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Research article

Interspecific competition impacts the occupancy and range limits of two ptarmigan species along the elevation gradient in Norway

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Many mountain species are expected to respond to climate change through upslope shifts of their range limits, but competition may restrict or alter this response. Under traditional range-limit theory, it is expected that lower-elevation species are better competitors than closely related higher-elevation species. However, recent work finds that this prediction is often unmet. We investigated evidence for the impact of competition during breeding season on the elevational range limits of a pair of closely related bird species, willow ptarmigan *Lagopus lagopus* and rock ptarmigan *L. muta*, in mainland Norway. The species share overlapping ranges that loosely divide slightly upslope from the treeline ecotone, with willow ptarmigan generally occupying lower sites and rock ptarmigan occupying higher sites. We used multi-species occupancy models to test four competing hypotheses for how competition may affect the range limit between willow ptarmigan and rock ptarmigan: 1) asymmetric competition that restricts the lower range limit of rock ptarmigan; 2) asymmetric competition that restricts the upper range limit of willow ptarmigan; 3) condition-specific competition that restricts both species' range limits; and 4) range limits unaffected by competition. We found evidence for a negative pairwise interaction between the two species. Changes in interaction strength along the elevation gradient suggested evidence for condition-specific competition. However, a strong positive correlation between rock ptarmigan and higher-elevation habitat resulted in a highly asymmetric outcome, where the upper range limit of willow ptarmigan was restricted but rock ptarmigan occupancy was fairly independent of willow ptarmigan. This outcome is opposite to the prediction of traditional range-limit theory and may suggest a greater climate threat to willow ptarmigan than has been previously projected. Thus, our results demonstrate the importance of considering biotic interactions at both the higher and lower ends of species' range limits along elevation gradients.

Keywords: elevation gradient, interspecific competition, occupancy, ptarmigan, range limits



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Introduction

Species in high-elevation and high-latitude environments are expected to be highly vulnerable to the effects of climate change (Fei et al. 2017, Pacifici et al. 2017, Scridel et al. 2021). These environments face rapidly warming temperatures, altered climate dynamics, and altered habitat structure, exacerbated by feedback loops (Pepin 2015). In response, the ranges of many species have shifted upward in elevation or poleward to track suitable conditions (Lehikoinen et al. 2013, Lenoir and Svenning 2014). However, species' ability to shift their range limits in response to changing climate conditions can be complicated by biotic interactions (Wisz et al. 2013, Godsoe et al. 2017, Sirén and Morelli 2020). Competition is expected to play an especially strong role in establishing the range limits of species that are closely related or share similar traits and ecosystem function (Simberloff and Dayan 1991, Freeman 2020). When potential competitors share overlapping distributions along an elevational or latitudinal gradient, the lower elevation or latitude species is traditionally thought to restrict the lower range limit of the higher species through asymmetric competition. This follows the long-standing theory that abiotic factors tend to set species' range limits at their more abiotically stressful range edges (e.g. higher elevation) while biotic interactions tend to set species' range limits at their less stressful range edges (e.g. lower elevation) (Darwin 1859, MacArthur 1972, Louthan et al. 2015, Freeman 2020).

The growing urgency of climate change threats to mountain species has led to a renewed focus on the role of biotic interactions in setting species' range limits along elevational gradients (Sirén and Morelli 2020, Lyu and Alexander 2022). Understanding the effect of biotic interactions on species' range limits is critical for characterizing the distinct climate threats faced by each species. Under the traditional theory that asymmetric competition will restrict the lower range limit of a higher elevation species, upward range expansion of a lower elevation species is expected to reduce the space available for the higher species in what has been termed an 'escalator to extinction' (Urban 2018, Freeman 2020, Paquette and Hargreaves 2021). However, it has become clear that the pattern of competitive dominance by lower elevation species is far from universal (Sirén and Morelli 2020, Lyu and Alexander 2022). Recent studies of species pairs have revealed a variety of alternative outcomes, including asymmetric competition that favors the higher elevation species (Twomey et al. 2008, Freeman 2020); condition-specific competition, where species' competitive dominance depends upon the environmental conditions such that each holds dominance along a portion of the elevation gradient (Sirén and Morelli 2020, Lyu and Alexander 2022, Mauro et al. 2022); and occurrence patterns with no evidence of spatial competitive exclusion (Sirén and Morelli 2020).

Here, we investigate evidence for the impact of competition on the elevation range limits of a pair of congeneric ptarmigan species in mainland Norway. Ptarmigan (*Lagopus* genus) are charismatic, cold-adapted grouse that occupy high

altitude and tundra habitat across the Holarctic (Fuglei et al. 2020, Scridel et al. 2021). Due to their distribution and their sensitivity to climate impacts, including temperature increase, snow loss, and changes in biotic interactions, they are recognized as sentinels of climate change (Storch 2007, Henden et al. 2017, Bowler et al. 2020, Hjeljord and Loe 2022). Habitat loss and upward shifts in range limits have already been observed for ptarmigan species in some circumstances and these are expected to continue, with some studies predicting regional losses of over 50% of habitat in coming decades (Scridel et al. 2017, Brambilla et al. 2022). However, the role of competition in shaping ptarmigan species' range limits is not well understood and has therefore not been explicitly accounted for in predictions of range shift (Scridel et al. 2021). Each species has separately been studied extensively, but relatively little research focuses on sympatric occurrence of the two species despite the fact that they share large portions of their ranges (Henden et al. 2017, Scridel et al. 2021). An improved understanding of competition between ptarmigan species is needed to understand the specific climate threats faced by this genus (Schai-Braun et al. 2021, Scridel et al. 2021).

The ranges of willow ptarmigan *L. lagopus* and rock ptarmigan *L. muta* overlap across a variety of alpine, subalpine, and tundra habitat conditions in Norway, ranging from high-aspect alpine and subalpine habitat found inland at higher elevations to lower-elevation coastal and northern mountain habitats and extending to tundra habitat farther north (Fuglei et al. 2020). Across these varied conditions, partitioning of habitat between the two species during the breeding season is loosely defined by the treeline ecotone (Wilson and Martin 2008, Fuglei et al. 2020). Willow ptarmigan commonly occupies lower elevation sites with dense thicket or treeline vegetation (Kvasnes et al. 2018, Montgomerie and Holder 2020), while rock ptarmigan more often occupies higher elevation habitat above the treeline, typically breeding in alpine meadows with rock, shrub, and heather ground cover (Wilson and Martin 2008, Pedersen et al. 2014, Fuglei et al. 2020). The shift from predominant occupancy by willow ptarmigan to predominant occupancy by rock ptarmigan, loosely centered on the treeline ecotone, therefore aligns with the species' known habitat preferences. However, theory about species pairs along elevation gradients suggests that they may also be influenced by a competitive interaction between the two species.

We used multi-species occupancy modeling (MacKenzie et al. 2002, Rota et al. 2016) to investigate evidence for competition between willow ptarmigan and rock ptarmigan in Norway. We describe four competing hypotheses corresponding to distinct ways that competition is expected to influence range limits of species pairs along elevation gradients (Table 1). The first hypothesis (H1) follows the traditional expectation (Darwin 1859, MacArthur 1972, Louthan et al. 2015) that asymmetric competition will favor the lower elevation species. The second hypothesis (H2) follows recent studies describing asymmetric competition that favors the higher elevation species (Freeman 2020,

Table 1. Four competing hypotheses and associated predictions that describe potential ways in which competitive interactions between willow ptarmigan and rock ptarmigan might affect the range limits of the two species. In the prediction plots in the rightmost column, the yellow (left) figures indicate predicted rock ptarmigan occupancy probability along the y-axis; the blue (right) figures indicate the same for willow ptarmigan. The x-axis indicates distance (in meters) from the treeline, where the left side of the x-axis is below the treeline and the right side of the y-axis is above the treeline. Solid lines indicate conditional occupancy probability in the absence of the other species and dashed lines indicate conditional occupancy probability in the presence of the other species.

Hypotheses	Species	Expected effect of competition on range limits	Expected evidence: model parameters	Predictions	
				Expected evidence: occupancy trends	Expected evidence: occupancy trends
				Rock	Willow
H1. Asymmetric competition favors willow ptarmigan	<i>Willow</i>	Range limits are unaffected	Conditional occupancy probability is independent of or increased in the presence of rock ptarmigan		
	<i>Rock</i>	Lower range limit is constricted	Conditional occupancy probability is reduced in the presence of willow ptarmigan		
H2. Asymmetric competition favors rock ptarmigan	<i>Willow</i>	Upper range limit is constricted	Conditional occupancy probability is reduced in the presence of rock ptarmigan		
	<i>Rock</i>	Range limits are unaffected	Conditional occupancy probability is independent of or increased in the presence of willow ptarmigan		
H3. Condition-specific competition favors rock ptarmigan at higher elevations and willow ptarmigan at lower elevations	<i>Willow</i>	Upper range limit is constricted	Conditional occupancy probability is reduced in the presence of rock ptarmigan		
	<i>Rock</i>	Lower range limit is constricted	Conditional occupancy probability is reduced in the presence of willow ptarmigan		
H4. Competition does not affect the species' range limits	<i>Willow</i>	Range limits are unaffected	Conditional occupancy probability is independent of or increased in the presence of rock ptarmigan		
	<i>Rock</i>	Range limits are unaffected	Conditional occupancy probability is independent of or increased in the presence of willow ptarmigan		

Lyu and Alexander 2022). The third hypothesis (H3) follows theory on condition-specific competition, where each species is dominant in its preferred habitat (Twomey et al. 2008, Sirén and Morelli 2020). Finally, the fourth hypothesis (H4) describes a scenario where the ranges of willow ptarmigan and rock ptarmigan are not influenced by competition between the two species. We fitted a set of candidate models to test the competing hypotheses.

Material and methods

Occurrence data

We extracted data on the detection and non-detection of willow ptarmigan and rock ptarmigan from Norwegian breeding bird monitoring surveys (<https://hekkefugloervakingen.nina.no/>) conducted between 2007 and 2021 (Kålås et al. 2022). Surveys are coordinated by the Norwegian Institute

for Nature Research, BirdLife Norway, and the Norwegian Environmental Agency, and are conducted once per year between weeks 22 and 28. This monitoring scheme includes 492 survey routes that were randomly selected from the approximately 1000 crossing points created by a grid of 18 × 18 km laid out across Norway. This provides a relatively even coverage of habitats across Norway. The number of routes surveyed annually has increased from approximately 100 routes in 2007 to stabilize at approximately 400 routes from 2016 (Kålås et al. 2022). The exact sampling date for each route is chosen to be as early as feasible within the indicated time window given seasonal conditions and site accessibility. Each survey route consists of between 12 and 20 observation points tracing the outline of a 1.5 × 1.5 km square, though due to topographical obstacles some of the sampling routes have adjustments in the square system (Fig. 1). At each observation point, counts of all species are performed for exactly 5 min (NBBMS 2023). Observations are performed by experienced birdwatchers and ornithologists.

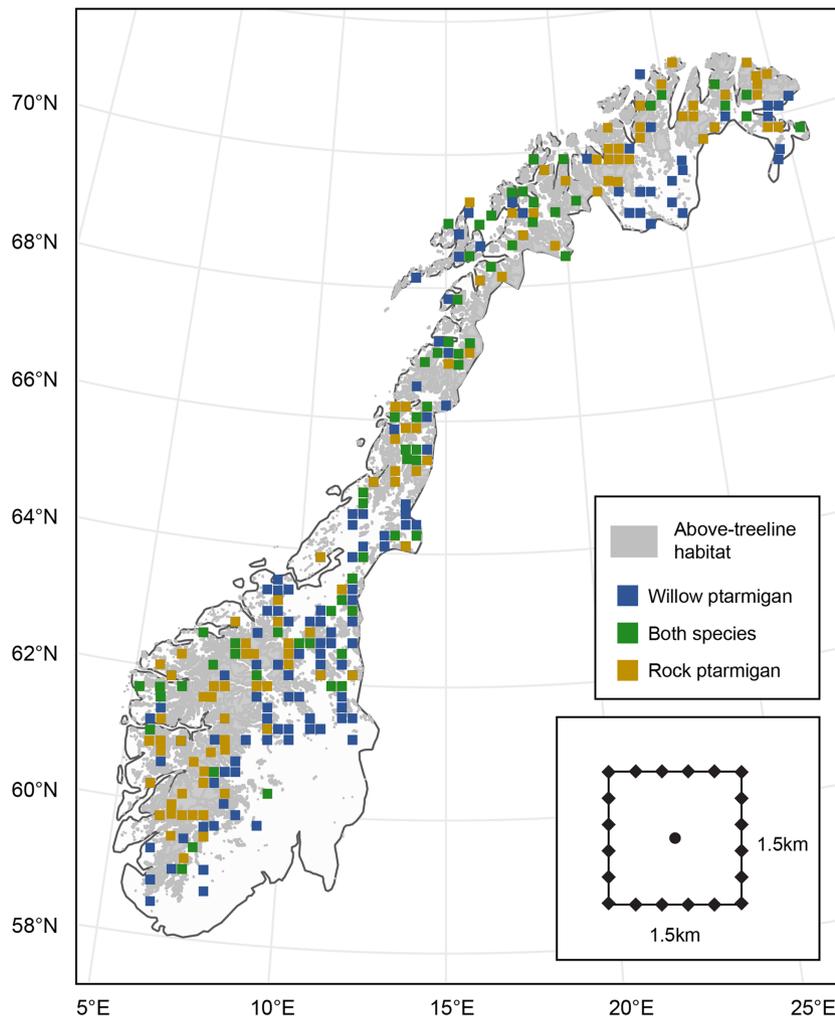


Figure 1. Map of all survey routes included in the study, indicating naive occupancy. Colors indicate whether either or both species of interest were recorded at the route at least once during any year of the study. Darker grey region indicates above-treeline habitat. The inset grid indicates the layout of each survey route, which consists of twenty observation points (represented by the diamonds) that were used as spatial replicates in this study. Due to topographical obstacles, some routes consist of fewer than the full twenty observation points, but all have at least twelve. The centroid (represented by the circle) was used to represent the route location when deriving covariates.

We included in our analysis all years of survey data for all survey routes at which at least one of the ptarmigan species has ever been observed during a survey ($n=282$). The percentage of routes at which each species was observed annually varied from 16 to 37% for willow ptarmigan (mean 26%) and 8 to 29% for rock ptarmigan (mean 19%). There was an overall positive trend in the percentage of routes occupied for both species, with a greater increase during the study duration for rock ptarmigan (Supporting information). Because we were not focused on change in occupancy between years, we chose to ‘stack’ the data for each survey route, using each unique combination of route and year (‘route-year’; hereafter, ‘site’) as a unit of analysis. This approach is recognized as an effective way to increase sample size, though at the risk of underestimating the error associated with parameter estimates due to potential pseudoreplication (Burnett and Roberts 2015). This ‘stacking’ approach also allowed our model to

accommodate the relative independence at each survey route expected between years, driven by high year-to-year mortality among willow and rock ptarmigan (Israelsen et al. 2020, Nilsen et al. 2020). As an ad hoc examination of potential spatial or temporal autocorrelation, we examined the residuals for signs of spatial or temporal bias introduced by this approach and found no issues (Supporting information). The twelve to twenty observation points within each site were used as spatial replicates, and the species counts at each observation point were converted to detection/non-detection data for occupancy analysis. Counts were low; for both species, the mean number of individuals counted at each site where the species was present was 2, which remained relatively consistent throughout the study duration (Supporting information). The final dataset consisted of 2325 sites, each associated with a sampling history of between twelve and twenty replicates, where the data for each replicate consisted

of either a '1' or '0' for each species to indicate its detection or non-detection.

Environmental data

We considered the potential relationship of two environmental variables to the ptarmigan species' occupancy: 1) the distance from the centroid of the survey route to the treeline and 2) the elevation of the treeline nearest to the centroid of the survey route. The location of the treeline was derived from an empirical model of the boundary between forest and mountain habitat across mainland Norway at a 25 m resolution (Bryn and Porthoff 2018). Elevation values were derived from the Norwegian Digital Elevation Model (www.kartverket.no) at a resolution ranging from 25 m (at 71.09°N) to 40 m (at 48.50°N).

Distance from the survey route to the treeline was calculated as the shortest distance, in meters, between the centroid of the route and the nearest point on the modeled treeline. Distances above the treeline were assigned positive values and distances below the treeline were assigned negative values. This approach was selected based on a preliminary comparison of two alternative measures of distance from the treeline: the along-the-ground measurement previously described, as well as the vertical distance, calculated as the difference in elevation between the centroid of the survey route and the nearest treeline point. The correlation between along-the-ground and vertical distance was relatively high ($r=0.51$) so we did not include them in any models together but rather compared their performance using the AIC_c model selection approach described below. Vertical distance performed substantially worse ($\Delta AIC_c > 220$; Supporting information) so it was excluded from further analyses and along-the-ground distance (hereafter, 'distance') was retained as the only measure of distance between sampling locations and the treeline. Due to the size of the survey route (1.5×1.5 km), it should be noted that routes within approximately 1000 m of the nearest treeline may include one or more observation points on the opposite side of the modeled treeline from the route centroid (Fig. 1).

Statistical analysis

We modeled the occupancy probability of willow ptarmigan and rock ptarmigan using the multi-species occupancy modeling framework introduced by Rota et al. (2016). This framework extends single-species occupancy modeling (MacKenzie et al. 2002) to model species' occupancy probability contingent on spatial covariates as well as on the modeled occupancy probability of one or more other species. It estimates detection probability (p) and occupancy probability (ψ) for each species and each pairwise interaction specified in the model (Rota et al. 2016). A different set of covariates can be specified for the occupancy and detection probabilities of each species and interaction. The observed occupancy of each species is considered to be conditional on both the

modeled detection probability and the latent true occupancy state. Observed and true occupancy are modeled as Bernoulli random variables, where Z = the true occupancy state, y = the observed data, p = detection probability, ψ = occupancy probability, i = sites, j = sampling replicates, and s = species or pairwise interaction:

$$Z_{is} \sim \text{Bernoulli}(\psi_{is})$$

$$y_{ijs} | Z_{is} \sim \text{Bernoulli}(Z_{is} p_{ijs})$$

Occupancy and detection probabilities for each species and pairwise interaction are modeled as a function of covariates:

$$\text{logit}(\psi_{is}) = \beta_{0s} + \beta_{\psi s} \text{cov}_{is}$$

$$\text{logit}(p_{is}) = \beta_{0s} + \beta_{ps} \text{cov}_{ijs}$$

We specified a full model that included the same occupancy covariates for each species and for their pairwise interaction: the additive and interaction effects (e.g. the product) of distance from treeline and treeline elevation (Table 2). We derived a set of candidate models ($n=150$) that consisted of all possible combinations of the occupancy covariates included in the full model, with and without the inclusion of the model formula for a pairwise interaction. We used AIC_c model selection to identify the best fitting combination of covariates to model the occupancy of each individual species as well as their pairwise interaction. Continuous covariates were centered and scaled for analysis by subtracting the mean and dividing by one standard deviation. In each candidate model, we included year as a categorical occupancy covariate for both species to account for potential annual variation in the species' populations. In all candidate models, we allowed the probability of detection to vary with two detection covariates: week of the survey (weeks 22–28), to account for variation in behavior of the species throughout the survey season; and openness of habitat, as represented by a binary classification of above or below treeline.

We included a minimal set of variables because we expected the selected variables to have the greatest effect on habitat partitioning between the two ptarmigan species. Distance from treeline was included in the full model for each species' occupancy because it was expected to serve as an effective proxy for many correlated attributes of the species' habitat preferences (Kvasnes et al. 2018), and it was included in the full model for the species' interaction to allow for the possibility that interactions would vary along the elevation gradient. Elevation of the nearest treeline was included to allow for potential variation in the species' habitat preferences and interactions throughout mainland Norway, which is characterized by a gradient in the elevation of treeline from higher in the south and inland to lower in the north and

Table 2. Candidate full model. For occupancy covariates, ‘distance’ indicates along-the-ground distance between survey route centroids and the nearest treeline point, ‘treeline_elevation’ indicates the elevation of the nearest treeline point, and ‘year’ is a categorical variable indicating the year the survey was conducted. For detection covariates, ‘week’ indicates the numerical week (22–28) in which the survey was conducted and ‘treeline’ indicates whether the survey route centroid was above the treeline (in more open habitat) or below the treeline. The ‘year’, ‘week’, and ‘treeline’ covariates were retained in all candidate models.

	Occupancy model (ψ)	Detection model (p)
Willow	distance × treeline_elevation + year	week + treeline
Rock	distance × treeline_elevation + year	week + treeline
Willow-rock	distance × treeline_elevation	(.)

along the coast. To minimize the risk of capturing additional unmodeled habitat variables related to the species’ habitat preferences in the model outputs, we restricted the sampling locations included in our model to those where at least one of the ptarmigan species had been observed at least once during the sampling period between 2007 and 2021.

We used Akaike’s information criterion for small sample sizes (AIC_c) to rank the set of candidate models derived from the full model. All models within 2.0 AIC_c values of the best fitting model were considered competitive and the results of all competitive models were examined. All analyses were conducted in R ver. 4.1.2 (www.r-project.org). Models were fitted with the R package ‘unmarked’ using the *occuMulti()* function (Fiske and Chandler 2011) and model selection was performed with the ‘AICcmodavg’ R package (Mazerolle 2023).

Results

The best fitting models ($\Delta AIC_c < 2.0$; Fig. 2, Table 3) offer partial support for both hypothesis H2 (asymmetric competition that favors rock ptarmigan) and H3 (condition-specific competition). These models fit substantially better than any of the candidate models that did not include the effect of interspecific interactions ($\Delta AIC_c > 40$; Supporting information), suggesting that the range limits of ptarmigan species in Norway are set not only by habitat preferences but also by interspecific interactions. The parameter estimates differ little among the best fitting models; therefore, we present the model with the lowest AIC_c value here (Table 3–4). Rock ptarmigan showed a stronger relationship to the environmental variables than willow ptarmigan; in all thirteen best fitting models, both environmental occupancy covariates were included in the model formula for rock ptarmigan. In contrast, the relationship between willow ptarmigan and the environmental occupancy covariates was less clear.

In environments near the treeline, the modeled occupancy probability of rock ptarmigan is reduced in the presence of willow ptarmigan (Fig. 2; treeline [2018]: willow absent $\psi_{\text{rock}} = 0.48 \pm 0.06$; willow present $\psi_{\text{rock}} = 0.36 \pm 0.06$). The modeled occupancy probability of willow ptarmigan at the treeline is also reduced in the presence of rock ptarmigan (treeline [2018]: rock absent $\psi_{\text{willow}} = 0.42 \pm 0.04$; rock present $\psi_{\text{willow}} = 0.31 \pm 0.05$). At greater distances above the treeline, the negative association between the two species grows stronger (Fig. 2, Table 4). However, the strong positive relationship between rock ptarmigan occupancy probability and distance above the treeline (Fig. 2, Table 4) means that

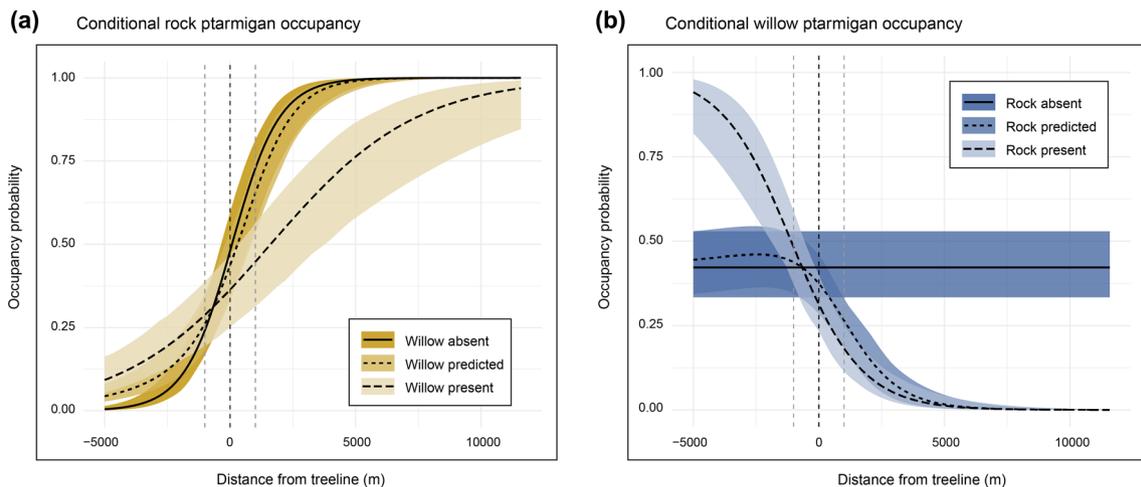


Figure 2. Conditional occupancy probability of (a) rock ptarmigan and (b) willow ptarmigan under three distinct modeled conditions. Model structure is described in Table 4. For both species, the solid line indicates occupancy probability given the absence of the other species; the dotted line indicates occupancy probability given the modeled occupancy of the other species; and the dashed line indicates occupancy probability given the presence of the other species. Ribbons indicate 95% confidence intervals. Elevation of the nearest treeline is held constant at its mean value and the year is held constant at 2018, which is the year with parameter estimates closest to the mean for all years (see Supporting information for plots of all years). Because distance from the treeline was calculated from the centroid of the 1.5×1.5 km survey route, the dashed lines indicate the range of estimated distance values that could refer to survey routes with one or more observation points potentially on the opposite side of the treeline from the route centroid.

Table 3. The occupancy formulas of the thirteen models considered to be competitive ($\Delta AIC_c < 2.0$; see Supporting information for full list of candidate models). Detection model formulas are consistent as described in Table 2.

Model	AIC _c	ΔAIC_c	<i>k</i>	AIC _c weight
ψ willow: 1 + year	17193.54	0	51	0.08
ψ rock: distance * treeline_elevation + year				
ψ willow-rock: distance				
ψ willow: distance + year	17193.79	0.25	52	0.07
ψ rock: distance * treeline_elevation + year				
ψ willow-rock: distance				
ψ willow: elevation + year	17193.8	0.25	52	0.07
ψ rock: distance * elevation + year				
ψ willow-rock: distance				
ψ willow: distance + elevation + year	17193.8	0.25	53	0.07
ψ rock: distance * elevation + year				
ψ willow-rock: distance				
ψ willow: 1 + year	17194.26	0.72	50	0.06
ψ rock: distance + elevation + year				
ψ willow-rock: distance				
ψ willow: distance + year	17194.38	0.83	51	0.06
ψ rock: distance + elevation + year				
ψ willow-rock: distance				
ψ willow: 1 + year	17194.79	1.25	52	0.04
ψ rock: distance * elevation + year				
ψ willow-rock: distance + elevation				
ψ willow: 1 + year	17194.84	1.3	52	0.04
ψ rock: distance + elevation + year				
ψ willow-rock: distance * elevation				
ψ willow: distance + year	17195.1	1.56	53	0.04
ψ rock: distance + elevation + year				
ψ willow-rock: distance * elevation				
ψ willow: distance + year	17195.13	1.59	53	0.04
ψ rock: distance * elevation + year				
ψ willow-rock: distance + elevation				
ψ willow: distance + elevation + year	17195.25	1.71	52	0.04
ψ rock: distance + elevation + year				
ψ willow-rock: distance				
ψ willow: elevation + year	17195.28	1.73	51	0.04
ψ rock: distance + elevation + year				
ψ willow-rock: distance				
ψ willow: distance * elevation + year	17195.47	1.93	54	0.03
ψ rock: distance * elevation + year				
ψ willow-rock: distance				

the predicted negative impact of willow ptarmigan on rock ptarmigan decreases with greater distance above treeline. The opposite is true for willow ptarmigan; the predicted negative impact of rock ptarmigan on willow ptarmigan increases with greater distance above treeline (Fig. 2). These trends suggest a dynamic of condition-specific competition (H3), where each species is expected to exert a stronger negative influence under the conditions that align more closely with their known habitat preferences.

However, consideration of the species' occupancy probabilities conditioned upon the predicted occupancy of the other species – rather than on the presence of the other species – suggests that the outcome of competition between rock and willow ptarmigan more closely resembles asymmetric competition that favors rock ptarmigan (H2). Because rock ptarmigan has a strong positive relationship with distance above treeline and willow ptarmigan does not, the rock ptarmigan occupancy probability under conditions of predicted

willow ptarmigan occupancy does not, at any point above the treeline, differ significantly from under conditions of willow ptarmigan absence (Fig. 2). In contrast, the occupancy probability of willow ptarmigan under conditions of predicted rock ptarmigan occupancy is significantly lower than under conditions of rock ptarmigan absence (Fig. 2). At sites lower than approximately 500 m of distance below the treeline, our results indicate a positive relationship between the two species (Fig. 2, Table 4). This suggests either a direct positive relationship or that, in below-treeline habitat conditions, habitat preference is more important to species occupancy probability than the negative relationship that occurs over most of the elevation gradient.

All of the best fitting models included the treeline elevation covariate in at least one of the model formulas (Table 3). The occupancy probability of rock ptarmigan was slightly lower in locations with higher treeline elevations, suggesting that the negative effect of competition on willow

Table 4. Parameter estimates (reported in multivariate logit scale) for the best fitting model. Estimates are followed by standard errors in brackets.

Parameter	Rock	Willow	Rock: Willow
<i>Occupancy model (ψ)</i>			
Intercept	-2.879 [\pm 0.617]	-0.385 [\pm 0.349]	0.888 [\pm 0.272]
Distance	3.473 [\pm 0.398]		-2.340 [\pm 0.407]
Treeline elevation	-0.194 [\pm 0.096]		
Distance: Treeline elevation	-0.263 [\pm 0.159]		
2008	0.461 [\pm 0.745]	0.334 [\pm 0.481]	
2009	0.112 [\pm 0.731]	-0.408 [\pm 0.475]	
2010	-0.162 [\pm 0.757]	-0.499 [\pm 0.459]	
2011	0.249 [\pm 0.680]	-0.310 [\pm 0.424]	
2012	0.381 [\pm 0.676]	-0.351 [\pm 0.421]	
2013	0.107 [\pm 0.682]	-0.804 [\pm 0.429]	
2014	0.982 [\pm 0.646]	-0.319 [\pm 0.409]	
2015	1.039 [\pm 0.638]	0.104 [\pm 0.401]	
2016	1.307 [\pm 0.626]	0.253 [\pm 0.395]	
2017	1.493 [\pm 0.629]	-0.092 [\pm 0.397]	
2018	0.776 [\pm 0.626]	0.073 [\pm 0.392]	
2019	0.940 [\pm 0.629]	0.515 [\pm 0.395]	
2020	1.093 [\pm 0.633]	0.247 [\pm 0.398]	
2021	1.468 [\pm 0.625]	0.256 [\pm 0.392]	
<i>Detection model (p)</i>			
Intercept	-3.023 [\pm 0.406]	-2.445 [\pm 0.199]	
Above treeline	0.037 [\pm 0.105]	-0.123 [\pm 0.141]	
Week 23	0.254 [\pm 0.435]	0.109 [\pm 0.220]	
Week 24	-0.022 [\pm 0.422]	0.136 [\pm 0.207]	
Week 25	0.407 [\pm 0.414]	-0.287 [\pm 0.210]	
Week 26	0.313 [\pm 0.415]	-0.350 [\pm 0.219]	
Week 27	0.205 [\pm 0.421]	-0.660 [\pm 0.266]	
Week 28	-0.039 [\pm 0.463]	-2.124 [\pm 0.651]	

ptarmigan may be somewhat lessened in places where the treeline elevation is high (Supporting information).

Discussion

Our results suggest that the range limits of Norway's two ptarmigan species are determined by competition in addition to the species' habitat preferences. The predicted effect of competition is asymmetrical, favoring rock ptarmigan at higher altitudes. This predicted competition may result in a restriction of the upper range limit of willow ptarmigan but is not expected to restrict the lower range limit of rock ptarmigan to the same extent. This is opposite to the traditional expectation that lower elevation species will be dominant competitors and, relatedly, that upper range limits will be set by abiotic factors rather than biotic interactions (Louthan et al. 2015, Freeman 2020).

The predicted asymmetric competition is driven by a strong predicted association between rock ptarmigan and above-treeline habitat, which is not shared by willow ptarmigan. These habitat associations align with many empirical studies of the species' distribution and habitat use (Wilson and Martin 2008, Ehrich et al. 2012, Pedersen et al. 2014, Kvasnes et al. 2018, Fuglei et al. 2020). Our results additionally suggest that the species' habitat associations also drive their relative competitive dominance. The negative effect of

rock ptarmigan presence on willow ptarmigan occupancy is expected to be stronger at greater distances above treeline, whereas the negative effect of willow ptarmigan presence on rock ptarmigan occupancy is expected to be stronger closer to, though still above, the treeline. This resembles a scenario of condition-specific competition (Freeman 2020, Sirén and Morelli 2020).

Condition-specific competition has been shown to drive the range boundaries between other closely related species pairs along elevational gradients (Althuler 2006, Malenke et al. 2011, Srinivasan et al. 2018), so it is not surprising that it could also affect the distribution of ptarmigan species. A noteworthy aspect of our results, however, is that the full range of predicted competitive interactions occurs in the above-treeline habitat that is known to be preferred by rock ptarmigan and less preferable to willow ptarmigan. As a result, the expected negative impact of competition on willow ptarmigan occupancy is much stronger than the expected negative impact on rock ptarmigan occupancy. This results in a highly asymmetrical impact where willow ptarmigan's upper range limit is restricted but rock ptarmigan occurs fairly independently of willow ptarmigan occupancy.

In a scenario of condition-specific competition, willow ptarmigan would be expected to hold the greatest competitive advantage near and below the treeline, which is its preferred habitat (Kvasnes et al. 2018). However, our results

do not reveal a negative interaction in most below-treeline habitat, but rather indicate a positive interaction beginning at approximately 500 m of distance below the modeled treeline. This may indicate that, within this elevation range, competitive interactions are mediated by the available habitat or favorable abiotic conditions. It is possible that the vegetation community near and below the treeline could play a mediating role in supporting the co-occurrence of willow ptarmigan and rock ptarmigan. Such mediating interactions are described in the recently outlined interactive range limit theory, which posits that biotic factors can play a mediating role to extend species' range limits despite the existence of other negative conditions (Sirén and Morelli 2020). Rock ptarmigan's strong association with higher elevations means that it does not frequently occur below the modeled treeline, but the results suggest that when it does occur in below-treeline habitats it is more likely to occur in the presence of willow ptarmigan than to occur separately.

Our results do not allow us to infer anything about potential mechanisms for interactions between willow and rock ptarmigan. The predicted competitive impact of rock ptarmigan is somewhat surprising because rock ptarmigan does not meet many conditions typically expected of competitively dominant species (Freeman 2020): it is smaller than willow ptarmigan (Hannon et al. 2020), expected to be similarly or less aggressive than willow ptarmigan (Moss 1972, Hannon et al. 2020), and occurs in the position along the elevation gradient traditionally expected to be held by weaker competitors (Louthan et al. 2015). One potential mechanism for competitive dominance by the higher-elevation species in a pair is suggested by Freeman (2020), who speculates that selection for competitive ability in higher-elevation species may be linked to the conditions present at the lower end of their range, because this is where they tend to encounter competition. This explanation does not seem likely here, however, because our results show that the negative impact of rock ptarmigan occupancy on willow ptarmigan occupancy grows stronger at higher elevations. Another potential explanation relates to ptarmigan behavior and ecology. Competition tends to be driven by territoriality during the breeding season (Moss 1972). Rock ptarmigan tend to nest in rocky, open areas above the treeline (Pedersen et al. 2014, Hannon et al. 2020) whereas willow ptarmigan tend to nest at somewhat lower elevations with greater vegetation cover (Montgomerie and Holder 2020). It is possible that rock ptarmigan are therefore more driven to engage in direct competitive interactions above the treeline, producing a stronger negative effect on willow ptarmigan, while the mediating effect of treeline habitat structure prevents an equivalent dynamic from establishing in the preferred breeding habitat of willow ptarmigan.

Because our study is observational, we cannot fully exclude the possibility that the results are produced by correlation with one or more unmodeled habitat variables rather than by interspecific interactions. This is especially likely to play a role in explaining the results for the below-treeline portion of the elevation gradient, where the species display a

positive association. Although this positive association may suggest a mediating effect of below-treeline vegetation that dampens the impact of competition, an alternative interpretation is that it may simply indicate the latent effect of patches of habitat that are suitable for both species. Either or both interpretations may explain the results, and additional research will be required to investigate potential mechanisms behind the modeled species associations. It is possible that the latent effect of unmodeled habitat variables drives the results near and above the treeline as well, though it is somewhat less likely that unmodeled variables are the main driver of the results at higher elevations; sites within a short distance above the treeline are part of the core habitat of both species, and the greater sample size in this region makes it less likely that correlation with habitat is a major driver of the model outcomes. A post hoc examination of the land cover at each survey route, based on available satellite data, further suggests that the observed patterns of species co-occurrence occur independent of any specific habitat type (Supporting information). To further investigate the potential effects of interspecific interactions between rock and willow ptarmigan, it would be instrumental to follow up this study with additional targeted ptarmigan monitoring. The low modeled probability of detection (Table 4; [below treeline, week 24] $p_{\text{willow}} = 0.09 \pm 0.01$, $p_{\text{rock}} = 0.05 \pm 0.01$) and broad time span characteristic of our survey dataset, while necessary to obtain its spatial and temporal extent, are limitations that could be addressed with targeted follow-up monitoring.

Our results contribute to a better understanding of the climate threats faced by ptarmigan species. Although there is wide variation in the response of the species' ranges to climate change, upward shifts in ptarmigan range limits have been demonstrated in some circumstances and habitat loss is projected to continue (Pernollet et al. 2015, Scridel et al. 2018, Fuglei et al. 2020, Brambilla et al. 2022). In Norway, and in Fennoscandia more broadly, the population of ptarmigan species is in decline (Lehikoinen et al. 2013, Fuglei et al. 2020, Hjeljord and Loe 2022). Both willow ptarmigan and rock ptarmigan were added to the Norwegian IUCN Red List for the first time in 2015 (Hjeljord and Loe 2022). After a modest population increase through 2020, they were removed from the Red List, but the population remains low compared to historical levels (Nilsen and Rød-Eriksen 2020, Hjeljord and Loe 2022). It is possible that the slight increase in occupancy shown in our data (Supporting information) reflects this recovery.

Despite the recent modest population increase, habitat loss is expected to continue for both willow and rock ptarmigan (Fuglei et al. 2020, Scridel et al. 2021, Hjeljord and Loe 2022). Although the species' responses to climate change are complex and interrelated with other drivers of population trends, including land use change and the population dynamics of predator and alternative prey species, it is generally expected that climate change may drive the loss of portions of ptarmigan species' lower-elevation habitat (Freeman 2020, Fuglei et al. 2020, Hjeljord and Loe 2022). As the

higher elevation species, rock ptarmigan may experience more severe habitat loss than willow ptarmigan, potentially driving upward range shifts (Scridel et al. 2021). This aligns with the traditional ‘escalator to extinction’ theory, which posits that the lower elevation species in a pair will expand its range limits to track climate conditions at the expense of the higher elevation species, whose range is then forced to contract (Urban 2018, Freeman 2020).

However, our results suggest that this outcome is not guaranteed, but rather indicate that negative interactions with rock ptarmigan may limit the upper range edge of willow ptarmigan. Competitive dominance of rock ptarmigan above the treeline could prevent upslope range expansion of willow ptarmigan, a scenario that Freeman (2020) has termed ‘kings of the mountain’. It is possible that the greater positive trend in the population of rock ptarmigan than willow ptarmigan throughout the duration of our study is evidence that such an outcome is already taking place, although there are many other potential explanations for these population trends as well. The degree to which competition continues to shape the species’ ranges may depend in part on the velocity of climate-driven shifts in the treeline ecotone habitat. The vegetation community that forms the treeline is broadly predicted to shift upslope in response to climate change, but these shifts are expected to be highly heterogeneous in terms of extent and velocity (Harsch et al. 2009, Rannow 2013, Bryn and Potthoff 2018, Mienna et al. 2022). At sites where the treeline community shifts upslope, our results suggest that this shift may support increased sympatry between willow ptarmigan and rock ptarmigan as these species are themselves driven upslope. Alternatively, however, the velocity of range shifts for ptarmigan species may exceed that of the treeline, a scenario that may hamper the ability of willow ptarmigan to track climate conditions. Simultaneous changes in treeline habitat due to changing land use patterns, particularly livestock grazing, may further reduce the presence of mediating habitat structure. Thus, our results demonstrate that interspecific competition introduces new complexity into the question of predicting ptarmigan species’ responses to climate change. This reinforces the general importance of considering biotic interactions at both the upper and lower range limits of species pairs along the elevation gradient.

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Author contributions

Caitlin P. Mandeville: Conceptualization (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Anders G. Finstad:** Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **John A. Kålås:** Data curation (lead); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Bård G. Stokke:** Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Ingar J. Øien:** Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Erlend B. Nilsen:** Conceptualization (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal).

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Data availability statement

Biodiversity data are available in aggregated form from the Norwegian Institute for Nature Research (Kålås et al. 2022). The Norwegian Digital Elevation Model is accessible from the Norwegian Mapping Authority (<https://www.kartverket.no>). R scripts used in analyses are available on Open Science Framework (Mandeville 2023; <https://osf.io/ab89k/>).

Supporting information

The Supporting information associated with this article is available with the online version.

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