

Rapid population decline in McKay's Bunting, an Alaskan endemic, highlights the species' current status relative to international standards for vulnerable species

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ABSTRACT

The McKay's Bunting (*Plectrophenax hyperboreus*) is endemic to Alaska, breeds solely on the remote and uninhabited St. Matthew and Hall islands (332 km²) in the central Bering Sea, and is designated as a species of high conservation concern due to its small population size and restricted range. A previous hypothesized population estimate (~2,800 to 6,000 individuals) was greatly increased (~31,200 individuals) after systematic surveys of the species' entire breeding range in 2003, establishing McKay's Bunting as one of the rarest passerines in North America. In 2018, we replicated the 2003 surveys and used density surface models to estimate breeding season densities, distributions, and population change over the intervening time period. Our results indicate that the McKay's Bunting population declined by 38% (95% CI: 27 to 48%) from ~31,560 to 19,481 individuals since 2003. Spatial model predictions showed no areas with an increase of birds on either St. Matthew or Hall islands but revealed declines across 13% (42 km²) of St. Matthew Island. Declines disproportionately occurred both in marginal habitats with reduced rocky nesting substrate and in high-density hotspots along the coast of St. Matthew Island. The total area occupied by breeding adults decreased by 8%, and high-density hotspots shifted inland from the coast of St. Matthew Island to higher elevations on both islands, the latter potentially responses to exceptionally warm weather and reduced spring snow cover in 2018. Additionally, we observed low numbers of predators and interspecific competitors in 2018, suggesting that these did not cause the decline. Our findings indicate that McKay's Bunting meets international standards for elevating its conservation status from Least Concern to Endangered based on the International Union for Conservation of Nature Red List of Threatened Species ranking criteria. Additional population monitoring and studies to identify the causal mechanisms of the recent population decline of this rare species could assist future population assessments.

Keywords: Alaska, Bering Sea, conservation concern, density surface model, endemic, McKay's Bunting, *Plectrophenax hyperboreus*, population decline

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LAY SUMMARY

- Bird populations are declining across the Arctic, but the causes of the declines are not well understood because many of these populations are poorly monitored.
- McKay's Bunting is endemic to Alaska and only occurs in the Bering Sea region where its entire population breeds on 2 remote and uninhabited islands.
- This species is of conservation concern because it has one of the smallest populations and geographic ranges of any songbird in North America.
- We surveyed adult McKay's Buntings across their entire breeding range in 2018 and detected a 38% population decline since 2003 (3% decline per year).
- McKay's Bunting meets international criteria to elevate its conservation status to higher classifications of vulnerability.

La rápida disminución poblacional en *Plectrophenax hyperboreus*, una especie endémica de Alaska, destaca el estado actual de la especie en relación con los estándares internacionales para especies vulnerables

RESUMEN

Plectrophenax hyperboreus es endémica de Alaska, se reproduce únicamente en las remotas e inhabitadas islas St. Matthew y Hall (332 km^2) en el Mar de Bering central, y está designada como una especie de gran preocupación para la conservación debido a su pequeño tamaño poblacional y su rango restringido. Una estimación poblacional hipotética realizada con anterioridad (~2,800–6,000 individuos) aumentó significativamente (~31,200 individuos) después de realizarse censos sistemáticos en todo el rango reproductivo de la especie en 2003, estableciendo a *P. hyperboreus* como uno de los paseriformes más raros de América del Norte. En 2018, replicamos los censos de 2003 y utilizamos modelos de superficie de densidad para estimar las densidades en la temporada de cría, las distribuciones y los cambios poblacionales a lo largo del período intermedio. Nuestros resultados indican que la población de *P. hyperboreus* disminuyó en un 38% (IC del 95%: 27–48%) de ~31,560 a 19,481 individuos desde 2003. Las predicciones del modelo espacial no mostraron áreas con un aumento de aves en las islas St. Matthew o Hall, y revelaron disminuciones en el 13% (42 km^2) de la isla St. Matthew. Las disminuciones ocurrieron desproporcionadamente tanto en hábitats marginales con menor cantidad de sustrato rocoso para anidar como en puntos de alta densidad a lo largo de la costa de la isla St. Matthew. El área total ocupada por adultos reproductores disminuyó un 8%, y los puntos de alta densidad se desplazaron tierra adentro desde la costa de la isla St. Matthew a elevaciones más altas en ambas islas, esto último posiblemente en respuesta a un clima excepcionalmente cálido y a una reducción en la cobertura de nieve en primavera en 2018. Además, observamos bajos números de depredadores y competidores interespecíficos en 2018, lo que sugiere que estos no fueron la causa de la disminución. Nuestros hallazgos indican que *P. hyperboreus* cumple con los estándares internacionales para elevar su estatus de conservación de Preocupación Menor a En Peligro, según los criterios de clasificación de la Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza. El monitoreo adicional de la población y estudios para identificar los mecanismos causales de la reciente disminución poblacional de esta especie rara podrían ayudar en las evaluaciones poblacionales futuras.

Palabras clave: Alaska, disminución poblacional, endémico, Mar de Bering, modelo de superficie de densidad, *Plectrophenax hyperboreus*, preocupación para la conservación

INTRODUCTION

Greater than 50% of Arctic bird species across the United States and Canada have experienced population declines since 1970 (Rosenberg et al. 2019), with similar proportions of Arctic bird populations declining in other circumpolar regions (Smith et al. 2020). The causes of these declines are not well understood but are thought to include loss and alteration of key habitats along migration paths and in nonbreeding areas (Kubelka et al. 2022), and climate-mediated changes to ecosystems and food webs in Arctic breeding areas (Smith et al. 2020). Environmental changes in breeding areas are of particular concern because Arctic and subarctic biomes are warming at a rate 4 times the global average (IPCC 2022, Rantanen et al. 2022). Despite widespread declines, nearly half of Arctic bird populations are poorly monitored, including many species and subspecies with small and geographically restricted populations (Smith et al. 2020). These taxa have limited options to shift their ranges and are more prone to fluctuate widely in abundance (Cuervo and Möller 2017), factors which increase their risk of extinction from environmental change (Ehrlich et al. 1980, Shaffer 1981, Manne and Pimm 2001). Identifying factors governing population trends in small and vulnerable bird populations is critical for implementing effective conservation initiatives.

The Bering Sea region between Alaska and the Russian Far East has exceptionally high endemism of Arctic birds that evolved in isolation in Beringia, the largest ice-free refugium during the repeated glacial maxima of the Pleistocene Epoch (Winker et al. 2002, 2023, Gibson and Byrd 2007). McKay's Bunting (*Plectrophenax hyperboreus*) is a year-round resident endemic to the region, believed to have evolved from a small founding population that diverged from Snow Buntings (*P. nivalis*) ~18 to 73 thousand years ago (kya) (Maley and Winker 2010). The population expanded in size and range across Beringia during the last glacial maximum, and then declined in population size and range when the sea-level increased and submerged the Bering Land Bridge ~11 to 13 kya

(Maley and Winker 2010, Farmer et al. 2023). McKay's Buntings now breed solely on the uninhabited St. Matthew and Hall islands (332 km^2), located ~400 km west of mainland Alaska in the central Bering Sea (Kessel and Gibson 1978). The species' nonbreeding distribution ($72,000 \text{ km}^2$) spans the Bering Sea coast from Kotzebue Sound to the Alaska Peninsula (Sealy 1972, BirdLife International and Handbook of the Birds of the World 2020).

McKay's Bunting has been designated as a species of high conservation concern due to its small population size and restricted range (Rosenberg et al. 2016, Handel et al. 2021, Partners in Flight 2021). The species' first hypothesized population estimate was low (~2,800 to 6,000 individuals) and based on extrapolations of mean and maximum breeding densities of Snow Buntings in Canada from 1940 to 1982 (Lyon and Montgomerie 1995). The first empirically derived population estimate was greatly increased (~31,200 individuals) after systematic surveys of the species' entire breeding range in 2003, establishing McKay's Bunting as one of the rarest passerines in North America (Matsuoka and Johnson 2008). The population status of McKay's Bunting was assumed to be stable (BirdLife International 2023) due to the species' remote breeding and nonbreeding habitats. However, the McKay's Bunting population had not been monitored since 2003.

Recent environmental changes in the Bering Sea region potentially impact the population size and breeding distribution of McKay's Buntings (Matsuoka and Johnson 2008, Johnson et al. 2013). Record-breaking climate extremes are causing disruptions to ecological systems and processes (Overland and Stabeno 2004, Stabeno and Bell 2019). In this region, rapid warming is reducing the duration of terrestrial snow cover and increasing coastal erosion and flooding (Macander et al. 2014, Baker et al. 2020), processes that may influence the availability of rock crevices in coastal sea cliffs and talus, important habitats used by breeding McKay's Buntings (Johnson et al. 2013). For example, the extent of June snow

cover in the Northern Hemisphere declined 18% per decade from 1979 to 2011 and exceeded sea ice loss in September during that same period (-11% per decade, [Derksen and Brown 2012](#)). Additionally, coastal erosion on St. Matthew and Hall islands ([Hanna 1920](#), [Renner and Jones 2005](#)) has impacted the availability of nesting habitat for crevice-nesting birds ([Klein and Kleinleder 2015](#)). Dynamic landscape perturbations, such as slumping, mudslides, and rockslides, may alter the availability of rock crevices for nesting ([Klein and Kleinleder 2015](#)) and could impact McKay's Buntings by decreasing access to important breeding habitats.

In addition to direct physical alteration of McKay's Bunting breeding habitats driven by recent climatic changes, climate-mediated ecological shifts may also be occurring on St. Matthew and Hall islands. For example, a shift in the terrestrial predator community has been noted where red foxes (*Vulpes vulpes*) have largely displaced Arctic foxes (*V. lagopus*, [Klein and Sowls 2015](#)), a pattern observed in other high latitude regions as red foxes expand their ranges northward with climate warming ([Elmhagen et al. 2017](#)). Although foxes will occasionally prey upon McKay's Buntings ([DeGange and Sowls 1978](#)) and their nests ([Johnson et al. 2013](#)), they feed principally on endemic singing voles (*Microtus abbreviatus*), seabirds and their eggs, and beach-cast marine mammals ([DeGange and Sowls 1978](#), [Klein and Sowls 2015](#)). Moreover, interspecific competition from Snow Buntings, a closely related and ecologically similar sister species, could impact McKay's Buntings if Snow Buntings expand their range and colonize St. Matthew and Hall islands. However, Snow Buntings have only been observed in small numbers on St. Matthew and Hall islands and have not yet been documented breeding ([Winker et al. 2002](#), [Robinson et al. 2020](#)). The extent to which changes in predator communities and potential interspecific competitors has affected McKay's Buntings is unknown.

In this study, we estimated changes in McKay's Bunting breeding distribution and total abundance during a 15-year interval. In 2018, we replicated the 2003 line transect surveys of adult McKay's Buntings ([Matsuoka and Johnson 2008](#)) across St. Matthew and Hall islands and analyzed the count data using a density surface modeling approach ([Hedley and Buckland 2004](#), [Miller et al. 2013](#)). Our primary objectives were to (1) measure change in population size between 2003 and 2018, (2) identify topographic features and habitats associated with density and population change, (3) measure changes in the extent and distribution of the core breeding range and high-density hotspots, (4) assess the potential threat of predators and interspecific competitors to breeding McKay's Buntings, and (5) review the current conservation status of the species based on international ranking criteria.

METHODS

Study Area

We conducted our study on St. Matthew Island (314 km^2 , 60.42°N , 172.76°W) and Hall Island (18 km^2 , 60.66°N , 173.09°W) in the central Bering Sea, Alaska ([Figure 1](#)). Both islands are uninhabited and managed as wilderness by the U.S. Fish and Wildlife Service Alaska Maritime National Wildlife Refuge. Topographic features include broad valleys, gently to steeply sloping hills, and coastal sea cliffs. Maximum elevations are 507 m on Hall Island

and 459 m on St. Matthew Island ([DeGange and Sowls 1978](#)). The islands' flora was characterized by subarctic tundra vegetation dominated by graminoids at lower elevations, transitioning to dwarf shrubs with interspersed bryophyte, lichen, and forb communities as elevation increased. Mid-to-high elevations included tundra and alpine habitats with rock scree, talus, and boulder slopes. Freshwater and brackish lakes, ponds, and numerous streams occurred on St. Matthew Island while lakes and ponds were absent from Hall Island.

Field Surveys

We replicated surveys of adult McKay's Buntings along line transects using distance sampling techniques ([Buckland et al. 2001](#)) between June 6 and 11, 2018. We followed the sampling protocol reported by [Matsuoka and Johnson \(2008\)](#) and surveyed transects placed perpendicular to the length of each island, including 34 transects spaced 1.5 km apart that totaled 181.9 km on St. Matthew Island and 12 transects spaced 0.5 km apart that totaled 22.1 km on Hall Island ([Figure 1](#)). Eight observers independently conducted surveys throughout the day and counted birds out to 100 m on either side of the transect while walking at a steady pace. For each detection, we recorded the side of the transect on which an individual or cluster of birds was located, marked the position on the transect perpendicular to each detection using a handheld global positioning system unit, and then used a laser rangefinder to measure the perpendicular distance to the location where the detection first occurred ([Buckland et al. 2001](#)). When birds were encountered in clusters, we recorded the total number of birds and measured the perpendicular distance from the transect to the center of the cluster ([Buckland et al. 2001](#)). We also counted adult foxes during surveys and tallied all observations of Snow Buntings encountered on and off transects.

Environmental Covariates

We derived topographic covariates from the National Elevation Dataset ([U.S. Geological Survey 2020](#)) and a habitat covariate from one land cover classification (June 2016 Landsat 8, 30-m resolution, [Fleming 2019](#)) and used these variables as predictors in both the 2003 and 2018 models of McKay's Bunting density and population change. Covariates were selected a priori and represented site characteristics associated with breeding McKay's Buntings ([Montgomerie and Lyon 2020a](#)): elevation (m), slope (degrees), distance to the coast (m), and proportional cover by rocky tundra habitat. We chose the topographic covariates because the species had been categorized as abundant along the coast ([Gabrielson and Lincoln 1959](#), [DeGange and Sowls 1978](#)) and nests primarily on slopes in rock crevices within rock scree, talus, and boulder fields ([Johnson et al. 2013](#)). For the habitat covariate, we combined 6 of the 19 land cover classes to include alpine and rocky areas as a single rocky tundra class ([Supplementary Material Table 1](#)). We considered shrub tundra habitat and normalized difference vegetation index as covariates in our models but did not include these variables because they were strongly correlated with rocky tundra habitat ($r \geq -0.6$). We also considered but excluded sedge and coastal habitats because of low coverage (<15%) across the sampled areas ([Supplementary Material Table 1](#)).

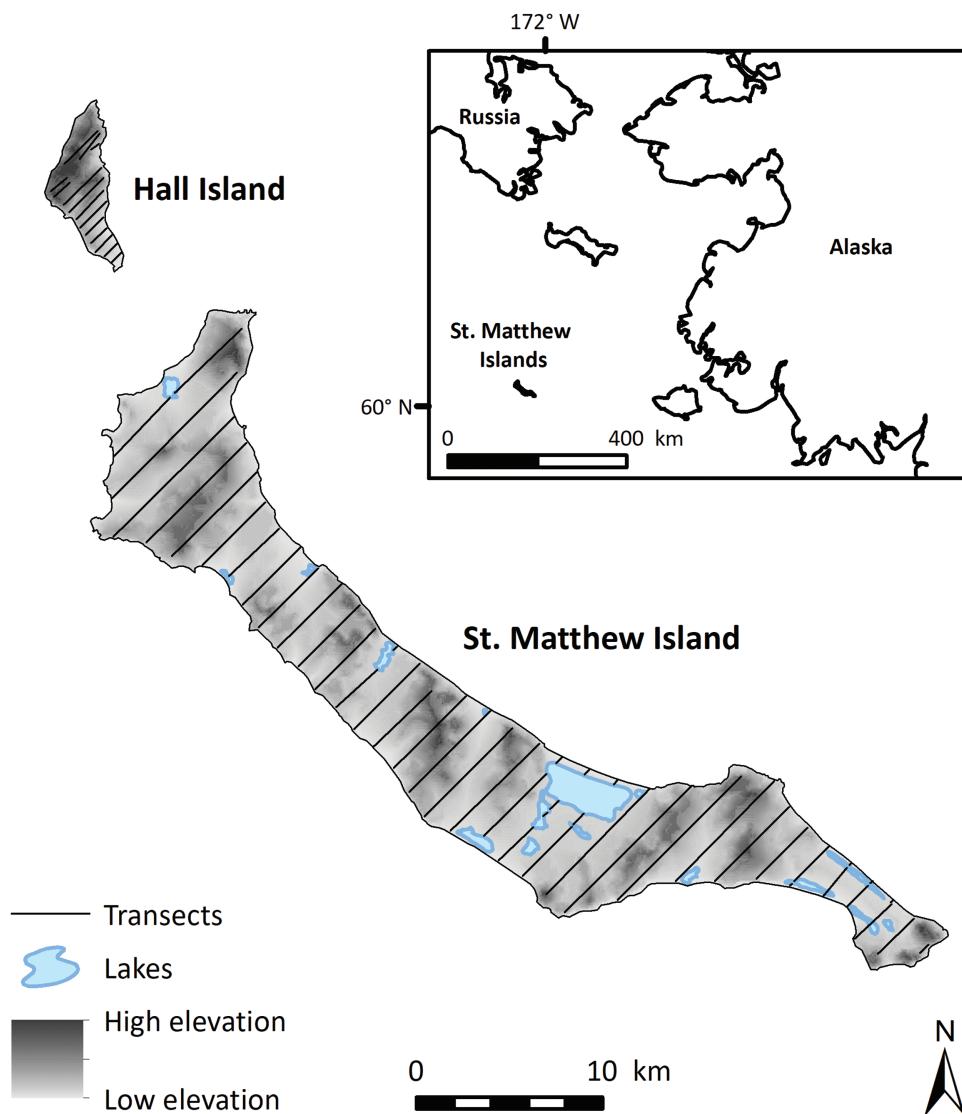


FIGURE 1. Line transects surveyed for breeding McKay's Buntings on St. Matthew and Hall islands, Alaska, 2003 and 2018. Elevation is displayed in shaded relief. The inset map shows the proximity of the St. Matthew Island group to mainland Alaska.

Statistical Analyses

Detection probability

We modeled detection probability by using multiple-covariate distance sampling (Marques and Buckland 2003, Marques et al. 2007) to adjust the bird counts in 2003 and 2018 for (1) the decreasing probability of detecting birds as their perpendicular distance from the transect increased (Buckland et al. 2001), and (2) variation in detection probability relative to detectability covariates. We pooled detections across years and first fit the half-normal and hazard-rate detection functions without covariates or adjustment terms to the unbinned count data and then selected the function with the lowest Akaike's information criterion (AIC) score (Burnham and Anderson 2002) to serve as the distance-only model. We then used the selected global detection function to assess the univariate effects of observer rank, cluster size, day within season, habitat, and year to account for major sources of spatiotemporal bias in detection.

Detectability covariates were fit as continuous variables except for habitat and year, which were fit as 2-level categorical

variables. For habitat, we assigned each detection location to 1 of 2 condensed land cover classes: "rocky tundra" or "other" (i.e., shrub tundra, sedge, and coastal; Supplementary Material Table 1). For observer rank, we first fit an observer-only model and then used their relative detection probabilities to rank each observer's detection probability from low to high as a measure of observer survey skill. This approach allowed us to include the effect of the observer on detection while minimizing the number of model parameters. We selected the detection function model with the lowest AIC score for inference and assessed model performance with a Q-Q plot and a Cramér-von Mises goodness-of-fit test (Burnham et al. 2004).

Density surface modeling

We estimated McKay's Bunting density and breeding distribution in 2003 and 2018 via generalized additive models (GAM, Wood 2017) fit within a density surface model (DSM) framework (Hedley and Buckland 2004, Miller et al. 2013). DSMs simultaneously adjust counts for detection probability while incorporating spatial environmental covariates on

density. We modeled the bivariate effect of latitude and longitude (projected as Universal Transverse Mercator coordinates) by island, and the univariate effects of elevation (m), slope (degrees), distance to the coast (m), and proportional cover by rocky tundra habitat as thin plate regression splines (Wood 2003) with the default basis size for each smooth term (covariate). We partitioned each transect into ≤ 250 -m-long contiguous segments ($n = 844$) and calculated, for each segment, the mean of the spatial covariates within a 200-m buffer centered on the segment line (Supplementary Material Table 2). We treated the buffered line segments as the units of sampling in the DSMs and accounted for variation in the area of each segment by including segment area as an offset term in the models.

We created separate DSMs for 2003 and 2018 to evaluate changes in McKay's Bunting population size, breeding distribution, and habitat associations between survey years. We examined the negative binomial and Tweedie distributions for count data for each year separately, thereby fitting 2 models with all covariates per year. We selected the model with the lowest AIC score in each year and then used the selected models to predict density by year in each 300×300 -m pixel ($n = 3,853$) across a grid covering the 332-km^2 study area. Within each pixel, we summarized the spatial covariates in the same manner as we did for the buffered line segments (Supplementary Material Table 2) and excluded pixels with $>90\%$ water ($n = 96$, 8 km^2) from predictions.

To estimate population size for each year, we summed the pixel-level predictions of abundance across the islands (Miller et al. 2013) and then calculated population change between 2003 and 2018 as the difference between the annual estimates of population size. We calculated pixel-level predictions, population size estimates, and their uncertainty using a simulation-based method that incorporates variance and covariance in both the detection function model and GAM (Miller et al. 2022). We fit 5,000 realizations of the predictions from the combined models and calculated the mean predictions, mean estimates, and 95% confidence intervals (95% CIs) from the posterior distribution.

Temporal changes in density and distribution

To delineate areas and habitats where density changed between 2003 and 2018, we first assigned pixels to 1 of 3 population change categories depending on whether 95% CIs in predicted density (1) overlapped between years (stable), (2) did not overlap and were lower in 2018 (decreasing), or (3) did not overlap and were higher in 2018 (increasing). We then mapped the population change categories to identify areas where changes in density were concentrated, and we compared the distributions of topographic and habitat covariates between pixels with stable density versus decreasing density to identify habitat conditions where declines were prevalent.

To delineate the core breeding range and high-density hotspots, and evaluate shifts in distribution over time, we first created an index of relative density for each year. We defined pixels across both islands as "low" density if the upper 95% CI was lower than the annual mean density, "average" density if the 95% CI overlapped the annual mean density, and "high" density if the lower 95% CI was higher than the annual mean density. To measure changes in breeding range size, we defined the core breeding range as areas with "average" and "high" density pixels, calculated the change between years, and then

mapped the density dynamics to identify shifts in the distribution of the core breeding range and high-density hotspots.

Finally, we estimated the area of occupancy (AOO) of breeding McKay's Buntings on St. Matthew and Hall islands because AOO was not included in the species' most recent assessment for listing on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (BirdLife International 2023). We followed the IUCN Standards and Petitions Committee (2022) guidelines and measured AOO by overlaying a 2×2 -km grid over the islands and summing the terrestrial area of grid cells occupied by McKay's Buntings during our systematic breeding surveys in 2003 and 2018 separately. We did not include in our breeding AOO estimate any June or July observations of McKay's Buntings from St. Paul Island and St. Lawrence Island (Sullivan et al. 2009) because the species is not observed annually during the breeding season on these islands (Rogers 2005, Montgomerie and Lyon 2020a, Withrow 2020).

All analyses were performed in R software 4.2.2 (R Core Team 2022) using the packages *Distance* 1.0.2 (Miller et al. 2019), *dsm* 2.3.1 (Miller et al. 2021), *mgcv* 1.8-39 (Wood 2022), and *reldistr* 1.0.3 (Lee et al. 2019). We present estimates \pm standard error, coefficient of variation (CV), and all confidence intervals are 95% CIs.

RESULTS

Total McKay's Bunting counts across both islands included 2,398 birds from 1,412 detections across 201.8 km of transects in 2003 and 1,547 birds from 916 detections across 204.1 km of transects in 2018, a decrease of 851 birds detected during surveys. We excluded from analysis detections of birds recorded beyond 100 m, in long direct flights overhead, or with no recorded GPS location (Matsuoka and Johnson 2008), resulting in a final data set that included 2,260 birds from 1,324 detections in 2003 and 1,382 birds from 798 detections in 2018. Cluster size averaged 1.71 ± 0.02 birds (range: 1 to 6 birds) in 2003 and 1.73 ± 0.03 birds (range: 1 to 8 birds) in 2018. Tallies of adult foxes during surveys across both islands decreased by 36% from 2003 (Arctic fox = 14, red fox = 5, and unidentified fox = 3) to 2018 (Arctic fox = 5, red fox = 7, and unidentified fox = 2). Tallies of Snow Bunting sightings both on and off transects were low in both years and decreased by 40% from 2003 (5 male off transects, Matsuoka and Johnson 2008) to 2018 (1 male and 1 female on transects, 1 female off transects).

Detection Probability and Density Surface Models

Observer rank (i.e., survey skill) was the most influential factor affecting the detectability of McKay's Buntings during line transect surveys across years. Detection probability was best explained by a hazard-rate key function ($AIC = 18,998$) compared to a half-normal key function ($\Delta AIC = 25$). Detection probability improved with higher ranked observer survey skill ($\beta = 0.06 \pm 0.01$, Supplementary Material Figure 1) and there was no support for the other detectability covariates ($\Delta AIC \geq 20$, Supplementary Material Table 3). The estimated average detection probability was 0.58 ± 0.02 ($CV = 0.03$, Supplementary Material Table 3) and detection probabilities ranged from 0.45 to 0.69 among observer ranks. For the DSMs, the Tweedie distribution provided a better fit to the data than the negative binomial, with

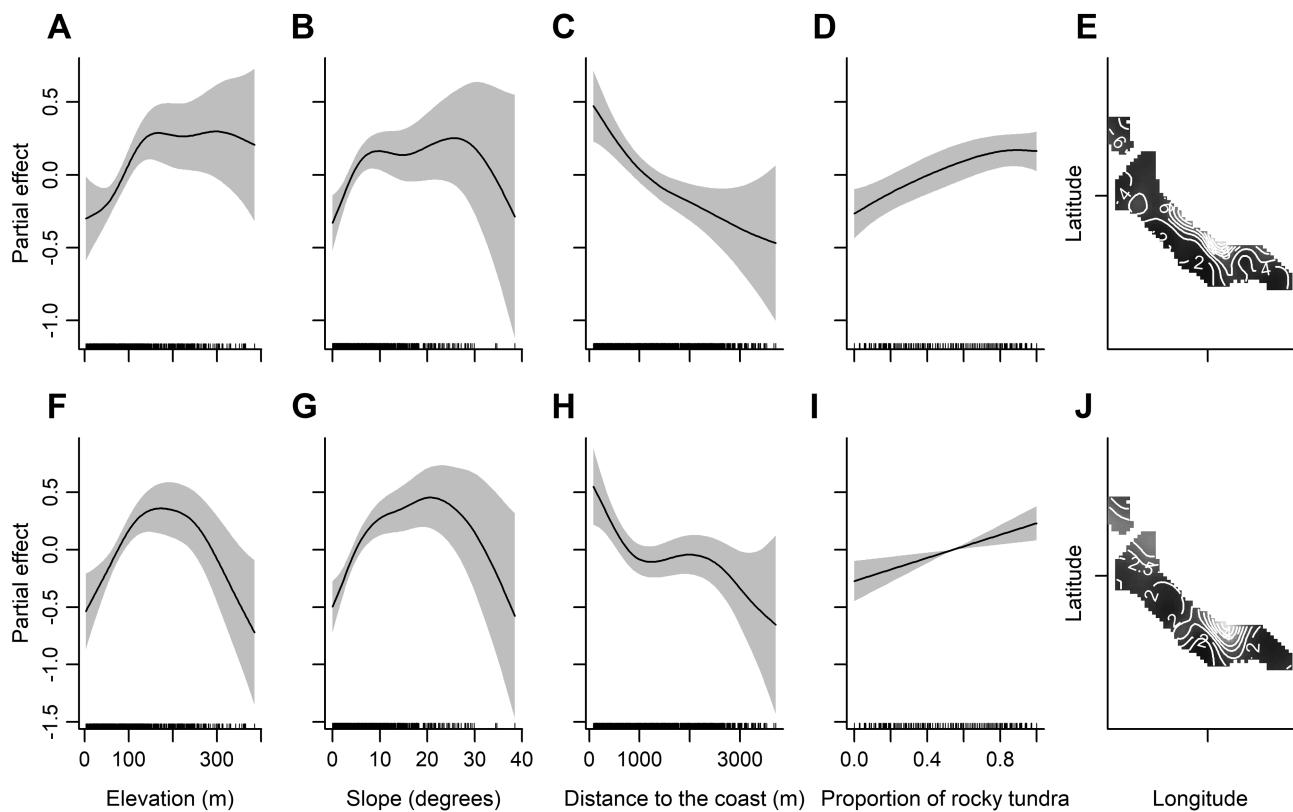


FIGURE 2. Partial effects of the environmental covariates used to predict McKay's Bunting breeding density on St. Matthew and Hall islands, Alaska, were similar between (A–E) 2003 and (F–J) 2018. Shaded polygons denote the 95% CIs. Vertical ticks along the x-axes indicate observed covariate values. Lighter shades in (E) and (J) represent larger predictions, the darker shades are smaller predictions, and the axis tick marks indicate coordinates 60.5°N and 172.6°W.

lower AIC scores ($\Delta\text{AIC}_{\text{NegBin}} > 100$ points higher in both years) and higher deviance explained (2003_{NegBin} = 23% vs. 2003_{Tweedie} = 26%, 2018_{NegBin} = 22% vs. 2018_{Tweedie} = 26%) for both years. In general, covariate effects were similar between years (Figure 2) except for a decrease in McKay's Bunting density at the highest elevations in 2018 (Figure 2F). The highest predicted densities occurred at elevations between 150 and 200 m, on slopes between 10° and 25°, closest to the coast, and in areas with higher proportions of rocky tundra habitat.

Estimates of Density and Total Abundance

Estimates of McKay's Bunting breeding density and total abundance differed between islands and were considerably lower in 2018 compared to 2003. In 2003, the mean predicted density was higher on Hall Island (135 birds per km², 95% CI: 104–177) compared to St. Matthew Island (94 birds per km², 95% CI: 83–107, Figure 3A). In 2018, the mean predicted density was lower overall than in 2003 but was substantially higher on Hall Island (105 birds per km², 95% CI: 78–144) compared to St. Matthew Island (56 birds per km², 95% CI: 49–64, Figure 3A). Total abundance in 2018 (19,481 birds, 95% CI: 17,305–21,890) was lower than 2003 (31,560 birds, 95% CI: 28,205–35,446), lower on St. Matthew Island in 2018 (17,548 birds, 95% CI: 15,518–19,752) compared to 2003 (29,042 birds, 95% CI: 25,843–32,638), and lower on Hall Island in 2018 (1,932 birds, 95% CI: 1,476–2,569) compared to 2003 (2,518

birds, 95% CI: 1,960–3,213, Figure 3B). Population size declined 40% on St. Matthew Island and 23% on Hall Island, but 95% CI in annual population size estimates overlapped on Hall Island. For the islands combined, the population declined by 38.3% (95% CI: 27.2–47.9%) with a loss of 12,079 birds between 2003 and 2018. This equates to an average 3.2% (95% CI: 2.1–4.3%) decline per year and a 27.5% (95% CI: 19.1–35.3%) decline per decade.

Spatial Patterns in Density and Population Change

The annual density surface maps showed both spatial and temporal variation in McKay's Bunting density, with lower density across both islands in 2018 compared to 2003 (Figure 4). For St. Matthew Island, we detected significant declines in 13% of pixels across 42 km² of the island area and stable densities between years in 84% of pixels across 264 km². The remaining 3% of pixels represented areas with >90% water, which were removed from predictions. Areas with significant declines were concentrated in 3 locations along the north and southeastern-facing shoreline and 1 location on the northwestern-facing shoreline (Figure 4). For Hall Island, our results showed stable densities between years across the entirety of the island (18 km²; Figure 4). No pixels showed substantial increases in density on either island. The density distributions of environmental covariates suggested that pixels with stable density occurred at similar elevations as pixels with declines in density, but that declines occurred on lower slope angles that were generally <2,000 m from

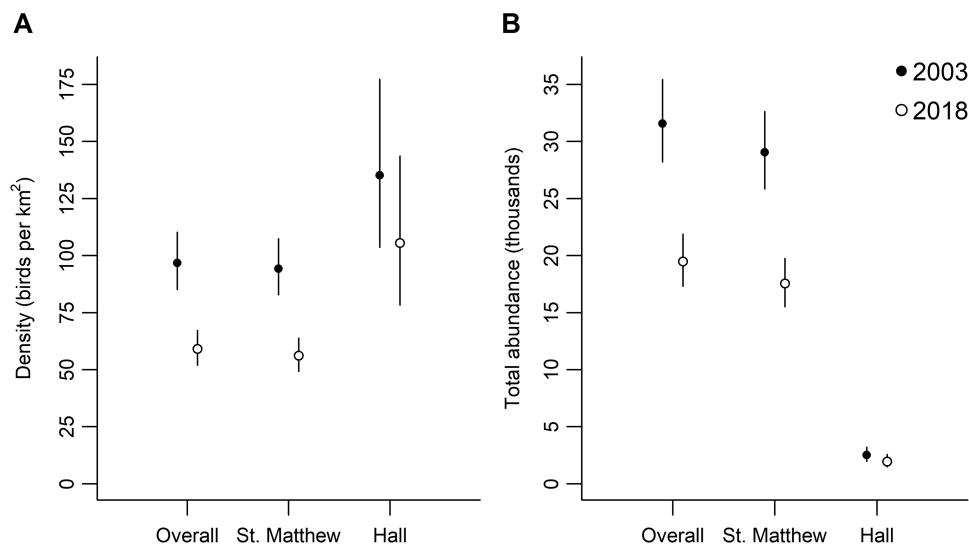


FIGURE 3. Estimates of McKay's Bunting (A) breeding density and (B) total abundance on St. Matthew and Hall islands, Alaska, were lower in 2018 compared to 2003, and breeding density was lower on St. Matthew Island compared to Hall Island in both years. Error bars denote the 95% CIs.

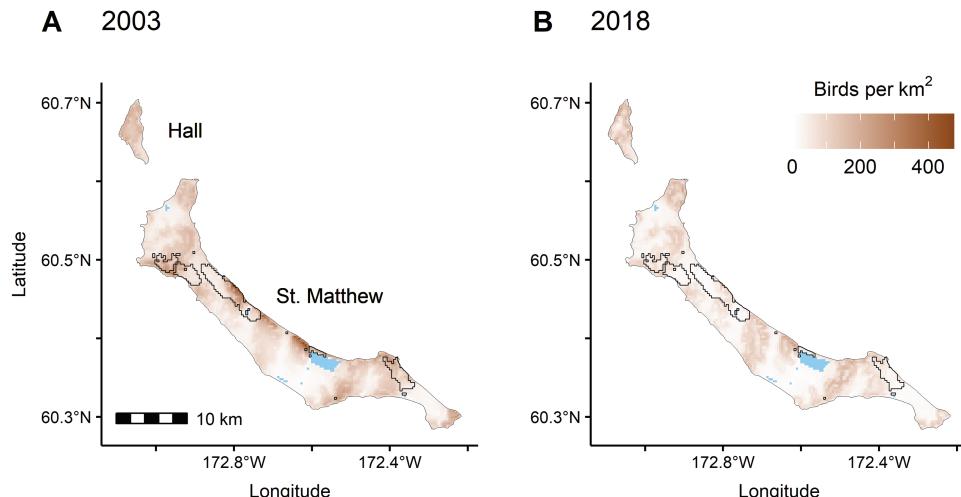


FIGURE 4. Spatial distribution of McKay's Bunting breeding density on St. Matthew and Hall islands, Alaska, varied between (A) 2003 and (B) 2018. Significant declines in breeding density (black outline) occurred only on St. Matthew Island and there were no areas with an increase of birds on either island. Areas in blue have >90% water and were masked from model predictions.

the coast and contained less rocky tundra habitat (Figure 5). Pixels with stable density showed a bimodal distribution in rocky tundra habitat and were more likely to occur where the proportion of rocky tundra was either low or high (Figure 5).

The McKay's Bunting breeding range size, measured as terrestrial AOO, contracted by an estimated 8% from 286 km² in 2003 (86% of island area) to 262 km² in 2018 (79% of island area). Our post-hoc analysis on shifts in breeding distribution between years suggests that small shifts in core breeding range, which included high-density hotspots, occurred primarily on St. Matthew Island. All 18 km² of Hall Island remained core breeding range in both years, while on St. Matthew Island the core breeding range covered 268 km² in 2003 but decreased by 11 km² in 2018 (Figure 6A). High-density hotspots in 2003 were only located across 8 km² of St. Matthew Island and occurred primarily along the northeastern coast (Figure 6B). Compared to 2003, high-density hotspots in 2018 increased by 2 km² on Hall Island, decreased by

0.4 km² on St. Matthew Island, and shifted inland to higher elevations on both islands (Figure 6B).

DISCUSSION

Based on our survey information, the McKay's Bunting total population size declined by 38% from 2003 to 2018. Declines were concentrated both in marginal habitats with reduced rocky nesting substrate and in high-density hotspots, which shifted from the coast to higher elevation areas inland. This indicates that there may be a combination of processes influencing the species' breeding distribution through time. We did not assess the causes of the reduction in the species' population size, but because we observed low numbers of predators and interspecific competitors in 2003 and 2018, these potential threats were likely not the primary reason for the species' decline. As this is the first estimate of population change for McKay's Bunting, additional surveys would help

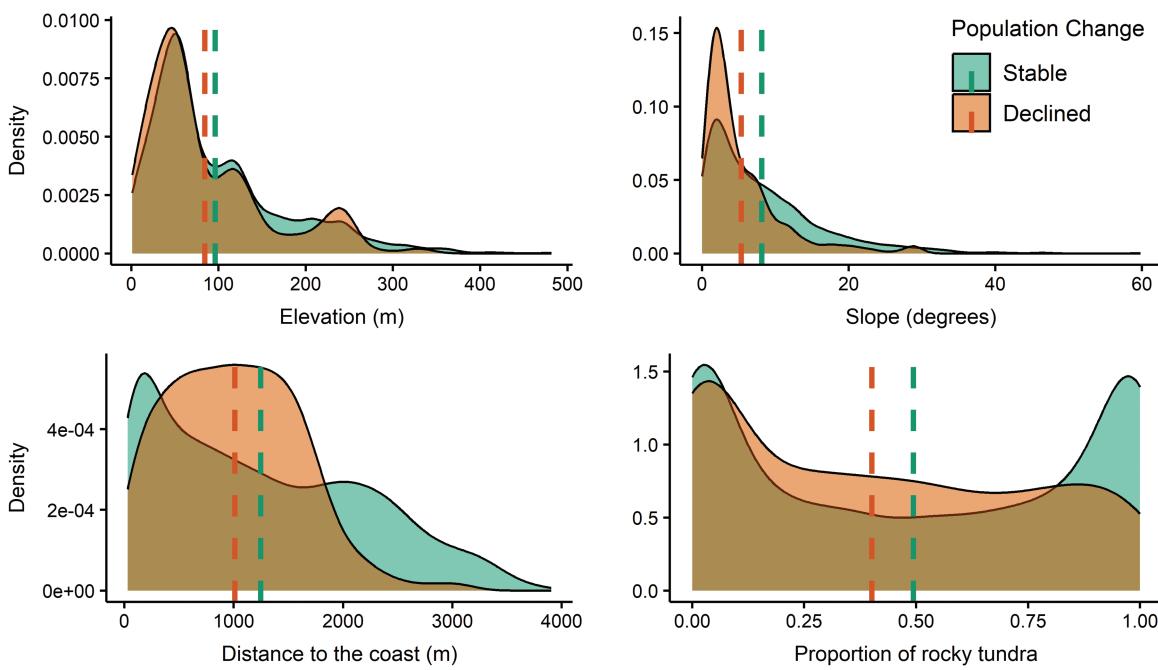


FIGURE 5. Areas with significant declines in McKay's Bunting breeding density between 2003 and 2018 were located on lower slope angles, closer to the coast, and contained less rocky tundra habitat as shown by the distributions of environmental covariate values on St. Matthew and Hall islands, Alaska. Vertical-dashed lines denote mean values.

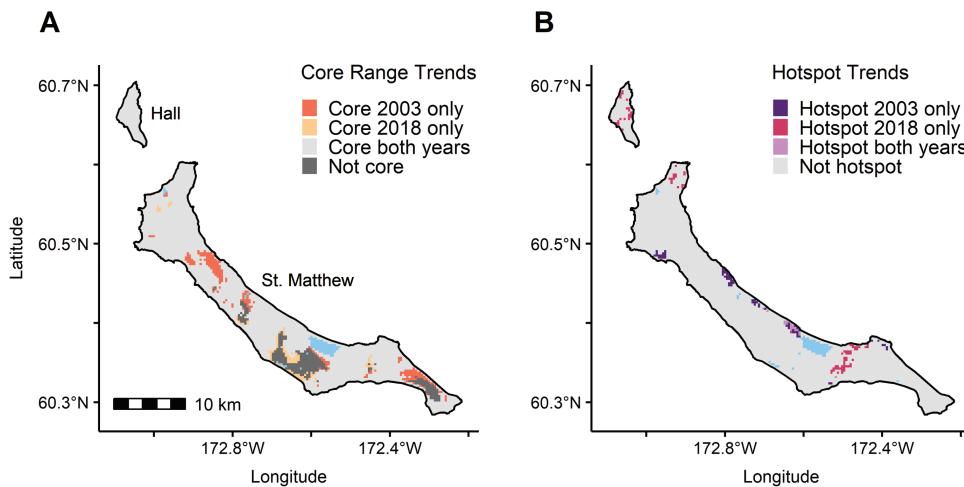


FIGURE 6. McKay's Bunting (A) core breeding range decreased only on St. Matthew Island and (B) high-density hotspots shifted inland to higher elevations on both St. Matthew and Hall islands, Alaska, between 2003 and 2018. Core breeding range includes areas with average and above-average annual density and high-density hotspots denote areas with above-average annual density (see Methods for details). Areas in blue have >90% water and were masked from predictions.

distinguish whether the current decline is a short-term fluctuation from higher numbers in 2003, or part of an ongoing and longer-term trend. If the current estimated annual rate of decline continues, we project that the 2018 population of McKay's Buntings will be halved and fall below 10,000 birds in 2040.

Reduced Breeding Population Size

In 2003, McKay's Buntings on St. Matthew and Hall islands bred at exceptionally high densities that were 7 to 10 times greater than the average breeding densities of ecologically similar and closely related Snow Buntings (mean = 12 birds per km^2 ; see Appendix 1 of Montgomerie

and Lyon 2020b). The high densities may have led to nest site and food limitations because adult females that year often nested in lower-quality shallow rock crevices that suffered high predation rates and produced smaller clutches compared to Snow Buntings nesting at similar latitudes (Johnson et al. 2013). Thus, it is plausible that the population may have been at or above carrying capacity in 2003. By 2018, the densities of McKay's Buntings were significantly reduced across 13% of St. Matthew Island with no signal of local increase on either island; however, the species in that year still bred at 5 to 7 times the average breeding densities of Snow Buntings across northern Canada.

Future breeding surveys of McKay's Buntings could clarify whether the population decline we observed between 2003 and 2018 is short-term, part of a fluctuating population pattern, or a longer-term and ongoing reduction. Notably, there is no prior evidence that the McKay's Bunting breeding population cycles widely in size. Since the species' breeding grounds were discovered (Townsend 1887), nearly all ornithologists visiting the islands in summer have described the McKay's Bunting as common or abundant and never has the species been noted as uncommon, rare, or absent (Gabrielson and Lincoln 1959, Winker et al. 2002). Regardless, McKay's Buntings have a small population size and restricted geographical range making them inherently more susceptible to demographic and environmental stochasticity, local catastrophes, and puts them at greater risk of extinction (Lande 1993, Purvis et al. 2000, O'Grady et al. 2004).

Habitat Use and Changes in Breeding Distribution

Habitat patterns in the density of McKay's Buntings were consistent between years and reflected the selection of territories with high-quality nest sites (Johnson et al. 2013). Thus, the shifts in the species' breeding distribution we observed through time likely reflected a combination of a reduction in the use of lower-quality nesting habitats as the population declined and a possible separate shift in the availability of higher-quality nesting habitats from the coast to higher elevations inland. Our model predictions of breeding density both increased linearly with proportion of rocky tundra habitat, where 79% of nests were placed in rock crevices, and peaked on moderate slopes near the 27° average used for nesting in 2003 (Johnson et al. 2013). Similarly, Snow Bunting nest densities were lowest in vegetated tundra areas with few rock crevices for nesting (Montgomerie and Lyon 2020b). Significant declines in the density of McKay's Buntings disproportionately occurred in lower-quality nesting habitats with low proportions of rocky tundra on low-angle slopes. This is consistent with the hypothesis that as populations decline, birds will persist the longest in high-quality habitats, as individuals move to prime areas when vacancies arise and any density-dependent regulation of breeding density fades (Fretwell 1972, Wilcove and Terborgh 1984).

However, McKay's Buntings also declined in high-density areas closer to the coast, where our models predicted high breeding densities in both years and where ornithologists previously described the species to be most abundant (Hanna 1917, 1923, DeGange and Sowls 1978). High-density hotspots shifted away from the coast in 2003 to higher elevations inland in 2018. This pattern was consistent with previous shifts in the species' habitat use and timing of breeding that appeared to be responses to changes in spring snow cover (Johnson et al. 2013). We encountered little snow cover on the islands during our surveys in 2018, which followed a winter with exceptionally warm ocean and air temperatures and record low sea-ice coverage across the Bering Sea region (Stabeno and Bell 2019). Thus, warm conditions and more extensive loss of spring snow cover likely allowed McKay's Buntings to nest at higher elevations further inland, and possibly earlier than in 2003.

It is less certain whether coastal erosion from storms or permafrost thaw on St. Matthew and Hall islands (Klein and Kleinleder 2015) contributed to the species' shift away from the coast. McKay's Buntings also nest in rock crevices in

coastal cliffs (DeGange and Sowls 1978, Johnson et al. 2013), which appear highly sought-after given their higher proportional use as nest sites (12% of 83 nests, Johnson et al. 2013) compared to proportional availability (2% of island area, Supplementary Material Table 1). However, coastal erosion would likely only be detrimental to the breeding population of McKay's Buntings if erosion processes resulted in a net loss of nesting habitats in coastal areas, the likelihood of which is unknown.

Potential Causes of Decline

We gained little insight from the breeding ground surveys as to the possible roles of predators or interspecific competitors in the population decline of McKay's Buntings. It is unlikely that Arctic and red fox predation contributed to the decline, given that fox sightings during surveys decreased by 36% between 2003 and 2018. Moreover, limited evidence suggests that foxes are infrequent predators of McKay's Buntings (DeGange and Sowls 1978) and their nests (Johnson et al. 2013). Evidence that interspecific competition contributed to the decline is similarly scant. We found that McKay's Buntings remain geographically isolated from Snow Buntings while breeding on St. Matthew and Hall islands. Snow Buntings were uncommon during our surveys in 2003 and 2018, with only 8 detected across both sets of surveys. Furthermore, there is no evidence that Snow Buntings breed on St. Matthew and Hall islands (Winker et al. 2002, Robinson et al. 2020, Withrow 2020, this study). Therefore, McKay's Buntings do not currently seem vulnerable to genetic or demographic swamping (Todesco et al. 2016). Finally, we note that a multiyear marine heatwave in the Bering Sea occurred between our surveys with marked effects on seabirds (Romano et al. 2020) and may have similarly disrupted St. Matthew and Hall islands' terrestrial environments in ways that negatively affected the McKay's Bunting breeding population. These detailed topics aside, McKay's Buntings are poorly studied and most vital rates for the species are unknown. As such, future studies identifying changes in McKay's Bunting vital rates could assist population assessments.

Because we found no obvious increases in predators, competitors, or habitat loss on the species' remote and uninhabited breeding islands, events during the nonbreeding season may be contributing to the reduction in the McKay's Bunting population size. Currently, no information is available on the nonbreeding ecology of McKay's Buntings, a period when the species overwinters primarily on the Yukon-Kuskokwim Delta along the Bering Sea coast of western Alaska (Fink et al. 2022). This region recently experienced several large and damaging extratropical cyclones during 2004 to 2006, 2011, and 2022; the size of which had not been seen since 1974 (Mason et al. 1996, Terenzi et al. 2014, Thoman 2022). These powerful storms caused extensive coastal flooding across up to 3,200 km² of the Yukon-Kuskokwim Delta alone and may have altered winter habitats (Terenzi et al. 2014) or caused direct mortality of birds, as has been documented for Snow Buntings during other large storms (Sutton 1932). With continued climate warming, extreme weather events across western Alaska are projected to increase in magnitude and frequency through the end of the century (Bieniek et al. 2018, Redilla et al. 2019) and may contribute to future declines of McKay's Buntings and other birds overwintering in the region. Snow Buntings also winter along the Bering Sea

coast and often occur in mixed-species flocks with McKay's Buntings (Sealy 1972). Snow Buntings have experienced steep declines in this region (Meehan et al. 2022), and nonbreeding studies of these sister species along the Bering Sea coast of western Alaska could provide important insights into the possible factors underlying recent population declines.

Conservation Status

Our findings indicate that McKay's Bunting meets international criteria to elevate its conservation status to higher classifications of vulnerability. We estimated that the McKay's Bunting total population size declined at an average rate of 3.2% per year from 2003 to 2018, a rate of decline among the 4th percentile of population trends for landbird species breeding in the United States and Canada (Partners in Flight 2021). The magnitude of the recent decline now qualifies McKay's Bunting for Partners in Flight's Red Watch List, which currently includes 39 of 705 bird species in the United States and Canada that are considered "highly vulnerable and in urgent need of special attention" (Panjabi et al. 2021, Partners in Flight 2021). In addition, the McKay's Bunting decline, combined with its small breeding range (AOO <500 km²) on only 2 islands, meets IUCN criteria to elevate the species' status from the IUCN Red List category of Least Concern to Endangered. Only 15 other bird species in the United States and Canada are currently listed as Endangered by the IUCN (Partners in Flight 2021), a classification meaning that a taxon is "facing a very high risk of extinction in the wild" (IUCN Standards and Petitions Committee 2022). These higher classifications of vulnerability further emphasize the importance of continuing population monitoring of McKay's Buntings as well as identifying the causal mechanisms underlying the steep decline of this rare species.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

This research was approved by the U.S. Geological Survey Institutional Animal Care and Use Committee.

Author contributions

SMM, JAJ, MDR, and ART conceived the idea and acquired the funding. RMR, SMM, JAJ, and MDR collected the field data. MDF contributed the land cover data. RMR and CLA analyzed the data. RMR wrote the article with important contributions from CLA and SMM. All authors provided input and gave final approval for publication.

Conflict of interest statement

This article has been peer reviewed and approved for publication consistent with U.S. Geological Survey Fundamental Science Practices. The authors declare no conflicts of interest.

Data availability

Analyses reported in this article can be reproduced using the data provided by Richardson and Matsuoka (2023).

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