future (Flather & Bevers, 2002; Nilsen, Finstad, Næsje, & Sverdrup-Thygeson, 2013). The various ways in which climate can affect the dynamics of bird populations has been studied extensively (Crick, 2004). Still, there is a need for more research on bird populations residing in high mountainous areas, from basic ecological studies to more intensive studies on the demographic parameters that control the distributions of species (Chamberlain et al., 2012; Chamberlain, Brambilla, Caprio, Pedrini, & Rolando, 2016). There are various reasons for a shortage of research on these bird species. First, the logistics of performing research at high altitudes are always demanding and will therefore require lots of resources (Nilsen, Pedersen, Brøseth, & Pedersen, 2012). Second, weather conditions are often extreme in these areas (Martin & Wiebe, 2004), causing further practical complications when performing research at high elevations.

The rock ptarmigan (*Lagopus muta*) is a bird species in the grouse family that has a circumpolar distribution and inhabits polar and alpine habitats (Kaltenborn & Andersen, 2009; Sahlman, Segelbacher, & Hoglund, 2009). In Norway, it is the only species in the

Tetraonidae family that occupies alpine habitats throughout the year (Nilsen et al., 2012). Alpine species are highly specialized to their habitats (Revermann, Schmid, Zbinden, Spaar, & Schröder, 2012), often with narrow climatic niches that make them particularly vulnerable to extinction (Sekercioglu, Schneider, Fay, & Loarie, 2008). It is therefore expected that species such as the rock ptarmigan will be affected by changes to these habitats. Rock ptarmigan numbers declined considerably in the period 2007 – 2013 (Kålås, Husby, Nilsen, & Vang, 2014) and have as a result been classified as near threatened (NT) on the Norwegian red list of species (Henriksen & Hilmo, 2015). Thus, gaining more knowledge about the rock ptarmigan population in Norway is deemed necessary (Nilsen et al., 2012). Alpine grouses in general and rock ptarmigan in particular, are often seen as excellent sentinel species for indicating alterations in the environment due to climate change (Imperio et al., 2013; Novoa, Astruc, Desmet, & Besnard, 2016; Patthey, Wirthner, Signorell, & Arlettaz, 2008; Pernollet, Korner-Nievergelt, & Jenni, 2015; Revermann et al., 2012).

The aim of this study is to provide insight into how climate change induced habitat change might affect an alpine bird species, the rock ptarmigan. In this study, I will use a dynamic site occupancy model (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003) on eight years (2011-2018) of Norwegian breeding bird census data (Kålås et al., 2014). A dynamic site occupancy model can test if the variation in occupancy of sites between seasons can be explained by environmental variables (MacKenzie et al., 2003). Any changes in site occupancy between seasons are in this model explained by the dynamic processes colonization (γ) and local extinction (ε) (MacKenzie et al., 2003). According to Hanski (1994), large patches are more likely to be occupied than smaller patches. Large patches also tend to have a higher probability of being colonized (Hill, Thomas, & Lewis, 1996). Hence, it is expected that large patches have a more stable occupancy dynamics, as smaller patches have a higher probability of going locally extinct (Hanski, 1991). Based on the above arguments, one could deduce that occupancy of rock ptarmigan is more variable for sites located in small patches compared to large patches, and more variable for sites close to the forest edge than for sites further away. A reduction in available habitat will also decrease the distance from the habitat patch edge to the centre of the habitat patch. Consequently, a change in distance to forest edge and its influence on the occupancy dynamics is also investigated.

Therefore, I predict (1) that sites located in habitats with a large area have a higher probability of being colonized, and that (2) sites located in habitats with a large area will have a lower probability of going locally extinct. Increases in abundance from the periphery of a species' range to the centre of their range can be seen for many bird species (Brown, Mehlman, & Stevens, 1995). One reason for this relationship is that the habitat closer to the edge tend to be clearly distinct from the habitat located towards the centre (Ries, Fletcher Jr, Battin, & Sisk, 2004). Consequently, I also predict (3) that sites located at the interior of the habitat range will have a higher probability of being colonized than sites located towards the edge. Finally, I predict (4) that the sites located at the periphery of the habitat range will have a higher probability of going locally extinct than sites located towards the interior.

Methods

Field data collection

Here, I only give a brief overview of field data collection, for a detailed description see Kålås et al. (2014) and (Program for terrestrisk naturovervåking, 2019). The project "Extensive monitoring of breeding birds (TOV-E)" was established to monitor the changes in the most common terrestrial bird populations in Norway. As a result, 493 monitoring sites were distributed across mainland Norway. The distribution of sites follows a random stratified sampling scheme. First, mainland Norway was intersected by 18 km x 18 km grid cells, and monitoring sites were then randomly drawn from the > 1000 intersections between grid cells. Sampling was done after stratifying on region (Eastern Norway, Southern Norway, Western Norway, Central Norway, Nordland, and Troms & Finnmark). Each monitoring site consists of 20 observation points, 300 m apart from each other, located along the edge of a 1.5 km x 1.5 km quadrant. Each point is registered with a GPS position to ensure that the same point can be visited every year. The observations start in the most south-western point and continue in a clockwise direction. If for some reason there are a lot of points that cannot be used, the whole site can be rotated 90, 180 or 270°. If one or several of the 20 points are still unavailable (due to steep cliffs, houses, the point is in a body of water etc.) the point(s) can be moved to a new location. However, it should not exceed a maximum distance of 100 m away from the original point and not be closer than 250 m to other points. Therefore, for some of the sites less than 20 points were surveyed.

The observer is instructed to visit each observation point for exactly 5 minutes and record all sightings of any terrestrial bird species included in the TOV-E project. Each observation is placed in one of two categories: closer than 50 m away or farther than 50 m away. However, for this study, both are collapsed into one presence-absence column of observations. In addition, the observer also records any sightings when moving between the predefined points in the quadrant. These observations are only recorded as the total number of sightings of rock ptarmigan when the observer was moving between the observation points and therefore no information identifying between which of the 20 observation points the sighting was made is available. The uncertainty in the location of observations between points meant that it was not possible to include these observations in the dynamic site occupancy model used in this study. If the observer considers any observations of rock ptarmigan in two or more observation points to be the same bird, the observation is limited to the point where it was first observed only. The time of year the sites are surveyed varies with both latitude and altitude, however, they are done in the breeding season, usually within the time frame of 23rd of May – 8th of July. Data collected for the TOV-E project between 2011 and 2018 was used in this study. All fieldwork was carried out by trained volunteers from the Norwegian Ornithological Society (NOF).

Defining suitable rock ptarmigan habitat

Rock ptarmigans can be found breeding mostly in high altitude areas (above 600 meters above sea level) in southern parts of Norway (Pedersen, 1991). Further north, breeding pairs can be observed down to 100 meters above sea level (Pedersen & Karlsen, 2007). The treeline seem to follow a similar relationship with latitude, showing a decrease in elevation as the latitude increases (Sveinbjörnsson, 2000). Suitable rock ptarmigan habitat was therefore defined as all habitat above the treeline. A model of the habitat above the treeline in mainland Norway was used to meet the definition of suitable rock ptarmigan habitat. This model is a raster map (100 m x 100 m cells), where the locations of the treelines are based on altitude and various climate variables (See Blumentrath and Hanssen (2010) for a more detailed description). From this model, polygons of the area above the treeline were imported into the geographic information software ArcGIS, version 10.6 (ESRI, 2017). To avoid bias in the estimate of distance from a site to the nearest forest edge, all water sources were treated as terrestrial habitat. All the 493 monitoring sites were overlaid on the suitable rock ptarmigan habitat polygons as points using their central coordinates, of which 339 sites were removed from the analysis as they fell outside the suitable habitat polygons, yielding 154 sites within the ptarmigan habitat polygons. The areas (km^2) of all the habitat polygons were calculated using the geometry tool in the attribute table, as well as the distance (km) from the site to the nearest polygon edge using the near tool in the proximity toolset in ArcGIS, version 10.6

(ESRI, 2017). These statistics were appended to the attribute table of the site polygons with the spatial join tool before the site shapefile and suitable habitat shapefile was imported to R (R Core Team, 2017) to be used in the occupancy analysis. Out of the 154 sites, five sites were excluded because they had not been surveyed over the course of the study period. Another 12 sites that had only been surveyed one year were excluded, since it is not possible to estimate colonization and local extinction probabilities for sites that do not have any transitions. In total, 137 sites were used in the analysis (Figure 1).

Figure 1. Suitable rock ptarmigan habitat (green polygons) and the 137 included monitoring sites (black dots).

Fitting site occupancy models

When sampling at a site, there are two processes that generate the observed detection-nondetection data (MacKenzie et al., 2006). First, the ecological process (ψ), dependent on the intrinsic characteristics of each site, the species may be present or absent (Kéry & Schaub, 2011). Second, the observation (p) or detection process is based on the conspicuousness of the species and the ability of the observer to detect the species when present (Kéry & Schaub, 2011). Naïve occupancy (i.e. proportion of sites with at least one observation) is estimated assuming perfect detection of the species and so gives only a rough assessment of occupancy (MacKenzie et al., 2006). Site occupancy models, such as those described by MacKenzie et al. (2002) and Tyre et al. (2003), on the other hand, account for the uncertainty in the detection process by having repeated surveys (in space or time) of a site during a season. Here, I treat the 20 observation points (See Methods - Field data collection above) as repeated surveys within a season. From the observation process, two sources of error arise. First, the observer may record an absence when the species was in fact present, referred to as a false-negative error (Kéry & Royle, 2015). Second, the observer misidentifies the species of interest, a so-called false-positive error (Kéry & Royle, 2015). Although false-positives (i.e. recording a presence when in fact there is none) are possible, it was assumed that false-positive error rates were negligible and therefore not accounted for in this study. A single-season occupancy model can be fitted by combining the ecological process model with the detection process model in a joint likelihood model:

$$L(\psi, p \mid h_1, h_2, \ldots, h_s) = \prod_{i=1}^{s} P(h_i) \qquad (1)$$

Here, occupancy and detection probability (ψ, p) are estimated based on the observed detection history (h_i) of each site. P(h_i) represents the probability statement for the observed data at site i. For a more detailed description of single-season models, see MacKenzie et al. (2002).

In R (R Core Team, 2017) the function “occu” of the unmarked package (Fiske et al., 2017), was used to model single-season occupancy. In addition to the observed detection history for each site, this function allow a vector of sites that are known to be occupied to be included (Fiske et al., 2017). As such, the observations of rock ptarmigan made when the observer was moving between observation points could be included in the single-season models. Three estimates of occupancy were compared to assess the applicability of site occupancy models with the observed data; naïve occupancy for each season and estimated occupancy from eight single-season models, with and without including information of known occupied sites. In addition, based on eight single-season occupancy models (i.e. fitted to data from a single year), a visual assessment was conducted of the extent to which the inter-annual variation in predicted occupancy was more variable in small vs large patches (hypothesis 1) and close vs far from the forest edge (hypothesis 2). It was also assessed if the eight occupancy predictions revealed similarities in their estimates. Specifically, if there was a clear trend in the direction of the predicted change in occupancy with habitat size and distance to forest edge.

A formal test of the hypotheses was performed using the dynamic site occupancy model described by MacKenzie et al. (2003). When applying such a model the occupancy in season *t* can be modelled as a first-order Markov chain, where the initial occupancy (ψ_1) is estimated the first season and any changes in occupancy between seasons is estimated using the dynamic parameters, local extinction (ε_t) and colonization (γ_t) probabilities (MacKenzie et al., 2006)(Figure 2). In addition to initial occupancy and detection probabilities, the likelihood statement now includes local extinction and colonization probabilities:

$$L(\psi_1, \boldsymbol{\gamma}, \boldsymbol{\varepsilon}, \mathbf{p} \mid \mathbf{h_1}, \mathbf{h_2}, \ldots, \mathbf{h_s}) = \prod_{i=1}^{s} P(\boldsymbol{h_i}) \qquad (2)$$

It is the dynamic occupancy parameters that are of primary interest in this study. An occupied site in season *t* can go locally extinct between seasons *t*, and *t*+1, with a given probability (ε_t), or keep its occupied state with probability ($1 - \varepsilon_t$). Similarly, an empty site in season *t* can become colonized between seasons *t* and *t*+1, with a given probability (γ_t), or stay unoccupied with probability ($1 - \gamma_t$). Some parameters in Eq. 2. are outlined in bold, signifying that they are now written on vector form. For more details about dynamic site occupancy models, see MacKenzie et al. (2003). Habitat size and distance to forest edge were used as covariates attempting to explain the spatiotemporal variation in the dynamic occupancy parameters of the model. The dynamic occupancy models were all fitted in R (R Core Team, 2017) using the “colext” function of the unmarked package (Fiske et al., 2017).

The site occupancy models used in the analysis are based on certain assumptions (MacKenzie et al., 2006). These are: (1) No unmodeled heterogeneity in any of the parameters. (2) No misidentifications. (3) The detection of a species and the detection histories of each site are independent of each other. (4) Closure in occupancy within a season, that is, there cannot be a change in the occupancy state of a site within a season. If one or more of these assumptions are violated the estimated parameters may be biased and any inferences based on these parameters may be erroneous.

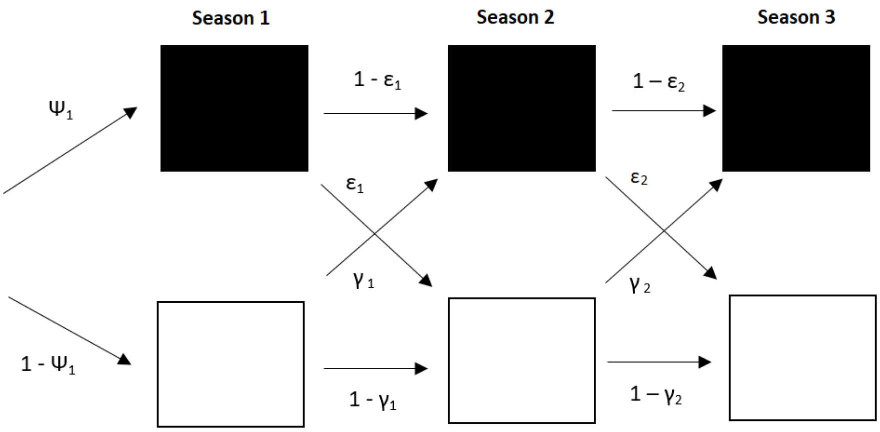

Figure 2. Illustration of a dynamic site occupancy model re-drawn from Figure 7.2 in MacKenzie et al. (2006, p. 189). White squares denote an empty site and black squares an occupied site.

Model selection and Model averaged predictions

To examine the support for the hypothesis outlined in the introduction, I performed a model selection routine where I compared a set of ecologically plausible dynamic site occupancy models. Beyond the variables of interest (habitat size and distance to forest edge), I also included latitude to control for potential confounding effects, as the population dynamics of a species often vary with latitude (Sæther et al., 2003). To test if there is variation between years in the ability to detect rock ptarmigan, year was included as an effect on detection probability (p). Since initial occupancy probability (ψ_1) was not of interest in my analysis, I did not include any covariates in the sub model for initial occupancy. This reduces the number of potential models to compare in the model selection procedure. Habitat size and distance to forest edge were also included as second-degree terms to test for the presence of any non-linear relationships. All variables (habitat size, distance to forest edge and latitude) were standardized by subtracting the mean and dividing by their respective standard deviations (SD). Hence, the most complex model for the model selection process was:

$$\text{logit}(\psi_1) \sim 1$$

$$\text{logit}(\gamma) \sim \text{habitat area} + (\text{habitat area})^2 + \text{distance to edge} + (\text{distance to edge})^2 + \text{latitude}$$

$$\text{logit}(\varepsilon) \sim \text{habitat area} + (\text{habitat area})^2 + \text{distance to edge} + (\text{distance to edge})^2 + \text{latitude}$$

$$\text{logit}(p) \sim \text{year}$$

The overall (all eight years) number of observations of rock ptarmigan per site was calculated and plotted against observed distance to forest edge to visually assess the habitat quality assumption made by prediction three and four (See Appendix A, Figure A1).

Prior to analysis, the correlation between the predictor variables was estimated (Table 1), because highly correlated variables should not be included in the same model (Graham, 2003). Overall, the correlations were moderate to low. As a precautionary measure the model selection procedure was performed twice, both with and without including latitude in the global model.

Table 1. Pearson correlation table for habitat size, distance to forest edge and latitude.

	Distance to forest edge	**Habitat size**
Habitat size	0.42	
Latitude	-0.06	-0.55

For this study, an information theoretic approach for testing competing hypotheses was taken. Using the Akaike's Information Criterion, corrected for small sample sizes (Hurvich & Tsai, 1989) the best models amongst a set was identified. Models are listed according to the relative difference in AIC_C value to the most supported model, ΔAIC_C. The Akaike weights (w_i) of each model is a measure of the weight of evidence for the given model being the best model in the set of models, given that the best model is included (Burnham & Anderson, 2002). Both ΔAIC_C and Akaike weights are measures that can be used for comparing support for various models in a set (Burnham & Anderson, 2002). When there is no single model with substantially more support, basing inferences on a single model does not account for the uncertainty in the model selection process (Grueber, Nakagawa, Laws, & Jamieson, 2011; Symonds & Moussalli, 2011). Basing inferences on a confidence set of models is then recommended (Grueber et al., 2011). A confidence set of models is when a set of models used in the model selection is subset based on some sort of support criterion (Burnham & Anderson, 2002). Usually, the confidence set is established from the models with an $\Delta AIC_C \leq 2$ (Burnham & Anderson, 2002), $\Delta AIC_C \leq 6$ (Richards, 2008), $\Delta AIC_C \leq 10$ (Bolker et al., 2009) or a sum of Akaike weights equal to 0.95 (Burnham & Anderson, 2002). Here, a confidence set of models that had a $\Delta AIC_C \leq 2$ was used to calculate the relative importance of each covariate and further used for inferences. The relative importance of a variable is calculated as the sum of the Akaike weights for all models in which the parameter of interest is included in the confidence set (Burnham & Anderson, 2002). The Akaike weights of the models in the confidence set were rescaled so that the weights in the set of models sum to 1. To visualize the effect of the covariates, a weighted estimate of the predicted values for all models in the confidence set of models was calculated following Burnham and Anderson (2002).

The model selection process was performed in R (R Core Team, 2017) using the "dredge" function from the MuMIn package (Barton, 2018). The confidence set of models was created using the "get.models" function from the MuMIn package (Barton, 2018) and the weighted model averaged prediction was calculated using the "modavgPred" function in the AIC_Cmodavg package (Mazerolle, 2017).

Data exploration

In addition to the strict tests of the hypotheses outlined above, I also conducted a set of more exploratory tests to assess the robustness of my results. In general, these were conducted by testing the hypotheses on logically defined subsets of the data. The rationale for this was that (1) the habitat size covariate showed a clustered frequency distribution, and (2) if there is an effect of the variables of interest, it was expected that these would be more pronounced on shorter ranges.

Habitat size data gaps and influence of habitat size on short ranges

The spread of habitat sizes is not uniform across its range, but clustered below 5000 km^2, at approx. 8000 km^2 and at approx. 16000 km^2 (See Appendix B, Figure B1). Consequently, I also tested my hypotheses only including sites located in patches of size $\leq$ 15000 km^2 (n = 112) and only including sites located in patches of size $\leq$ 5000 km^2 (n = 103). In spring, male rock ptarmigans establish territories that can be as large as 1 km^2 (Nilsen et al., 2012). The observed habitat sizes span a range from 3 km^2 to 16580 km^2, that is, up to several orders of magnitude greater than the male rock ptarmigan territories. Hence, the habitat size hypotheses were tested only including sites located in relatively small patches. First for sites located in patches of size $\leq$ 500 km^2 (n = 47) and second for sites located in patches of size $\leq$ 1000 km^2

(n = 57). Only linear effects were investigated for the model selection process regarding small habitat patches due to small sample sizes.

Influence of distance to forest edge on short ranges

Also for distance to forest edge one could speculate that there might be more variation in the occupancy dynamics for sites located close to the forest edge, than for sites located further away. As such, the distance to forest edge hypotheses were tested only including sites located close to the forest edge. For sites located ≤ 0.5 km (n = 42) away from the forest edge and for sites located ≤ 1 km (n = 63) away from the forest edge. Only linear effects of distance to forest edge were tested due to small sample sizes.

Results

Overall, there was a positive trend in naïve occupancy (i.e. proportion of sites with at least one observation) from 2011 to 2016, followed by a decrease the last two years (Figure 3a). Estimating annual occupancy using single-season models resulted in similar trends, but as expected gave consistently higher occupancy estimates (Figure 3a). Also as expected, the detection probability, when accounting for sites that were known to be occupied were included, was lower than for the model not incorporating this information (Figure 3b). As a result of lower detection probability, the estimated occupancy probabilities for the single-season models accounting for sites that were known to be occupied were higher, except for the years 2015, 2016 and 2018 (Figure 3a). Estimated detection probabilities were overall quite low (mean = 0.07 and mean = 0.06, for the model without and the model with information on known occupied sites respectively). Based on the mean detection probabilities, the site-level probabilities of detecting rock ptarmigan (given that it was present) was estimated at 0.77 and 0.71 respectively.

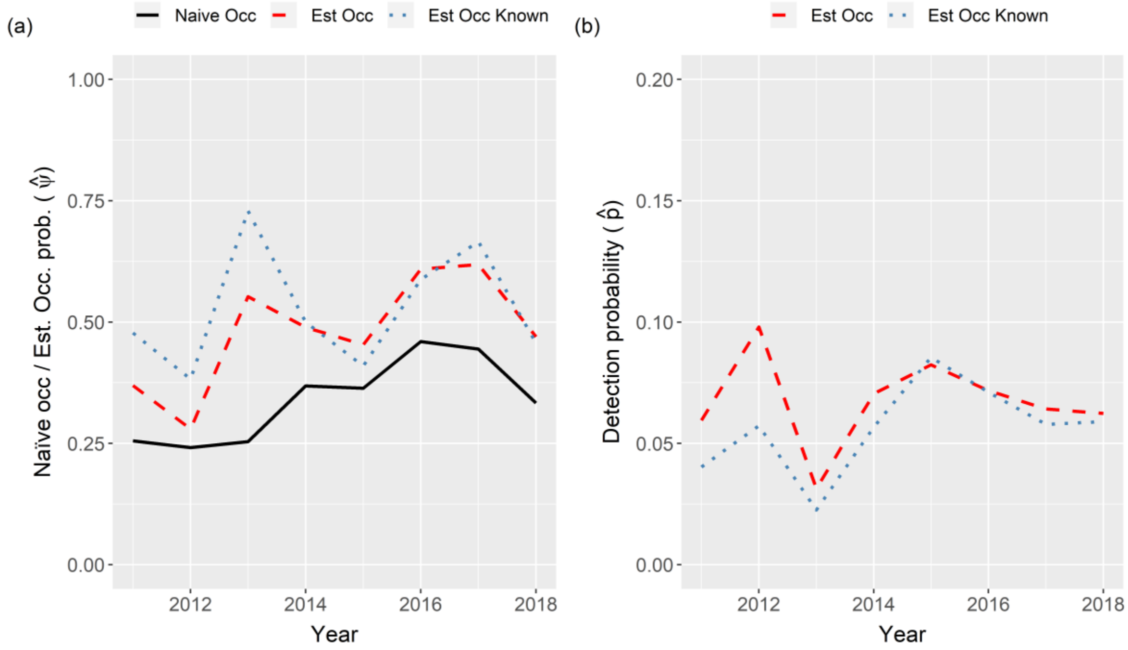

Figure 3. (a) Variation in naïve occupancy probability and the two estimated occupancy probabilities ($\hat{\psi}$), without information of sites known to be occupied (Est Occ) and with information of sites known to be occupied (Est Occ Known) over time. (b) Variation in estimated detection probabilities ($\hat{p}$), without information of sites known to be occupied (Est Occ) and with information of sites known to be occupied (Est Occ Known) over time.

Multi-season site occupancy dynamics

To formally test my four predictions, I assessed the relative support of the global model (outlined in the Methods) and all nested (i.e. simpler) models (n = 648), with the constraint that any non-linear terms had to be preceded by their respective linear term. Nine models had substantial support (Table 2), with an $\Delta AIC_C \leq 2$. Among the models with substantial support, a linear effect of distance to forest edge on colonization probability had a relative importance of 0.61 (included in six of the nine models), whereas the linear effect of habitat size on extinction probability had a relative importance of 0.39 (Table 3). All remaining effects of the variables of interest had only limited support. Weighted model averaged predictions for habitat size and distance to forest edge based on the nine models with substantial support is shown in Figure 4. Colonization probability had a predicted increase from 0.20 to 0.44 over the full range of distances to forest edge and local extinction probability a predicted increase from 0.15 to 0.24 over the full range of habitat sizes. Predicted changes in colonization probability with habitat size and local extinction probability with distance to forest edge were negligible. Latitude had a relative importance of 1 for an effect on both dynamic occupancy parameters, where both colonization- and local extinction probabilities showed positive weighted model averaged predictions (Figure 5). The predictions for colonization and local extinction probabilities over the full range of latitudes gave changes of 0.10 to 0.41 and 0.05 to 0.43, for the two dynamic occupancy parameters respectively. Repeating the model selection procedure when omitting the potential confounding effects of latitude, gave similar results (See Appendix C for AIC_C table and model selection table).

Table 2. Summary of model selection table, showing the nine models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the nine most supported models.

Model	**df**	**LogLik**	**AIC_C**	**ΔAIC_C**	**w_i**	**Rel. w_i**
M1	6	-1621.903	3256.397	0.000	0.038	0.178
M2	8	-1619.861	3256.751	0.354	0.032	0.150
M3	7	-1620.995	3256.783	0.386	0.031	0.146
M4	13	-1614.153	3257.002	0.605	0.028	0.131
M5	9	-1619.212	3257.719	1.322	0.019	0.089
M6	7	-1621.582	3257.958	1.561	0.017	0.08
M7	8	-1620.536	3258.101	1.704	0.016	0.075
M8	14	-1613.485	3258.105	1.708	0.016	0.075
M9	15	-1612.275	3258.159	1.762	0.016	0.075

Table 3. Model selection table for the nine models with substantial support and their effect sizes for all variables (V) on logit scale (±SE). Variable Relative Importance (RI), Initial Occupancy probability (I. Occ), Colonization probability (Col), Local extinction probability (Ext), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and year 2011-2018 as fixed factors (Y11-Y18).

V	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**	**M7**	**M8**	**M9**	**RI**
I. Occ. ($\hat{\psi}$)										
Int	-0.861	-0.793	-0.863	-0.746	-0.762	-0.839	-0.812	-0.76	-0.694	
	(±0.344)	(±0.351)	(±0.344)	(±0.378)	(±0.353)	(±0.346)	(±0.353)	(±0.376)	(±0.384)	
Col. ($\hat{\gamma}$)										
Int	-1.246	-1.109	-1.181	-1.27	-1.101	-1.233	-1.098	-1.211	-1.145	
	(±0.192)	(±0.211)	(±0.204)	(±0.201)	(±0.212)	(±0.194)	(±0.214)	(±0.209)	(±0.214)	
HS	-	-	-	-	-	-	-	-	-	0
HS^2	-	-	-	-	-	-	-	-	-	0
DFE	-	0.414	0.275	-	0.446	-	0.495	0.242	0.387	0.61
		(±0.225)	(±0.207)		(±0.229)		(±0.278)	(±0.211)	(±0.227)	
DFE^2	-	-	-	-	-	-	-	-	-	0
Lat	0.582	0.574	0.583	0.62	0.571	0.579	0.597	0.605	0.589	1
	(±0.203)	(±0.218)	(±0.210)	(±0.214)	(±0.218)	(±0.206)	(±0.216)	(±0.217)	(±0.225)	
Ext. ($\hat{\varepsilon}$)										
Int	-1.653	-1.450	-1.565	-1.71	-0.951	-1.631	-1.408	-1.628	-1.538	
	(±0.326)	(±0.333)	(±0.328)	(±0.339)	(±0.485)	(±0.338)	(±0.327)	(±0.340)	(±0.356)	
HS	-	0.536	-	-	1.027	0.280	-	-	0.576	0.394
		(±0.354)			(±0.547)	(±0.353)			(±0.380)	
HS^2	-	-	-	-	-0.451	-	-	-	-	0.089
					(±0.377)					
DFE	-	-	-	-	-	-	0.369	-	-	0.075
							(±0.342)			
DFE^2	-	-	-	-	-	-	-	-	-	0
Lat	0.811	0.975	0.742	0.87	0.822	0.962	0.714	0.797	1.061	1
	(±0.344)	(±0.405)	(±0.346)	(±0.359)	(±0.399)	(±0.416)	(±0.323)	(±0.361)	(±0.445)	
Det. ($\hat{p}$)										
Int (Y11)	-2.63	-2.62	-2.62	-2.779	-2.62	-2.63	-2.61	-2.768	-2.769	0.281
	(±0.071)	(±0.073)	(±0.071)	(±0.325)	(±0.072)	(±0.072)	(±0.072)	(±0.323)	(±0.324)	

Y12	-	-	-	0.332 (±0.382)	-	-	-	0.321 (±0.384)	0.339 (±0.388)	0.281
Y13	-	-	-	-0.64 (±0.397)	-	-	-	-0.640 (±0.397)	-0.633 (±0.398)	0.281
Y14	-	-	-	0.155 (±0.363)	-	-	-	0.152 (±0.362)	0.153 (±0.363)	0.281
Y15	-	-	-	0.316 (±0.357)	-	-	-	0.303 (±0.356)	0.311 (±0.357)	0.281
Y16	-	-	-	0.259 (±0.349)	-	-	-	0.255 (±0.347)	0.257 (±0.349)	0.281
Y17	-	-	-	0.182 (±0.351)	-	-	-	0.179 (±0.349)	0.187 (±0.351)	0.281
Y18	-	-	-	0.074 (±0.363)	-	-	-	0.079 (±0.362)	0.058 (±0.364)	0.281

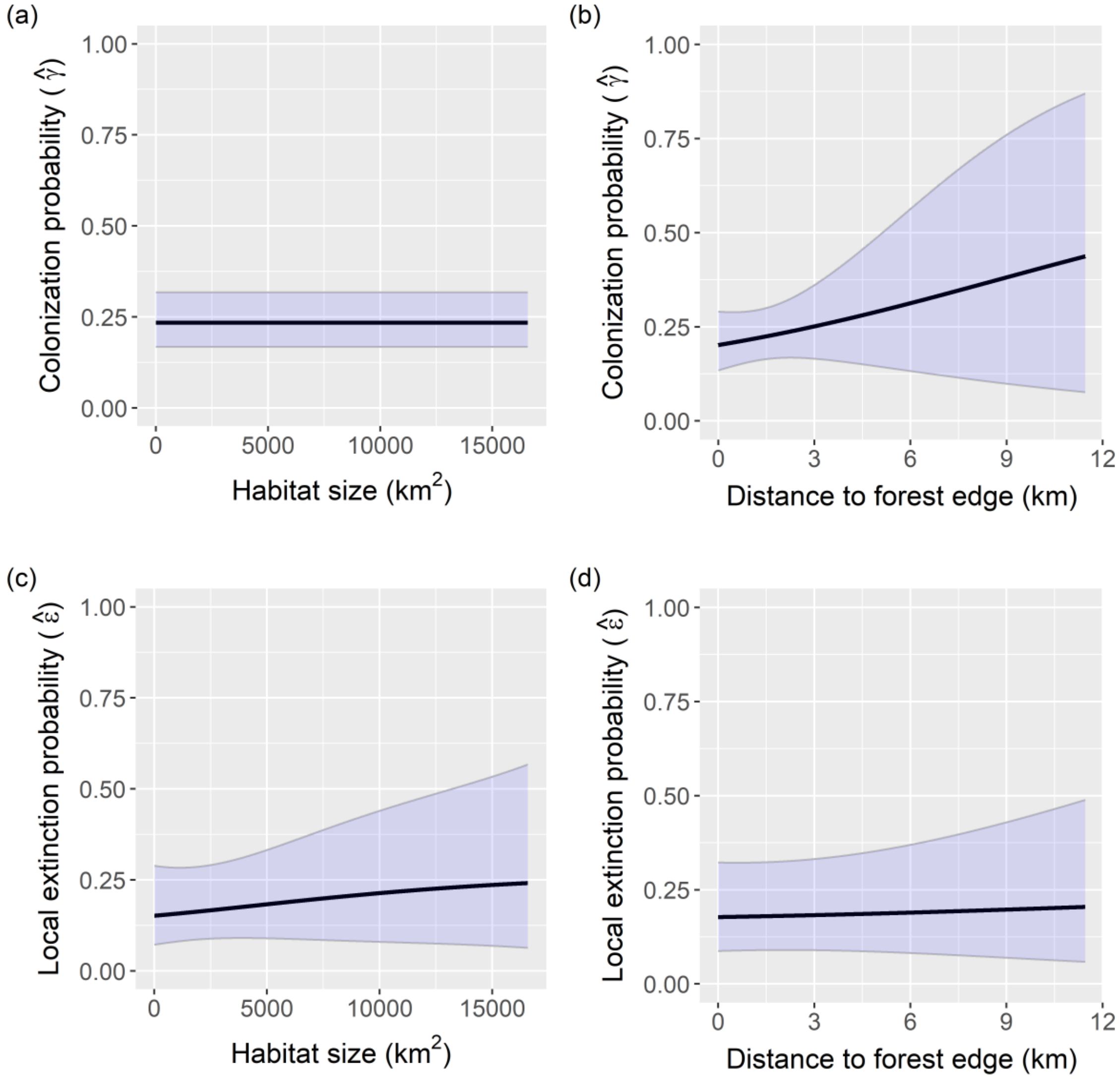

Figure 4. Predicted change in the dynamic occupancy parameters across the observed range of habitat sizes and distances from sites to the forest edge (black lines). (a, b) Predicted estimate for colonization probability ($\hat{\gamma}$). (c, d) Predicted estimate for local extinction probability ($\hat{\varepsilon}$). Shaded regions represent the 95% confidence interval for the predictions.

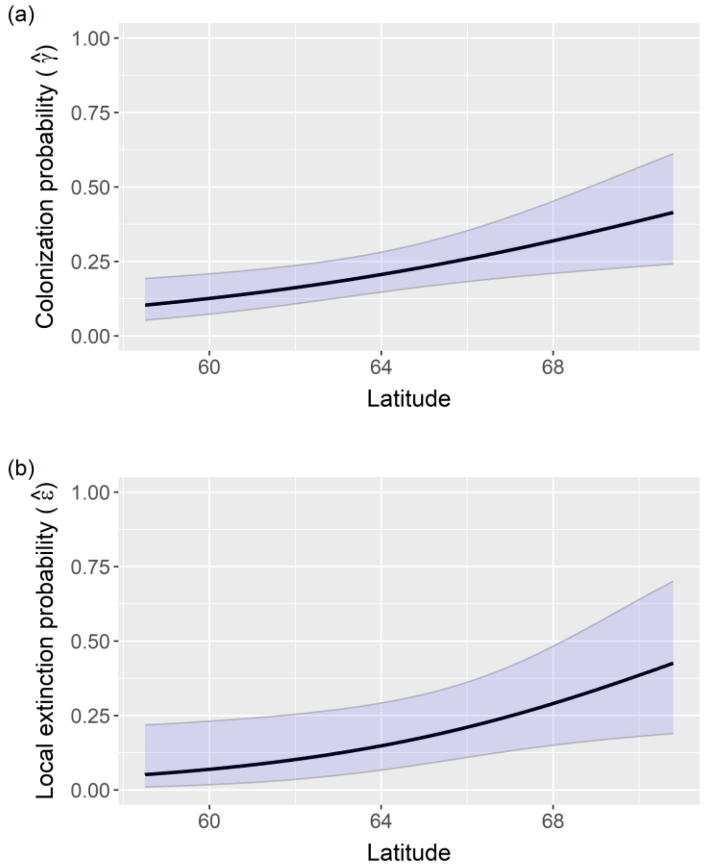

Figure 5. Predicted change in the dynamic occupancy parameters across the observed range of latitudes (black lines). (a) Predicted estimate for colonization probability ($\hat{\gamma}$*). (b) Predicted estimate for local extinction probability (*$\hat{\varepsilon}$*). Shaded regions represent the 95% confidence interval for the predictions.*

Single-season site occupancy models

To perform a visual assessment of the relative variation in site occupancy for sites located in small or large habitat patches and near or close to the forest edge, respectively, I also fitted eight single-season models. In agreement with the results from the multi-season occupancy model, there was no clear support for any of the hypotheses. In general, the predicted occupancy probability showed very little variation over the range of habitat sizes and distances to forest edge (Figure 6a, 6b). Additionally, there were no clear trends in the direction (negative or positive) of the predicted occupancy probabilities with habitat size or distance to forest edge. Occupancy also seem to follow the same pattern over time for various habitat sizes and distances to forest edge (Figure 6c, 6d). One should take note of the generally low support (except habitat size on occupancy in 2016 and 2017 with a relative importance of 0.81 and 0.80 respectively) for habitat size and distance to forest edge (See Appendix D for AIC$_C$ tables and model selection tables) in the single-season models, causing these predictions to have a high uncertainty.

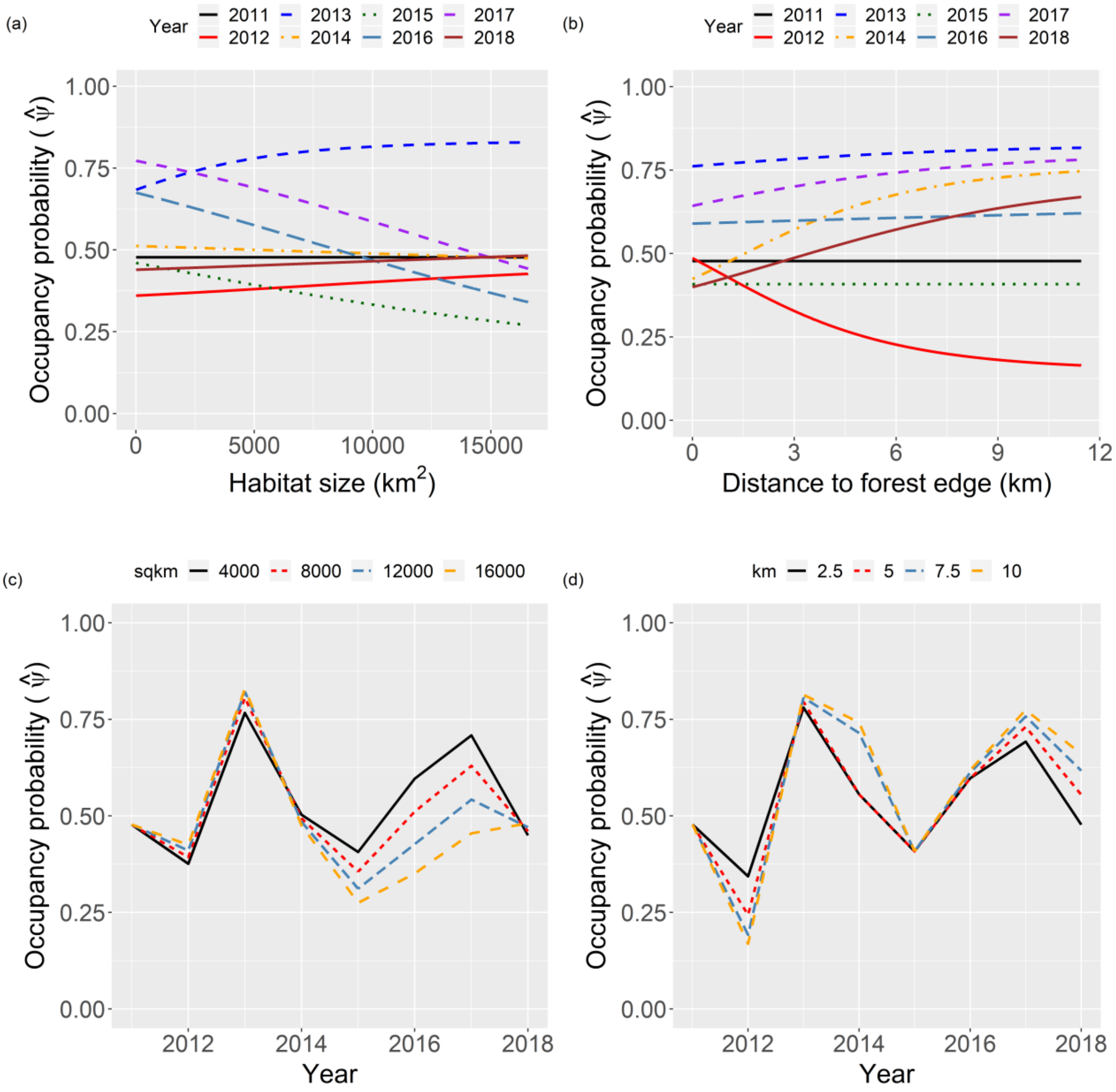

Figure 6. (a, b) Variation in occupancy probability ($\hat{\psi}$) with habitat size (km^2) and distance to forest edge (km) for each year included in the study. (c, d) The variation in occupancy probability over time for 4 habitat sizes (4000 km^2, 8000 km^2, 12000 km^2 and 16000 km^2) and 4 distances to forest edge (2.5 km, 5 km, 7.5 km and 10 km).

Data exploration

Habitat size data gaps and influence of habitat size on short ranges

The model selection process only including sites located in patches of size ≤ 15000 km^2 consisted of 64 models, where two models had substantial support (See Appendix E, Table E1). Two models with substantial support out of 64 potential models was found also for the model selection process only including sites located in patches ≤ 5000 km^2 (See Appendix E, Table E3). Neither of the two model selection processes revealed good support for habitat size or distance to forest edge explaining the observed variation in the dynamic occupancy parameters (See Appendix E, Table E2 and Table E4).

Out of the 16 models included in the exploratory analysis investigating the effect of habitat size on sites located in patches of size ≤ 500 km^2, one model had substantial support (See Appendix F, Table F1). Habitat size had a relative importance equal to 1 for both the colonization and local extinction parameters (See Appendix F, Table F2). Habitat size was estimated to positively affect colonization and local extinction probability, although it had a greater effect on colonization probability (Figure 7a, 7c). Colonization probability had a predicted increase from 0.05 to 0.93 with habitat size and local extinction probability a predicted increase from 0.06 to 0.90 with habitat size. For the sites located in patches of size ≤ 1000 km^2, 16 models were tested against each other, out of which four models had substantial support (See Appendix F, Table F3). Here, habitat size had good support for the colonization parameter with a relative importance equal to 0.78 and very weak support for the extinction parameter with a relative importance equal to 0.16 (See Appendix F, Table F4). Habitat size was predicted to have a positive effect on both colonization and local extinction probability (Figure 7b, 7d). The predicted changes in colonization probability with habitat size were relatively high, from 0.13 to 0.33, while only a slight change in predicted local extinction probability with habitat size was found, from 0.14 to 0.16.

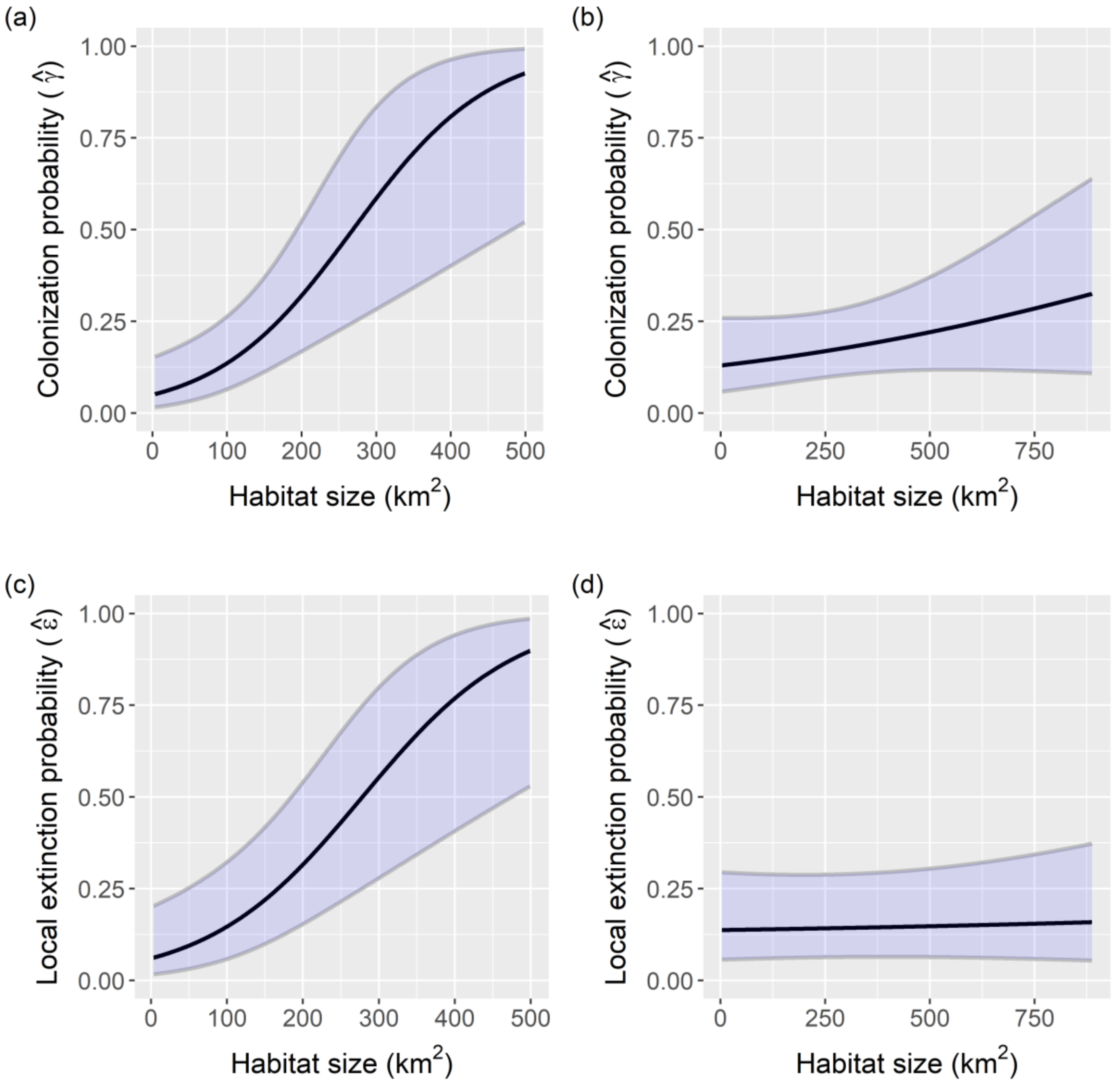

Figure 7. Predicted change in the dynamic occupancy parameters for sites located in patches of size ≤ 500 km^2 and size ≤ 1000 km^2 (black lines). (a, b) Predicted estimate of colonization probability ($\hat{\gamma}$). (c, d) Predicted estimate of local extinction probability ($\hat{\varepsilon}$). Shaded regions represent the 95% confidence interval for the predictions.

Influence of distance to forest edge on short ranges

Two subset data frames were created to investigate how distance to forest edge on shorter ranges influence the occupancy dynamics: sites ≤ 0.5 km and sites ≤ 1 km from the forest edge. Both model selection processes tested 16 potential models against each other. The model selection for sites located ≤ 0.5 km from the forest edge produced two models with substantial support (See Appendix G, Table G1). The distance to forest edge parameter had a relative importance of 0, that is, it was not included in either of the two models with substantial support (See Appendix G, Table G2). Similarly, the model selection for sites located ≤ 1 km from the forest edge produced two models with substantial support (See Appendix G, Table G3). Again, distance to forest edge had a relative importance of 0 (See Appendix G, Table G4).

Discussion

In this study, eight years of data (2011-2018) was used to investigate the effects of habitat size and distance to forest edge on the occupancy dynamics of rock ptarmigan in Norway. The colonization and local extinction parameters were found to not vary with habitat size. Colonization probability varied little-moderately with distance to forest edge, while local extinction probability showed only low variation. Both dynamic occupancy parameters varied greatly with latitude, suggesting increasingly more variable dynamics towards the north. Overall, there was only weak support for an effect of habitat size and distance to forest edge on either of the dynamic occupancy parameters. Eight single-season models created primarily to visually assess the variation in occupancy with habitat size and distance to forest edge, provided additional support to the main result of little to no effect of the variables of interest.

Habitat size was predicted to affect the occupancy dynamics, since smaller populations are found in smaller habitat patches and thereby have a higher probability of going extinct (Burkey, 1995). The first two predictions, increase in colonization- and decrease in local extinction probabilities with habitat size (1, 2), implicitly assume that rock ptarmigan populations in Norway are limited by available habitat. However, on the scale considered in this study, no habitat limitation was found. On smaller scales, there are some indications of an influence of patch size. An exploratory analysis on two subsets revealed a high relative importance of habitat size to both dynamic occupancy parameters on one subset, and moderate to high relative importance to colonization on the other. Male rock ptarmigans maintain small territories (up to 1 km^2) (Nilsen et al., 2012) relative to the observed habitat areas and it could be expected that the amount of available habitat would have a greater influence closer to the territory scale. Note that these analyses were performed as an exploratory analysis on a relatively small sample size (n = 47, n = 57) and should therefore not be treated as confirmatory (Nilsen, Bowler, & Linnell, 2019, April 29). Although the amount of alpine habitat is predicted to decrease (Harsch et al., 2009; Revermann et al., 2012), most habitat patches in Norway still maintain sizes several orders of magnitude greater than rock ptarmigan territories (80 % of sites are located in patches of size > 100 km^2). One could then suspect that climate change induced alterations of alpine habitat have not yet been so great as to affect rock ptarmigan occupancy dynamics in Norway. Novoa et al. (2016) conducted a study in the French Alps and Pyrenees investigating the effects of climate change on rock ptarmigan breeding biology. No apparent changes in breeding biology was found (Novoa et al., 2016), demonstrating the difficulties of directly linking climate change and rock ptarmigan biology. Nevertheless, some evidence exist for an altitudinal shift to higher elevations following climate change in the subspecies alpine rock ptarmigan (*Lagopus muta helvetica*)(Pernollet et al., 2015).

The premise for the third and fourth prediction, increase in colonization- and decrease in local extinction probabilities with distance to forest edge (3, 4), was that habitat quality should increase from the forest edge towards the centre. However, the location of a site in relation to the treeline, did not seem to affect the occupancy dynamics of rock ptarmigan. Also, an exploratory analysis revealed no indication that distance to forest edge had a more pronounced effect on shorter ranges as found for habitat size. Habitat quality might not vary as first assumed, supported by the fact that rock ptarmigan utilizes all available habitat from the treeline towards the centre (See Appendix A, Figure A1). Interestingly, the number of rock ptarmigan observations do not increase with distance to forest edge, but rather show a slight decrease. This may be due to the fact that monitoring is done during the breeding season, causing rock ptarmigan to prefer the habitat at more intermediate altitudes (Pedersen et al., 2014). Consequently, rock ptarmigan may not see the forest edge as the poor-quality edge habitat assumed in this study and might only be absent from areas below the treeline as a result of interspecific competition with willow ptarmigan (*Lagopus lagopus*) (Moss, 1974; Wilson & Martin, 2008) and/or higher predation rates (Angelstam, Lindström, & Widén, 1984). From a climate change perspective, this could mean that rock ptarmigan in Norway will remain unaffected by the relative increase in edge habitat that follows from a reduction in patch size. On the other hand, distance to forest edge was included in 6 of the 9 models with substantial support for the colonization parameter, with a relative importance of 0.61. Granted, there is not enough support to confidently state that distance to forest edge affect the colonization probability of a site, but its influence should not be disregarded completely. Especially since the predicted change in colonization probability spans from 0.20 to 0.44 over the range of distances. Unfortunately, few sites are located further away than 4 km from the forest edge (See Appendix B, Figure B1) causing a high uncertainty in the predictions above this distance.

Rock ptarmigan occupancy dynamics in Norway was found to follow a north-south gradient, where both colonization- and local extinction probabilities are higher for sites located in Northern Norway. Occupancy state of a site at higher latitudes tend to change more between years, a higher turnover rate, than sites located further south. In relation to climate change, one could speculate that a shift towards a warmer climate could increase stability in the occupancy dynamics of rock ptarmigan for sites located at high latitudes, if all other factors remain unchanged.

Given that the rock ptarmigan is seen as a sentinel species for detecting environmental change (Imperio et al., 2013; Novoa et al., 2016; Pernollet et al., 2015), the findings of this study could in isolation suggest that alpine habitats in Norway are currently vast enough to leave the occupancy dynamics of montane avifauna more or less unaffected. However, studies predict that both the rock ptarmigan (including *L. muta helvetica*) habitat and population size will severely decrease in the next 30-50 years (Imperio et al., 2013; Revermann et al., 2012) and other alpine species will most likely experience similar processes (La Sorte & Jetz, 2010). In fact, Imperio et al. (2013) revealed that climate change, coupled with anthropogenic modifications to the habitat greatly increases the extinction risk of the rock ptarmigan. Provided that the projections of Revermann et al. (2012) and Imperio et al. (2013) come true, the numerous small patches of alpine habitat face a risk of disappearing in the coming decades, followed by a high risk for patches that currently have a great size. Not only could the rock ptarmigans face extinction in the near future, but Dirnböck et al. (2011) showed that various high-altitude endemic species are particularly vulnerable to habitat loss. Habitat patches that form stepping stone networks could potentially maintain dispersal, as seen for greater sage-grouse (*Centrocercus urophasianus*) (Bush et al., 2011). If these patches of habitat are used as stepping stones for dispersal between more contiguous habitat patches, dispersal patterns could be disrupted, resulting in isolated populations (Saura, Bodin, & Fortin, 2014). Rock ptarmigan and black grouse (*Tetrao tetrix*) are both species of grouse which tend to avoid dispersing across large areas of unsuitable habitat (Caizergues & Ellison, 2002; Constanzi, 2019). A reduction in the size of habitat patches make them less valuable as stepping stone habitats (Saura et al., 2014) and the loss of these patches could therefore have serious implications for the viability of the species dependent on them.

Given that rock ptarmigan occupancy dynamics were found not to be affected by patch size or site location (from the treeline to more central habitat), this suggest that other factors may have been the cause of the observed population decline. A change in climate has greatly affected the population dynamics of small rodent species, particularly alpine and arctic lemming populations (Kausrud et al., 2008), by altering snow conditions in alpine areas (Korslund & Steen, 2006). Rodent peaks in abundance have for the most part been absent or irregular since 1994 (Kausrud et al., 2008). Further, predation pressure on grouse species are linked to rodent population cycles, with predation pressure increasing in the absence of rodent abundance peaks (Kausrud et al., 2008). Additionally, upwards expansion of species' ranges with warming climate can amplify aggressive interactions between species, threatening local population viability (Jankowski, Robinson, & Levey, 2010). Finally, anthropogenic disturbance in mountainous areas and increasing hunting pressure (defined as total number of registered hunters)(Statistisk sentralbyrå, 2019) could affect population sizes by increasing mortality rates (Patthey et al., 2008; Smith & Willebrand, 1999; Watson & Moss, 2004) and decrease chick production (Støen, Wegge, Heid, Hjeljord, & Nellemann, 2010).

One drawback of the dynamic site occupancy model from the unmarked package (Fiske et al., 2017) is that the observations made when moving between the observation points could not be included (See Methods). The inconspicuous nature of rock ptarmigans means that there are numerous sightings as the observer moves between observation points. Movement can startle the bird and cause it to take off in flight and it is then that it is easiest to notice. Excluding these observations can cause an underestimation of the detection probability of the species and further result in underestimation of occupancy, as seen for the single-season models. Hopefully, future revisions of the unmarked package (Fiske et al., 2017) will contain the option to include information of sites that are known to be occupied in the dynamic occupancy model.

It was clearly illustrated that the estimated detection probabilities were low (Figure 3). This in turn gave estimated occupancy probabilities that were consistently higher than using a naïve measure of occupancy, demonstrating the applicability of site occupancy models to the presence/absence data used in this study. All statistical models make certain assumptions about the data being used (Casson & Farmer, 2014) and the site occupancy models employed here are not an exception to the rule. Royle (2006) separated the seasonal repeated surveys in time for their avian survey example, by visiting sites over one month. This helps to make sure that detection and the detection histories at each site are independent from each other, which is one of the assumptions of the dynamic site occupancy model (MacKenzie et al., 2006). However, as rock ptarmigans are highly mobile, surveying over several days could violate the closure assumption, that there must not be a change in occupancy between repeated surveys

(MacKenzie et al., 2006). The closure assumption is therefore more likely to hold when monitoring is performed as described above (See Methods). In fact, if the observer assumes that a sighting is a duplicate from a previous observation point, an observation is only recorded for the first observation point, to account for the non-independence between points (Program for terrestrisk naturovervåking, 2019). Another assumption of dynamic site occupancy models states that there are no false detections of the species (MacKenzie et al., 2006). Given that the observers are well versed in identification of bird species (Kålås et al., 2014), it was assumed that the false-positive error rate would be negligible. The three assumptions mentioned above, should therefore hold for most of the observations made in my study. The final assumption states that there should be no unmodeled heterogeneity in any of the rate parameters (MacKenzie et al., 2006). It is almost certain that this assumption is violated, as there are numerous potential covariates that have not been measured. Inferences made when assumptions are violated can result in biased estimates and produce erroneous relationships between covariates. However, exactly how the results are impacted when the unmodeled variation assumption is violated has not been thoroughly studied (MacKenzie et al., 2006) and should therefore be investigated further.

To conclude, the model selection procedures used here revealed only weak support for my hypotheses. Low levels of support for the variables of interest, habitat size and distance to forest edge, are found throughout the study. Latitude best explained the variance in the dynamic occupancy parameters, with a relative importance equal to 1 for both colonization- and local extinction probabilities. The two latitude estimates were both positive, indicating a more unstable site occupancy dynamic for sites located in the north. However, a lack of evidence for an effect of habitat size and distance to forest edge on the occupancy dynamics of rock ptarmigan, does not mean alpine habitats will not be affected in the near future, as predicted by Revermann et al. (2012) and Imperio et al. (2013). Interestingly, this study show that rock ptarmigans use all available habitat from the forest edge towards more centrally located habitats. This may indicate that the occupancy dynamics of rock ptarmigan could remain unaffected by the relative increase in edge habitat as the elevational shift of the treeline to higher altitudes reduces the size of alpine habitats. With regards to the abundance of rock ptarmigan in Norway, there are probably various other factors that could have caused the observed reduction, such as a rise in predation pressure following absence of rodent cycles (Kausrud et al., 2008), increased hunting pressure (Statistisk sentralbyrå, 2019) or anthropogenic disturbances (Støen et al., 2010). As such, I believe an investigation of the link between some or all of these processes to the decline in rock ptarmigan abundance is a natural next step.

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Appendix A – Rock ptarmigan observations

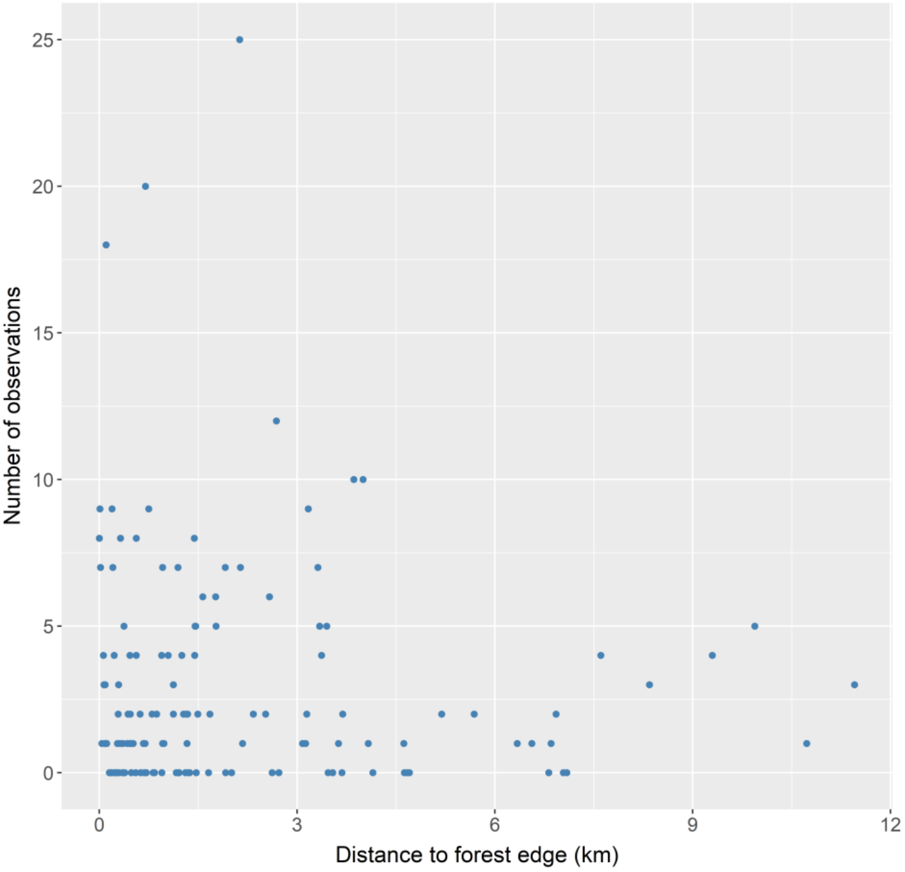

Figure A1. The total number of rock ptarmigan observations during this study with distance to forest edge.

Appendix B – Frequency distributions

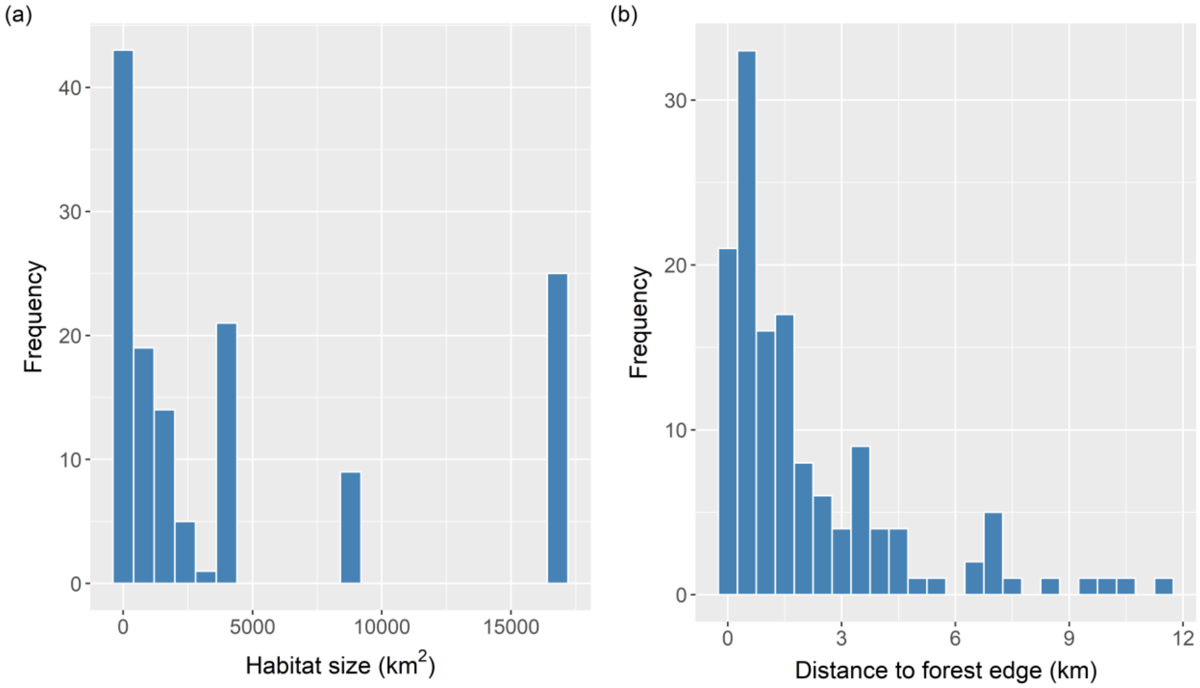

Figure B1. (a) Frequency distribution of the habitat size (km^2) variable. (b) Frequency distribution of the distance to forest edge (km) variable.

Appendix C – Model selection excluding latitude as a covariate: AIC$_C$ table and model selection table

Table C1. Summary of the model selection table, showing the 15 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the 15 most supported models.

Model	df	LogLik	AIC$_C$	ΔAIC$_C$	w_i	Rel. w_i
M1	6	-1623.916	3260.424	0.000	0.038	0.118
M2	5	-1625.120	3260.660	0.236	0.034	0.105
M3	4	-1626.476	3261.230	0.806	0.025	0.077
M4	7	-1623.265	3261.325	0.901	0.024	0.074
M5	12	-1617.577	3261.447	1.023	0.023	0.071
M6	11	-1618.837	3261.602	1.177	0.021	0.065
M7	6	-1624.508	3261.608	1.184	0.021	0.065
M8	8	-1622.294	3261.617	1.193	0.021	0.065
M9	13	-1616.509	3261.715	1.290	0.02	0.062
M10	8	-1622.433	3261.894	1.470	0.018	0.056
M11	7	-1623.586	3261.967	1.543	0.018	0.056
M12	6	-1624.788	3262.168	1.744	0.016	0.05
M13	8	-1622.596	3262.221	1.797	0.015	0.046
M14	9	-1621.493	3261.280	1.856	0.015	0.046
M15	10	-1620.410	3262.413	1.989	0.014	0.043

Table C2. Model selection table showing 10 out of the 15 models with substantial support and their effect sizes for all the variables (V) on logit scale (±SE). Variable Relative Importance (RI), Initial Occupancy probability (I. Occ), Colonization probability (Col), Local extinction probability (Ext), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and year 2011-2018 as fixed factors (Y11-Y18).

V	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	RI
I. Occ. ($\hat{\psi}$)											

Int	-0.823 (±0.347)	-0.793 (±0.346)	-0.805 (±0.346)	-0.734 (±0.347)	-0.671 (±0.383)	-0.68 (±0.385)	-0.761 (±0.348)	-0.776 (±0.345)	-0.702 (±0.384)	-0.795 (±0.35)	
Col. ($\hat{\gamma}$)											
Int	-1.304 (±0.198)	-1.342 (±0.197)	-1.37 (±0.196)	-1.310 (±0.198)	-1.389 (±0.207)	-1.42 (±0.208)	-1.304 (±0.199)	-1.45 (±0.194)	-1.355 (±0.207)	-1.297 (±0.196)	
HS	-0.251 (±0.167)	-	-	-	-	-	-	-	-0.240 (±0.170)	-0.258 (±0.200)	0.427
HS^2	-	-	-	-	-	-	-	-	-	-	0.089
DFE	0.393 (±0.393)	0.271 (±0.166)	-	0.376 (±0.181)	0.267 (±0.168)	-	0.335 (±0.175)	-	0.377 (±0.199)	0.454 (±0.206)	0.749
DFE^2	-	-	-	-	-	-	-	-	-	-	0
Ext. ($\hat{\varepsilon}$)											
Int	-1.6 (±0.326)	-1.61 (±0.325)	-1.67 (±0.335)	-1.014 (±0.434)	-1.71 (±0.334)	-1.77 (±0.345)	-1.561 (±0.322)	-1.554 (±0.555)	-1.7 (±0.336)	-0.967 (±0.440)	
HS	-	-	-	0.979 (±0.510)	-	-	0.261 (±0.227)	1.531 (±0.710)	-	0.818 (±0.522)	0.349
HS^2	-	-	-	-0.553 (±0.346)	-	-	-	-0.905 (±0.453)	-	-0.612 (±0.353)	0.284
DFE	-	-	-	-	-	-	-	-1.546 (±0.744)	-	-	0.26
DFE^2	-	-	-	-	-	-	-	0.475 (±0.253)	-	-	0.154
Det. ($\hat{p}$)											
Int (Y11)	-2.62 (±0.074)	-2.62 (±0.073)	-2.63 (±0.074)	-2.63 (±0.074)	-2.782 (±0.325)	-2.781 (±0.327)	-2.62 (±0.073)	-2.65 (±0.073)	-2.780 (±0.326)	-2.62 (±0.073)	0.198
Y12	-	-	-	-	0.32 (±0.381)	0.312 (±0.379)	-	-	0.308 (±0.383)	-	0.198
Y13	-	-	-	-	-0.638 (±0.398)	-0.646 (±0.398)	-	-	-0.638 (±0.398)	-	0.198
Y14	-	-	-	-	0.147 (±0.364)	0.140 (±0.365)	-	-	0.146 (±0.364)	-	0.198
Y15	-	-	-	-	0.283 (±0.357)	0.284 (±0.358)	-	-	0.276 (±0.358)	-	0.198
Y16	-	-	-	-	0.281 (±0.350)	0.274 (±0.351)	-	-	0.277 (±0.350)	-	0.198

Y17	-	-	-	-	0.203 (±0.352)	0.193 (±0.0.353)	-	-	0.201 (±0.352)	-	0.198
Y18	-	-	-	-	0.085 (±0.366)	0.069 (±0.366)	-	-	0.083 (±0.366)	-	0.198

Appendix D – Single-season occupancy models: AIC$_C$ tables and model selection tables

Table D1. Summary of the 2011 single-season model selection table, showing the model with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported model.

Model	df	LogLik	AIC$_C$	ΔAIC$_C$	w_i	Rel. w_i
M1	2	-89.929	184.131	0.000	0.421	1

Table D2. Model selection table for the 2011 single-season model with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	M1	RI
Occ. ($\hat{\psi}$)		
Int	-0.09 (±0.654)	
HS	-	0
DFE	-	0
Lat	-	0
Det. ($\hat{p}$)		
Int	-3.17 (±0.349)	

Table D3. Summary of the 2012 single-season model selection table, showing the 5 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the most supported models.

Model	**df**	**LogLik**	**AIC_C**	**ΔAIC_C**	**w_i**	**Rel. w_i**
M1	3	-126.462	259.369	0.000	0.258	0.308
M2	2	-127.728	259.674	0.305	0.222	0.265
M3	4	-125.997	260.748	1.379	0.13	0.155
M4	4	-126.081	260.916	1.547	0.119	0.142
M5	3	-127.338	261.12	1.751	0.108	0.129

Table D4. Model selection table for the 5 different 2012 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	**M1**	**M2**	**M3**	**M4**	**M5**	**RI**
Occ. ($\hat{\psi}$)						
Int	-0.537 (±0.474)	-0.478 (±0.439)	-0.578 (±0.492)	-0.547 (±0.521)	-0.505 (±0.447)	
HS	-	-	-	0.593 (±0.896)	-	0.142
DFE	-0.745 (±0.552)	-	-0.824 (±0.612)	-1.398 (±1.446)	-	0.605
Lat	-	-	-0.428 (±0.462)	-	-0.350 (±0.402)	0.284
Det. ($\hat{p}$)						
Int	-2.81 (±0.249)	-2.8 (±0.247)	-2.81 (±0.253)	-2.86 (±0.28)	-2.8 (±0.248)	

Table D5. Summary of the 2013 single-season model selection table, showing the 5 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the most supported models.

Model	**df**	**LogLik**	**AIC_C**	**ΔAIC_C**	**w_i**	**Rel. w_i**
M1	2	-110.82	225.827	0.000	0.232	0.282
M2	4	-108.654	225.953	0.126	0.218	0.265
M3	3	-110.285	226.950	1.123	0.132	0.161
M4	3	-110.374	227.128	1.301	0.121	0.147
M5	3	-110.389	227.158	1.331	0.119	0.145

Table D6. Model selection table for the 5 different 2013 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	**M1**	**M2**	**M3**	**M4**	**M5**	**RI**
Occ. ($\hat{\psi}$)						
Int	0.99 (±1.36)	1.70 (±1.705)	1.027 (±1.40)	0.720 (±1.060)	2.16 (±3.54)	
HS	-	1.39 (±0.904)	-	-	2.56 (±5.16)	0.41
DFE	-	-	-	0.581 (±0.826)	-	0.147
Lat	-	2.88 (±2.338)	0.813 (±1.05)	-	-	0.426
Det. ($\hat{p}$)						
Int	-3.77 (±0.376)	-3.69 (±0.261)	-3.72 (±0.338)	-3.69 (±0.341)	-3.8 (±0.283)	

Table D7. Summary of the 2014 single-season-model selection table, showing the 2 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported models.

Model	**df**	**LogLik**	**AIC$_C$**	**ΔAIC$_C$**	**w_i**	**Rel. w_i**
M1	2	-211.184	426.532	0.000	0.514	0.713
M2	3	-211.007	428.348	1.816	0.207	0.287

Table D8. Model selection table for the 2 different 2014 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Latitude (Lat) and Variable Relative Importance (RI). Distance to forest edge excluded due to high correlation.

V	**M1**	**M2**	**RI**
Occ. ($\hat{\psi}$)			
Int	-0.0004 (±0.41)	0.023 (±0.418)	
HS	-	-0.207 (±0.347)	0.287
Lat	-	-	0
Det. ($\hat{p}$)			
Int	-2.81 (±0.182)	-2.81 (±0.182)	

Table D9. Summary of the 2014 single-season model selection table, showing the 3 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported models.

Model	**df**	**LogLik**	**AIC$_C$**	**ΔAIC$_C$**	**w_i**	**Rel. w_i**
M1	2	-211.184	426.532	0.000	0.401	0.468
M2	3	-210.377	427.088	0.556	0.304	0.355
M3	4	-209.955	428.474	1.942	0.152	0.177

Table D10. Model selection table for the 3 different 2014 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI). Habitat size excluded due to high correlation.

V	M1	M2	M3	RI
Occ. ($\hat{\psi}$)				
Int	-0.0004 (±0.41)	0.100 (±0.543)	0.291 (±0.610)	
DFE	-	0.749 (±0.937)	1.425 (±1.202)	0.532
Lat	-	-	0.462 (±0.496)	0.177
Det. ($\hat{p}$)				
Int	-2.81 (±0.182)	-2.82 (±0.187)	-2.84 (±0.18)	

Table D11. Summary of the 2015 single-season model selection table, showing the 2 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported models.

Model	df	LogLik	AIC$_C$	ΔAIC$_C$	w_i	Rel. w_i
M1	3	-250.550	507.386	0.000	0.316	0.598
M2	2	-252.019	508.179	0.793	0.212	0.402

Table D12. Model selection table for the 2 different 2015 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	M1	M2	RI
Occ. ($\hat{\psi}$)			
Int	-0.375 (±0.290)	0.366 (±0.28)	
HS	-0.484 (±0.301)	-	0.598
DFE	-	-	0
Lat	-	-	0
Det. ($\hat{p}$)			
Int	-2.37 (±0.164)	-2.37 (±0.163)	

Table D13. Summary of the 2016 single-season model selection table, showing the 4 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the most supported models.

Model	df	LogLik	AIC_C	ΔAIC_C	w_i	Rel. w_i
M1	3	-330.5	667.25	0.000	0.329	0.426
M2	4	-330.074	668.5686	1.319	0.17	0.22
M3	3	-331.316	668.883	1.633	0.145	0.188
M4	4	-330.346	669.112	1.862	0.129	0.167

Table D14. Model selection table for the 4 different 2016 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	M1	M2	M3	M4	RI
Occ. ($\hat{\psi}$)					
Int	0.384 (±0.353)	0.399 (±0.360)	0.410 (±0.356)	0.365 (±0.348)	
HS	-0.618 (±0.291)	-0.483 (±0.317)	-	-0.685 (±0.320)	0.813
DFE	-	-	-	0.179 (±0.335)	0.167
Lat	-	0.307 (±0.340)	0.535 (±0.322)	-	0.408
Det. ($\hat{p}$)					
Int	-2.58 (±0.15)	-2.58 (±0.15)	-2.57 (±0.149)	-2.57 (±0.149)	

Table D15. Summary of the 2017 single-season model selection table, showing the 3 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the most supported models.

Model	df	LogLik	AIC_C	ΔAIC_C	w_i	Rel. w_i
M1	3	-310.148	626.549	0.000	0.398	0.425
M2	4	-309.175	626.776	0.227	0.355	0.379
M3	2	-311.987	628.099	1.550	0.183	0.196

Table D16. Model selection table for the 3 different 2017 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE) and Variable Relative Importance (RI).

V	M1	M2	M3	RI
Occ. ($\hat{\psi}$)				
Int	0.758 (±0.479)	0.803 (±0.512)	0.689 (±0.43)	
HS	-0.613 (±0.333)	-0.927 (±0.424)	-	0.804
DFE	-	0.541 (±0.440)	-	0.379
Det. ($\hat{p}$)				
Int	-2.79 (±0.167)	-2.8 (±0.167)	-2.79 (±0.169)	

Table D17. Summary of the 2018 single-season model selection table, showing the 5 models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the most supported models.

Model	df	LogLik	AIC_C	ΔAIC_C	w_i	Rel. w_i
M1	3	-238.776	483.804	0.000	0.285	0.352
M2	2	-240.445	485.016	1.211	0.155	0.192
M3	3	-239.463	485.179	1.374	0.143	0.177
M4	3	-239.676	485.605	1.801	0.116	0.143
M5	4	-238.643	485.711	1.907	0.11	0.136

Table D18. Model selection table for the 5 different 2018 single-season models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Occupancy probability (Occ), Detection probability (Det), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	**M1**	**M2**	**M3**	**M4**	**M5**	**RI**
Occ. ($\hat{\psi}$)						
Int	-0.185 (±0.350)	-0.174 (±0.334)	-0.194 (±0.394)	-0.197 (±0.342)	-0.225 (±0.345)	
HS	-	-	0.394 (±0.299)	-	-	0.177
DFE	0.585 (±0.407)	-	-	-	0.468 (±0.416)	0.488
Lat	-	-	-	-0.368 (±0.302)	-0.184 (±0.349)	0.279
Det. ($\hat{p}$)						
Int	-2.76 (±0.188)	-2.77 (±0.191)	-2.77 (±0.19)	-2.77 (±0.192)	-2.75 (±0.187)	

Appendix E – Habitat size data gaps: AIC$_C$ tables and model selection tables

Table E1. Sites located in patches ≤ 15000 km^2. AIC$_C$ table for the 2 dynamic occupancy models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported models.

Model	df	LogLik	AIC$_C$	ΔAIC$_C$	w_i	Rel. w_i
M1	7	-1329.519	2674.116	0.000	0.148	0.563
M2	6	-1330.916	2674.631	0.516	0.115	0.437

Table E2. Sites located in patches ≤ 15000 km^2. Model selection table for the 2 dynamic occupancy models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Initial Occupancy probability (Occ), Detection probability (Det), Colonization probability (Col), Local extinction probability (Ext), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	M1	M2	RI
I. Occ. ($\hat{\psi}$)			
Int	-0.818 (±0.386)	-0.875 (±0.383)	
Col. ($\hat{\gamma}$)			
Int	-1.094 (±0.207)	-1.114 (±0.207)	
HS	-	-	0
DFE	-	-	0
Lat	0.512 (±0.203)	-0.525 (±0.205)	1
Ext. ($\hat{\varepsilon}$)			
Int	-1.281 (±0.315)	-1.356 (±0.323)	
HS	0.454 (±0.252)	-	0.563
DFE	-	-	0
Lat	0.684 (±0.330)	0.695 (±0.348)	0
Det. ($\hat{p}$)			

Int	-2.57 (±0.078)	-2.57 (±0.078)	

Table E3. Sites located in patches ≤ 5000 km^2. AIC$_C$ table for the 4 dynamic occupancy models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported models.

Model	**df**	**LogLik**	**AIC$_C$**	**ΔAIC$_C$**	**w_i**	**Rel. w_i**
M1	6	-1260.956	2534.788	0.000	0.124	0.411
M2	6	-1261.356	2535.586	0.798	0.083	0.275
M3	7	-1260.727	2536.633	1.845	0.049	0.162
M4	7	-1260.796	2536.771	1.983	0.046	0.152

Table E4. Sites located in patches ≤ 5000 km^2. Model selection table for the 2 dynamic occupancy models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Initial Occupancy probability (Occ), Detection probability (Det), Colonization probability (Col), Local extinction probability (Ext), Habitat Size (HS), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	**M1**	**M2**	**M3**	**M4**	**RI**
I. Occ. ($\hat{\psi}$)					
Int	-0.837 (±0.408)	-0.732 (±0.399)	-0.829 (±0.407)	-0.83 (±0.408)	
Col. ($\hat{\gamma}$)					
Int	-1.035 (±0.216)	-1.138 (±0.231)	-1.032 (±0.221)	-1.032 (±0.217)	
HS	-	0.572 (±0.253)	0.155 (±0.231)	-	0.437
DFE	-	-	-	-	0
Lat	0.496 (±0.209)	-	0.417 (±0.239)	0.499 (±0.210)	0.725
Ext. ($\hat{\varepsilon}$)					
Int	-1.379 (±0.343)	-1.442 (±0.365)	-1.391 (±0.347)	-1.355 (±0.346)	
HS	-	0.743 (±0.323)	-	0.158 (±0.281)	0.427
DFE	-	-	-	-	0
Lat	0.857 (±0.384)	-	0.855 (±0.389)	0.787 (±0.401)	0.725
Det. ($\hat{p}$)					

Int	-2.57 (±0.08)	-2.58 (±0.083)	-2.57 (±0.08)	-2.56 (±0.08)	

Appendix F – Influence of habitat size on short range: AIC$_C$ tables and model selection tables

Table F1. Sites located in patches ≤ 500 km^2. AIC$_C$ table for the dynamic occupancy model with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported model.

Model	df	LogLik	AIC$_C$	ΔAIC$_C$	w_i	Rel. w_i
M1	6	-597.487	1209.075	0.000	0.59	1

Table F2. Sites located in patches ≤ 500 km^2. Model selection table for the dynamic occupancy model with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Initial Occupancy probability (Occ), Detection probability (Det), Colonization probability (Col), Local extinction probability (Ext), Habitat Size (HS), Latitude (Lat) and Variable Relative Importance (RI).

V	M1	RI
I. Occ. ($\hat{\psi}$)		
Int	-0.408 (±0.457)	
Col. ($\hat{\gamma}$)		
Int	-1.30 (±0.391)	
HS	1.62 (±0.496)	1
Lat	-	0
Ext. ($\hat{\varepsilon}$)		
Int	-1.26 (±0.477)	
HS	1.46 (±0.431)	1
Lat	5.67 (±2.76)	0
Det. ($\hat{p}$)		
Int	-2.53 (±0.108)	

Table F3. Sites located in patches ≤ 1000 km^2*. AIC_C table for the 4 dynamic occupancy models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the most supported models.*

Model	**df**	**LogLik**	**AIC_C**	**ΔAIC_C**	**w_i**	**Rel. w_i**
M1	5	-778.208	1567.593	0.000	0.245	0.410
M2	4	-780.022	1568.814	1.221	0.133	0.223
M3	6	-777.646	1568.972	1.38	0.123	0.206
M4	6	-777.891	1569.462	1.869	0.096	0.161

Table F4. Sites located in patches ≤ 1000 km^2*. Model selection table for the 4 dynamic occupancy models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Initial Occupancy probability (Occ), Detection probability (Det), Colonization probability (Col), Local extinction probability (Ext), Habitat Size (HS), Latitude (Lat) and Variable Relative Importance (RI).*

V	**M1**	**M2**	**M3**	**M4**	**RI**
I. Occ. ($\hat{\psi}$)					
Int	-0.505 (±0.457)	-0.506 (±0.457)	-0.568 (±0.465)	-0.507 (±0.456)	
Col. ($\hat{\gamma}$)					
Int	-1.61 (±0.322)	-1.57 (±0.311)	-1.516 (±0.319)	-1.608 (±0.317)	
HS	0.43 (±0.226)	-	0.465 (±0.234)	0.519 (±0.256)	0.777
Lat	-	-	0.306 (±0.286)	-	0.206
Ext. ($\hat{\varepsilon}$)					
Int	-1.82 (±0.459)	-1.82 (±0.469)	-1.7 (±0.437)	-1.814 (±0.443)	
HS	-	-	-	0.296 (±0.353)	0.161
Lat	-	-	-	-	0
Det. ($\hat{p}$)					
Int	-2.61 (±0.104)	-2.62 (±0.105)	-2.6 (±0.103)	-2.61 (±0.103)	

Appendix G – Influence of distance to forest edge on short range

Table G1. Sites located ≤ 0.5 km from the forest edge. AIC$_C$ table for the 2 dynamic occupancy models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC$_C$ values, relative difference in model AIC$_C$ values (ΔAIC$_C$), AIC$_C$ weight (w_i) and the relative AIC$_C$ weight (Rel. w_i) for the most supported models.

Model	**df**	**LogLik**	**AIC$_C$**	**ΔAIC$_C$**	**w_i**	**Rel. w_i**
M1	5	-423.27	858.206	0.000	0.360	0.627
M2	6	-422.422	859.244	1.038	0.214	0.373

Table G2. Sites located ≤ 0.5 km. Model selection table for the 2 dynamic occupancy models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Initial Occupancy probability (Occ), Detection probability (Det), Colonization probability (Col), Local extinction probability (Ext), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	**M1**	**M2**	**RI**
I. Occ. ($\hat{\psi}$)			
Int	-0.224 (±0.631)	-0.287 (±0.593)	
Col. ($\hat{\gamma}$)			
Int	-1.406 (±0.385)	-1.472 (±0.397)	
DFE	-	-	0
Lat	0.751 (±0.309)	0.941 (±0.358)	1
Ext. ($\hat{\varepsilon}$)			
Int	-0.966 (±0.479)	-1.161 (±0.516)	
DFE	-	-	0
Lat	-	0.695 (±0.579)	0.373
Det. ($\hat{p}$)			
Int	-2.59 (±0.147)	-2.57 (±0.142)	

Table G3. Sites located ≤ 1 km from the forest edge. AIC_C table for the 2 dynamic occupancy models with substantial support. Degrees of freedom (df), model log likelihoods (LogLik), AIC_C values, relative difference in model AIC_C values (ΔAIC_C), AIC_C weight (w_i) and the relative AIC_C weight (Rel. w_i) for the most supported models.

Model	**df**	**LogLik**	**AIC_C**	**ΔAIC_C**	**w_i**	**Rel. w_i**
M1	5	-638.68	1378.412	0.000	0.291	0.655
M2	6	-683.097	1379.693	1.282	0.153	0.345

Table G4. Sites located ≤ 1 km. Model selection table for the 2 dynamic occupancy models with substantial support and the effect sizes for all the variables (V) on logit scale (±SE). Initial Occupancy probability (Occ), Detection probability (Det), Colonization probability (Col), Local extinction probability (Ext), Distance to Forest Edge (DFE), Latitude (Lat) and Variable Relative Importance (RI).

V	**M1**	**M2**	**RI**
I. Occ. ($\hat{\psi}$)			
Int	-0.616 (±0.484)	-0.634 (±0.477)	
Col. ($\hat{\gamma}$)			
Int	-1.405 (±0.263)	-1.395 (±0.259)	
DFE	-	-	0
Lat	0.484 (±0.230)	0.605 (±0.255)	1
Ext. ($\hat{\varepsilon}$)			
Int	-0.971 (±0.354)	-1.006 (±0.347)	
DFE	-	-	0
Lat	-	0.376 (±0.348)	0.345
Det. ($\hat{p}$)			
Int	-2.56 (±0.111)	-2.55 (±0.109)	

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