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USING A MULTIMODEL APPROACH TO ESTIMATE THE POPULATION SIZE OF MCKAY'S BUNTINGS

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Abstract. We estimated the population size of McKay's Buntings (*Plectrophenax hyperboreus*) from surveys across their restricted breeding range on St. Matthew and Hall Islands, Alaska (326 km²). We used a multimodel approach to (1) estimate population size from counts with distance sampling, and (2) account for the effects of observers, habitat, flock size, and date on detectability. We counted 2400 buntings along 202 km of transects; most birds were in tundra (44%) or rocky uplands (46%). Breeding density was higher on Hall Island (154 ± 20 [SE] birds km⁻²) than St. Matthew Island (93 ± 7 birds km⁻²), possibly due to differences in habitat. Population size was $31\,200 \pm 2000$ birds ($CI_{95\%} = 27\,500\text{--}35\,400$ birds), 5–11 times greater than previously reported, but still small among North American passerines. Populations of this species should therefore be closely monitored and the focus of conservation.

Key words: Alaska, breeding density, distance estimation, McKay's Bunting, *Plectrophenax hyperboreus*, population size, St. Matthew and Hall Islands.

Uso de un Enfoque basado en Varios Modelos para Estimar el Tamaño Poblacional de *Plectrophenax hyperboreus*

Resumen. Estimamos el tamaño poblacional de *Plectrophenax hyperboreus* a partir de censos realizados a lo largo de su restringido ámbito de reproducción en las islas St. Matthew y Hall, Alaska (326 km²). Empleamos un enfoque basado en varios modelos para (1) estimar el tamaño de la población a partir de conteos con muestreos de distancia, y (2) tener en cuenta el efecto de los observadores, el hábitat, el tamaño de la bandada y la fecha sobre la detectabilidad. Contamos 2400 individuos a lo largo de 202 km de transectos: la mayoría de las aves estuvieron en tundra (44%) o en tierras altas rocosas (46%). La densidad de aves reproductoras fue mayor en Hall (154 ± 20 [EE] aves km⁻²) que en St. Matthew (93 ± 7 aves km⁻²), posiblemente debido a diferencias en el hábitat. El tamaño de la población

fue de $31\,200 \pm 2000$ individuos ($IC_{95\%} = 27\,500\text{--}35\,400$). Este valor es 5 a 11 veces mayor de lo que se había documentado previamente, pero aún pequeño en comparación con los tamaños poblacionales de otros passerinos de América del Norte. Por lo tanto, las poblaciones de esta especie deben ser monitoreadas de cerca, y deben representar el foco de programas de conservación.

Although known to science since 1884 (Ridgeway 1884), McKay's Bunting (*Plectrophenax hyperboreus*) remains one of the most poorly studied of North America's birds (Lyon and Montgomerie 1995). It is a close but distinct sister species to the Snow Bunting (*P. nivalis*; Lyon and Montgomerie 1995, Klicka et al. 2003, Maley and Winker 2007) that breeds entirely on St. Matthew Island and its smaller satellite, Hall Island, Alaska in the remote central Bering Sea (Gabrielson and Lincoln 1959, Kessel and Gibson 1978, Winker et al. 2002). Small numbers of birds also occur irregularly during the breeding season on St. Lawrence and the Pribilof Islands (Kenyon and Phillips 1965, Sealy 1967, 1969, Kessel and Gibson 1978), although breeding has not been confirmed. The species winters principally along the Bering Sea coast from the Seward to Alaska Peninsulas (Sealy 1972, Bailey 1974, Kessel and Gibson 1978, Lyon and Montgomerie 1995) and is the only avian species whose entire range is restricted to Alaska. Lyon and Montgomerie (1995) hypothesized that fewer than 2800 individuals comprise the species; however, surveys have never been conducted to estimate its abundance.

In this study, we report the first empirical estimate of population size for McKay's Bunting based on surveys we conducted across the species' restricted breeding range on St. Matthew and Hall Islands (326 km² combined). We also describe from our surveys the general use of habitats by this species. We used a multimodel approach (Burnham and Anderson 2002) to assess covariate effects on avian detectability and to estimate abundance of breeding McKay's Buntings from line transect surveys with distance sampling (Buckland et al. 2001, Marques et al. 2007). This improves upon the single-model approach typically used when analyzing distance data by: (1) measuring the relative effects of different ecological factors on detectability and abundance across a set of candidate models, and (2) incorporating model uncertainty into the variance structure of abundance (Burnham and Anderson 2002, Buckland et al. 2004, Marques et al. 2007).

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METHODS

STUDY AREA

We conducted our surveys on St. Matthew and Hall Islands ($60^{\circ}27'N$, $172^{\circ}50'W$; Fig. 1) within the Bering Sea Islands ecoregion, Alaska (Nowacki et al. 2001). These islands are uninhabited by people, >250 km from both the nearest landmass and human settlement, and protected as part of the U.S. Fish and Wildlife Service's Alaska Maritime National Wildlife Refuge. St. Matthew Island (309 km^2) is characterized by mixed topography reaching 459 m in elevation and a coastline comprised of extensive beaches and tall sea cliffs. Low-lying areas include small streams, ponds, and lakes as well as wet sedge meadows and tundra dominated by dwarf-shrubs or moss and lichens. Vegetation is generally <30 cm in height and becomes drier and sparser with increases in slope and elevation. Eventually, the vegetation gives way to rock talus on steep slopes and rock fields at high elevations. Hall Island reaches elevations up to 509 m and is distinguished from St. Matthew Island by its smaller size (17 km^2), steeper terrain, absence of lakes and beaches (Hanna 1917, DeGange and Sows 1978), and thicker mats of lichen-dominated tundra (Klein 1987). This latter difference resulted from overgrazing and trampling by reindeer (*Rangifer tarandus*), 29 of which were introduced to St. Matthew, but not Hall Island, in 1944. This herd increased to 6000 animals by 1963 and subsequently died off by 1982 (Klein 1968, 1987).

FIELD METHODS

We surveyed McKay's Buntings on both islands using line-transect surveys, with distances estimated to lone individuals or groups of birds (Buckland et al. 2001). We selected a random point on each island from which we distributed a systematic sample of parallel transects oriented 47° (true) and bisecting St. Matthew and Hall Islands along the short axis of the islands (Fig. 1). We surveyed 34 transects spaced 1.5 km apart on St.

Matthew Island from 30 May to 29 June 2003 and 12 transects spaced 0.5 km apart on Hall Island on 21 June 2003. We chose the smaller spacing between transects on Hall Island so that we would have sufficient samples to compare breeding densities between islands. We surveyed each transect once, typically starting and ending each survey in the supratidal zone or at the top of coastal cliffs on opposite coasts of the islands. Two transects on Hall Island (Fig. 1) were not completed due to limited time on this island. We did not survey or include in our estimates of transect length those sections of transects that crossed lakes or ponds.

Our surveys encompassed the breeding period from territory display and establishment through late incubation for McKay's Buntings (Winker et al. 2002). We conducted surveys throughout the day because activity of closely related Snow Buntings had not been found to vary diurnally during the breeding season (B. E. Lyon, University of California, Santa Cruz, pers. comm.). During surveys, we walked at a steady pace and noted the location and the side of the transect line on which each bird was observed. We walked to the point on the line that was perpendicular to each observation and then used a laser rangefinder to measure to the nearest meter the perpendicular distance from the transect line to the location of each lone individual bird, or to the center of each group of birds, when first detected. We noted whether distances were measured based on visual observations or estimated based on aural detections of birds, and recorded the coordinates on the transect line perpendicular to each observation with a global position system in order to map the locations of birds. We also recorded the habitat in the immediate vicinity (approximately 10-m radius) of each lone individual or group of birds, classified into one of four general categories: wet meadow, tundra, rocky uplands (rock talus or rock fields), or other habitats—the latter composed of beaches, sea cliffs, and snowfields. When we encountered birds in a group, we recorded the habitat used by the first bird encountered. We restricted our surveys to lone individuals and groups of birds whose flock centers were within 100 m of the transect line due to high densities. We recorded separately those birds observed in direct flights >200 m in length over survey transects (flyovers) and excluded these observations from analysis. We did not conduct surveys during periods of high winds, heavy rain, or thick fog. We distinguished McKay's from Snow Buntings by the greater amount of white on the wings, mantles, rumps, uppertail coverts, and tails of the former, following Byers et al. (1995), Lyon and Montgomerie (1995), and Pyle (1997). We most readily identified: (1) male McKay's Buntings by their white mantles, rumps, and uppertail coverts, (2) female McKay's Buntings by their white rumps and uppertail coverts and primarily white mantles with black centers, and (3) Snow Buntings by their mantles, rumps, and uppertail coverts having little to no white (Pyle 1997). When possible, we also distinguished McKay's from Snow Buntings by: (1) a lack of extensive black beyond the two innermost pairs of rectrices, and (2) outer primaries with white extending beyond the tips of the primary coverts (Pyle 1997); however, these characters were often difficult to discern in the field during surveys (Byers et al. 1995). Vocalizations are similar between these buntings (Lyon and Montgomerie 1995); thus, we could not use aural detections alone to identify species.

STATISTICAL ANALYSES

We used distance sampling models (Buckland et al. 2001, 2004) to adjust our counts for the decreasing probability of detecting birds with increasing distance from the transect line and to estimate

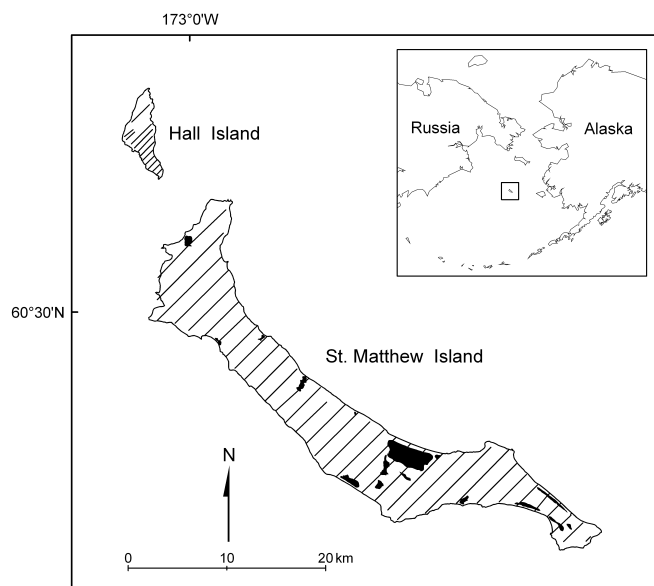


FIGURE 1. Systematic random sample of line transects surveyed for breeding McKay's Buntings in 2003 on St. Matthew and Hall Islands, Alaska ($n = 34$ and 12 transects, respectively).

density and total population size of breeding McKay's Buntings (Buckland et al. 2001). We first developed a preliminary model of abundance to evaluate whether observations were clustered at particular distances from transects and whether observations at larger distances should be removed to better fit the detection function near the line and to meet the assumption that detectability of birds was 100% on the line. We did not group data into distance categories or stratify counts in this model. We subsequently pooled data into 10-m intervals to improve model fit and truncated observations beyond 80 m because the detection probabilities from 81 to 100 m were below 0.15 (Buckland et al. 2001).

We then assessed the relative fit of different parametric key detection functions to select the function most appropriate for estimating abundance. We evaluated key detection functions with and without single-term series expansion for models that included no effects and the univariate effects of five covariates (observers, observer experience, habitats, date, and group size), which we later used to minimize bias in strata-specific estimates of density and population size (see descriptions below). For models without covariates, we assessed half-normal, hazard-rate (no expansion, cosine, and simple polynomial), and uniform key detection functions (cosine and simple polynomial; Buckland et al. 2001). For models with covariates, we assessed the same half-normal and hazard rate key detection functions included above (Marques and Buckland 2004). This resulted in 39 models (nine without covariates, 30 with covariates), among which we compared relative model fit based on Akaike's information criterion adjusted for small sample sizes (AIC_c). We expressed AIC_c as a relative likelihood of each model in the set (Akaike weight, w_i) and summed Akaike weights ($\sum w_i$) by key detection function to identify the function best supported by the data.

Next, we used the best-supported key detection function with and without single-term series expansion, and developed models of density and population size stratified by island and group size (lone individuals, two birds, and ≥ 3 birds). We stratified counts and detection functions by island because of differences in habitat and disturbance histories. We followed Buckland et al. (2001) and stratified counts by group size to account for variation in group size among detections and transects. We developed a total of 18 models of density and population size that included three models without covariates in the detection function and three models each for detection functions with the univariate effects of observers, observer experience, habitats, date, and group size. Each of these covariates had been found to affect detectability of birds (Buckland et al. 2001, Alldredge et al. 2007). We evaluated two separate covariates for observer effects: a covariate with a category for each of the five observers (observer) and a covariate for observer experience conducting line transect surveys (experience; 0 years vs. >1 year). Habitats were reduced to two classes (rock talus vs. all other categories combined) to meet the model requirement that detection probabilities of birds for all covariate levels exceed 0.1 (Marques and Buckland 2004). We predicted that detectability would: (1) be higher for experienced observers, (2) be relatively low in rock talus because buntings typically placed their nests in rock crevices (Winker et al. 2002), (3) decrease with date due to declines in singing rates and mate guarding as the breeding season progressed (Lyon and Montgomerie 1995), and (4) increase with group size.

We compared the relative fit among models of density and population size based on AIC_c and the relative likelihood of pairs of models using the ratio of Akaike weights (Burnham and Anderson 2002). For each of the models, we summed the group size stratum estimates of density (birds km^{-2}) and population size (number of birds) to estimate density and population

size for each island. For the islands combined, we estimated density by averaging the island estimates weighted by island area; we estimated total population size by summing the island estimates. We then calculated, by island and the islands combined, model-averaged estimates of density and population size, their associated variances, and their 95% log-based confidence intervals (Satterthwaite 1946, Buckland et al. 2001) following Burnham and Anderson (2002). We used SPSS (SPSS 1999) statistical package to calculate descriptive statistics; program DISTANCE 5.0, Release 2 (Thomas et al. 2006) to model the detection function and estimate abundance; and ArcGIS 9.0 to estimate the area of each island based on their perimeter at mean sea level. We present all estimates \pm SE.

RESULTS

We counted 2400 McKay's Buntings among 1415 groups along 201.9 km of survey transects. We did not encounter Snow Buntings on survey transects but observed five males away from transects from 27 May–5 June. We excluded from our analyses birds observed in direct flights of >200 m (71 groups, 110 individuals), birds for which we mistakenly did not record information on habitats used (7 groups, 13 individuals), and birds mistakenly recorded >100 m from observers (11 groups, 17 individuals). After truncation of birds observed at distances >80 m (111 groups, 196 individuals), we analyzed for abundance 1215 groups of birds totaling 2064 individuals—199 groups of birds totaling 313 individuals on Hall Island and 1016 groups of birds totaling 1751 birds on St. Matthew Island. This included 864 females, 1147 males, and 53 birds of unknown sex. Group size averaged 1.70 ± 0.02 birds and ranged from 1–6 birds. We detected 560 lone individuals, and 537 two-bird groups, 53 three-bird groups, 57 four-bird groups, five five-bird groups, and three six-bird groups. We measured distances to 1209 of these groups (99.5%) based on visual observations of birds and estimated distances to six lone individuals based on aural detections. We observed most birds in rocky upland (46% of groups and individuals; $n = 568$ groups, 953 individuals) and tundra habitats (44%; $n = 528$ groups, 911 individuals). We detected far fewer birds in meadows (8%; $n = 94$ groups, 155 individuals) and other habitats (2%; $n = 25$ groups, 45 individuals).

In our evaluation of models with different parametric key-detection functions, we found the most support for models using the half-normal key ($\sum w_i = 0.90$). We found far less support for models using hazard-rate ($\sum w_i = 0.10$) or uniform key functions ($\sum w_i < 0.01$). We therefore used the half-normal key function with and without a single adjustment term (cosine or simple polynomial) in all subsequent models. Among our 18 models of density and population size, we found the most support for models that included habitat ($\sum w_i = 0.72$). We found less support for models of the detection function that included experience ($\sum w_i = 0.23$), and little support for models with observers, cluster size, date, or no effects ($\sum w_i < 0.03$). The best-supported model ($w_i = 0.52$) included the covariate habitat and lacked an adjustment term in the detection function (Table 1). This model suggests that the detectability of buntings was lower in rocky uplands compared to other habitats, the latter the reference category ($\beta_{\text{habitat}} = -0.25 \pm 0.08$). The second-best model was 3.6 times less likely than the best model and included the covariate experience and lacked an adjustment term in the detection function ($w_i = 0.15$; Table 1). This model suggested that detectability of buntings was higher for new compared to experienced observers, the latter of which was the reference category ($\beta_{\text{experience}} = 0.22 \pm 0.08$). Thus, we found support for our predictions that detectability would be low in rocky

TABLE 1. Comparisons of models of the abundance of breeding McKay's Buntings in 2003 on St. Matthew and Hall Islands, Alaska (326 km²). Data are from line-transect surveys ($n = 46$ transects, 201.9 km total length), with distances measured to lone individuals or groups of birds ($n = 1215$ observations totaling 2064 birds) within 80 m of transect lines. We compared the fit among a total of 18 models of the detection function [$f(0)_{\text{covariates, adjustment term}}$] using Akaike's information criterion adjusted for small sample sizes (AIC_c) and the number of parameters (K) in the detection function that we estimated separately for each island. We present only results from models with model probabilities (w_i) ≥ 0.01 . Estimates of the effective strip half-width (ESW \pm SE m), density ($D \pm$ SE birds km⁻²), and population size ($n \pm$ SE individuals) are based on counts stratified by island and group sizes.

Model ^{a,b}	K	Log likelihood	ΔAIC_c	w_i	ESW	$D_{\text{St. Matthew}}$	D_{Hall}	n
$f(0)_{\text{habitat}}$	4	-2421.5	0.0	0.52	52.3 \pm 0.9	92.6 \pm 6.4	146.6 \pm 16.7	31 098 \pm 2001
$f(0)_{\text{experience}}$	4	-2422.8	2.6	0.15	52.1 \pm 0.9	92.4 \pm 6.4	146.8 \pm 16.7	31 058 \pm 1998
$f(0)_{\text{habitat, cos}}$	6	-2421.1	3.3	0.10	52.1 \pm 0.8	93.6 \pm 6.5	161.2 \pm 18.5	31 665 \pm 2029
$f(0)_{\text{habitat, sp}}$	6	-2421.2	3.4	0.10	52.0 \pm 2.5	92.5 \pm 6.4	153.6 \pm 20.4	31 207 \pm 2014
$f(0)_{\text{experience, sp}}$	6	-2421.7	4.5	0.05	52.1 \pm 2.7	92.7 \pm 6.4	154.2 \pm 20.8	31 274 \pm 2019
$f(0)_{\text{experience, cos}}$	6	-2422.3	5.6	0.03	52.0 \pm 0.8	93.4 \pm 6.4	161.1 \pm 18.5	31 595 \pm 2024
$f(0)_{\text{experience, cos}}$	2	-2427.0	6.8	0.02	51.2 \pm 2.1	92.1 \pm 6.6	146.1 \pm 18.3	30 952 \pm 2084

^aModels of $f(0)$ included those with univariate effects of habitats (rock talus vs. all other), observers ($n = 5$), observer experience (experience; 0 years vs. >1 year conducting line-transect surveys), and the number of birds in each observation (lone individuals or groups of 2–6 birds). All models of $f(0)$ used the half-normal key function either with or without single-term cosine (cos) or simple polynomial (sp) adjustment.

^bAIC_c of top model = 4851.1.

uplands. We did not find support, however, for our predictions that detectability would be higher for experienced observers or would decrease with date or cluster size.

Averaging models of density and population size with the half-normal key detection function (Table 1), we estimated that the effective strip half-width of our survey was 52.1 \pm 1.2 m. Thus, we effectively surveyed an area of 21.0 km² or 6.5% of St. Matthew and Hall islands combined. We used model averaging across models (Table 1) and estimated that the density of breeding McKay's Buntings was higher on Hall Island (154.0 \pm 20.2 birds km⁻²) than St. Matthew Island (92.7 \pm 6.5 birds km⁻²) and averaged 95.7 \pm 6.2 birds km⁻² across the islands combined. We estimated population size to be 31 200 \pm 2000 birds (CI_{95%} = 27 500–35 400 birds). Model averaging led to a 2% increase in the variance of density when compared to the best-fit model (Table 1).

DISCUSSION

Our estimate of 31 200 McKay's Buntings was 5–11 times greater than the population size of 2800–6000 birds that Lyon and Montgomerie (1995) reported based on extrapolations of average and maximum breeding densities of Snow Buntings in North America. Our raw count of 2400 birds alone was near their lower hypothesized population size. The high densities of McKay's Buntings breeding on St. Matthew and Hall Island (93 and 154 birds km⁻², respectively) were unique relative to Snow Buntings breeding in North America ($\bar{x} = 9$, range: 2–20 birds km⁻²) and Europe ($\bar{x} = 56$, range: 38–84 birds km⁻²; Lyon and Montgomerie 1995). It is unknown whether these differences in densities are due to disparities in predator regimes, breeding strategies, availability of nesting habitats, interspecific competition for nest crevices, or other factors. Our estimates of density were averaged across all habitats sampled—densities were likely even greater in tundra and rocky uplands, where we observed 90% of birds. These habitats were proportionately more common on Hall than St. Matthew Island and may in part account for differences in densities between islands. However, we may have underestimated densities on Hall Island because we did not complete surveys on two transects where these habitats were abundant.

The preponderant use of tundra and rocky uplands by McKay's Buntings was contrary to previous observations of bunting concentrating along beaches, shores of coastal lakes and ponds, and coastal cliffs (Hanna 1917, Gabrielson 1944, Gabrielson and Lincoln 1959, DeGange and Sowls 1978). We did not concentrate our sampling in these habitats and instead surveyed transects that were nearly perpendicular to the coast and the shores of most lakes and ponds. Our estimates of abundance might therefore be conservative despite high precision (CV = 6.5%) and thorough overall survey coverage (6.5% of islands effectively sampled). We conducted our surveys during the nesting period from 30 May to 29 June, whereas previous observations were later in the summer (26 June–27 July) and included adults feeding fledged young (Winker et al. 2002). Disparities between our observations and others may therefore reflect seasonal shifts in activity from interior nest sites to coastal areas with food and cover for postbreeding adults and juveniles.

We counted the greatest number of buntings (46%) in rocky uplands, the habitat in which we had the lowest probability of detecting birds. This suggests that previous researchers may have underestimated the use of rocky uplands by buntings. Future assessments of habitat selection in this species will need to account for detectability to reach valid conclusions (MacKenzie 2006). Rocky uplands provided deep nesting crevices protected from predators such as Arctic (*Alopex lagopus*) and red foxes (*Vulpes vulpes*), and Long-tailed (*Stercorarius longicaudus*) and Parasitic Jaegers (*S. parasiticus*), which we encountered frequently on the islands. Low detectability of birds in rocky uplands may have resulted from inconspicuous behavior of adults around nests or from difficulties in counting birds while traversing unstable talus and rock fields on often steep-sided slopes.

We did not encounter Snow Buntings on transects and observed only five male Snow Buntings away from transects during our study. Previous researchers either did not report Snow Buntings (Hanna 1917, Gabrielson 1944, DeGange and Sowls 1978) or considered the species uncommon on these islands (Winker et al. 2002). There appears to be little overlap in breeding range between these sister species; thus, hybridization is likely rare. We agree with Lyon and Montgomerie (1995) that further study is needed to assess whether birds with intermediate plumage between these

species (Sealy 1969, Rogers 2005) are hybrids or are within the natural range of plumage variability for either species.

We found McKay's Buntings to be more abundant than previously believed; however, only seven passerine species breeding in the United States or Canada have smaller population sizes (Rich et al. 2004)—four are federally listed as threatened or endangered (Committee on the Status of Endangered Wildlife in Canada 2004, U.S. Fish and Wildlife Service 2007). The small population and restricted range of McKay's Bunting heighten its vulnerability to extinction (Rich et al. 2004) as evidenced by these other passerines. Although these islands are remote and protected as part of the Alaska Maritime National Wildlife Refuge, they can still be threatened by introductions of invasive animals, environmental contamination, and changes in habitat from climate change. Plant and lichen communities have already been severely overgrazed and trampled by reindeer on St. Matthew Island (Klein 1968, 1987). The lower densities of buntings on St. Matthew compared to Hall Island may in part reflect the slow recovery of habitats from disturbance by reindeer (Klein 1987). Rats (*Rattus* spp.) have been introduced north of St. Matthew Island on mainland Alaska (Fritts 2007) and are most likely to colonize these islands from shipwrecks such as the 145-m long M/V *Milos Reefer*, which ran aground St. Matthew Island while carrying livestock and cargo in a November 1989 storm and spilled 880 kiloliters of fuel and oil onto the island's shores (Associated Press 1989). Fortunately, rats did not colonize the island during this event, and the oil spill was likely a small threat to upland-nesting buntings by the following summer. Finally, the Bering Sea region has undergone rapid climate warming in recent decades (Arctic Climate Impact Assessment 2005) that has been linked to increases in shrub height and cover across the Arctic (Tape et al. 2006). This could lead to large changes in the suitability of habitats used by breeding and wintering McKay's Buntings. We recommend periodic monitoring of the breeding population to better understand its status through time.

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