

Effects of Translocation on the Behavior of Island Ptarmigan

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Abstract. Evermann's Rock Ptarmigan (*Lagopus muta evermanni*) are endemic to the Near Islands of the western Aleutian Archipelago, Alaska, but introductions of nonnative arctic foxes extirpated ptarmigan from all islands except Attu Island. Fox removals were completed at Agattu Island in 1979 but natural recolonization did not occur, and 75 ptarmigan were translocated from Attu to Agattu during 2003–2006 to reestablish a breeding population. We used radiotelemetry to assess the impacts of translocation on the post-release movements, nest site selection, and brood movements of 28 females. Behavior of 11 translocated birds was compared to 17 established birds resulting from translocations completed in previous years. Nest sites of translocated females were not different from nest locations of established females with regard to topographical features or nest cover. Nest site selection was influenced by aspect and percent cover of rocks

and forbs, but not by slope or general habitat features. After hatching, translocated females moved their broods greater distances from nest sites than did established females (845 vs. 190 m), and all females moved their broods to higher elevations above the nest site (62 to 108 m). The size of the brood home range was similar for established (3.6 ha, SE = 1.6) and translocated females (6.7 ha, SE = 2.4). Overall, translocated and established ptarmigan had similar movements, nest site selection, and reproductive performance at Agattu. Our results are encouraging for future efforts to reestablish populations of endemic ptarmigan and land birds elsewhere in the Aleutian Islands.

Key Words: Agattu Island, Aleutian Archipelago, colonization, Evermann's Rock Ptarmigan, *Lagopus muta evermanni*, post-release movements, radiotelemetry, reintroduction.

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Oceanic island systems are highly susceptible to extinction, largely owing to reduced diversification, simplified food webs, and high rates of endemism, which make island species highly sensitive to ecological perturbations and disturbance (Moors 1993, Courchamp et al. 2003). Introduction of nonnative mammals has been a major cause of biodiversity loss on islands, due to the small size of island populations and a lack of adaptive behavioral responses among island species which have evolved without predators or competitors (Savage 1984, Atkinson 1985, King 1985, Moors and Atkinson 1984). Less than 20% of the world's bird species are restricted to islands, but over 90% of bird extinctions during historic times were island forms, largely attributed to the effects of introduced species (Johnson and Stattersfield 1990). Restoration of island ecosystems is an urgent need in conservation biology, but may also be one of the most feasible goals. If biodiversity loss has been due to impacts of introduced species, restoration via predator removal may be easier to achieve in closed island systems than mainland sites (Courchamp et al. 2003). Predator removals can restore island habitats, but direct intervention may still be needed to reestablish taxa with limited dispersal ability. Translocations of wild-caught animals are an important tool in conservation biology for reintroductions and supplementation of declining populations (Scott and Carpenter 1987, Griffith et al. 1989).

Translocations have been widely used to establish or reintroduce populations of ptarmigan (Braun et al. 1978, Hoffman and Giesen 1983), forest grouse (Woolf et al. 1984), and prairie grouse (Toepfer et al. 1990, Hoffman et al. 1992, Musil et al. 1993). Post-release monitoring of habitat selection and movements can provide insights into the behavioral mechanisms that contribute to successful settlement and establishment of new populations. Monitoring of recently released individuals can also help to determine the ecological requirements of a species, particularly during the early stages of colonization. If translocated individuals disperse from release sites before settlement, the new home ranges may indicate preferred environmental conditions (Hirzel et al. 2004). Field studies conducted during multi-year reintroduction projects have the added benefit of measuring the impacts of translocation by comparing performance of newly released birds with established individuals

and their offspring (Saltz and Rubenstein 1995, Sarrazin and Barbault 1996).

The Aleutian Islands are an archipelago of more than 200 islands extending from the Alaska Peninsula west toward Asia and geographically separating the North Pacific Ocean from the Bering Sea (Fig. 22.1). Historically, the Aleutian Islands had no native terrestrial mammals west of Umnak Island (Murie 1959, Gibson and Byrd 2007). Many island populations of native birds were negatively impacted by deliberate introductions of arctic foxes (*Alopex lagopus*) by fur trappers between 1750 and 1940 (Bailey 1993, Williams et al. 2003, Maron et al. 2006). Depredation of eggs, young, and breeding birds led to population declines and local extirpation of waterfowl, seabirds, and land birds from many islands (Murie 1959). In 1949, as part of the recovery efforts for the Aleutian Cackling Geese (*Branta hutchinsii leucopareia*), the U.S. Fish and Wildlife Service (USFWS) began systematic removal of foxes from Amchitka and Agattu Islands.

The Rock Ptarmigan (*Lagopus muta*, formerly *L. mutus*) is an arctic breeding bird with a Nearctic distribution (Holder and Montgomerie 1993). Within the Aleutian Archipelago, the species exhibits considerable phenotypic differentiation with a range of plumage coloration. Eight subspecies have been described from different groups of Aleutian Islands (Holder et al. 2000, 2004). In four subspecies, males have pale nuptial plumage, three subspecies have dark plumage, and only one subspecies has black plumage: Evermann's Rock Ptarmigan (*L. m. evermanni*). Genetic analyses based on mitochondrial DNA have shown that Evermann's Rock Ptarmigan are markedly different from all other Aleutian Rock Ptarmigan, and the origins of this isolated population remain unclear (Holder et al. 2000, Pruett et al. 2010). Evermann's Rock Ptarmigan once occurred throughout the Near Islands group (Fig. 22.1) in the western range of the Aleutians but were extirpated from all islands except Attu by 1936 (Turner 1886, Murie 1959). Following completion of fox removals in 1999, the extant population on Attu was estimated to be about 1,000 birds (Ebbert and Byrd 2002). Due to a small population size and limited geographic range, Evermann's Rock Ptarmigan was designated as a species of special management concern by the USFWS.

Regional migratory movements of Rock Ptarmigan are common in mainland Alaska and

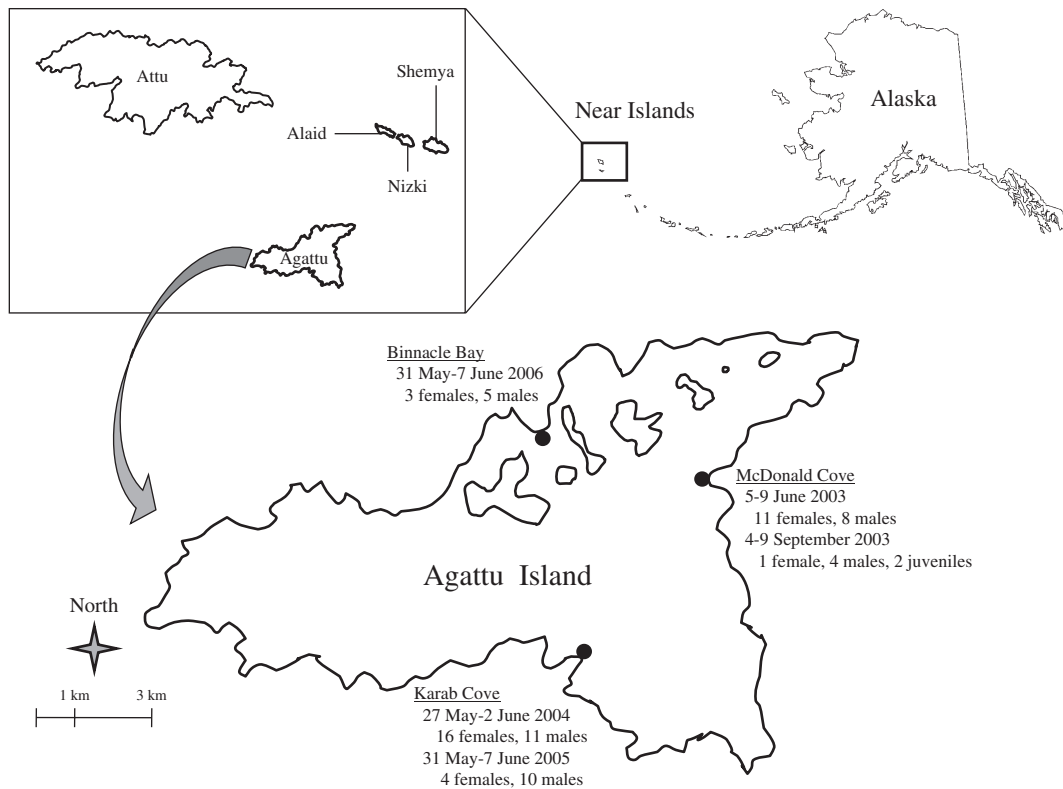


Figure 22.1. Location of field study of Evermann's Rock Ptarmigan at Agattu Island, part of the Near Islands group (inset), Alaska, 2005–2006. Evermann's Rock Ptarmigan once occupied the Near Islands (Attu, Agattu, Shemya, Nizki, and Alaid Islands), but predation by introduced foxes restricted their range to Attu by 1936. Ptarmigan were translocated from Attu to Agattu Island from 2003 to 2006 to restore birds to their former range. Outline of mountains in northeast portion of Agattu Island represents 300-m contour lines of montane habitats where ptarmigan nested. Points mark three coastal sites where ptarmigan were released after translocation from Attu to Agattu Island.

northern Canada, but ptarmigan in the Aleutian Islands are more sedentary. Long-distance movements have been reported for other species of ptarmigan (Hannon et al. 1998, Martin et al. 2000), including dispersal across marine waters (Zimmerman et al. 2005), but natural recolonization across the 28-km strait between the islands of Attu and Agattu did not occur during the 25-year period after foxes were successfully eradicated from Agattu. As part of a regional effort by the Alaska Maritime National Wildlife Refuge (NWR) to restore wildlife populations after the removal of nonnative predators, translocations were used to reestablish Evermann's Rock Ptarmigan at Agattu Island over a four-year period from 2003 to 2006. Previously, we compared the demographic performance of newly translocated birds with established birds from earlier translocations, and found that translocated birds delayed clutch initiation and laid smaller clutches, but that seasonal

productivity and survival rates of the two groups did not differ (Kaler et al. 2010). Here, we compare behavior of translocated and established birds to examine the settlement decisions, nest site selection, and brood movements of female ptarmigan during the early stages of establishment of a new population.

Our general objectives were to determine the ecological requirements of island ptarmigan and to develop translocation methods for restoration of endemic birds in the Aleutian Islands. We tested three hypotheses regarding habitat preferences of island ptarmigan: (1) If newly translocated females are unconstrained in their settlement decisions, they may select new habitats at Agattu compared to their capture sites at Attu; (2) if settlement decisions are constrained by presence of territorial birds, established females at Agattu might occupy preferred nesting habitats and recently translocated females might be

limited to nest sites in suboptimal sites; and (3) if habitat use is affected by timing of breeding or prior breeding experience, recently translocated females might have larger brood home ranges than established females with familiar nest and brood-rearing areas.

STUDY AREA

Attu Island (52.85° N, 173.19° E; 89,279 ha) and Agattu Island (52.43° N, 173.60° E; 22,474 ha) are in the Near Islands group in the western range of the Aleutian archipelago and are part of the Alaska Maritime National Wildlife Refuge (Fig. 22.1). Attu is a mountainous island, composed of steep hillsides rising from sea level to elevations up to 861 m. In contrast, Agattu is an island that is primarily maritime tundra <200 m in elevation, with a single mountain range covering the northern third of the island and a maximum elevation of 634 m. Climatic conditions in the Near Islands are characteristic of a maritime environment in the north Pacific and exhibit limited daily and annual variation. A weather station at Shemya Island, approximately 30 km to the northeast, reported a mean annual temperature of approximately 3.9°C, with precipitation occurring on >200 days and averaging 80.6 cm per year (1949–1995; Western Regional Climate Center). Wind velocities averaged 42 km per hour on Shemya and gusts of 165–200 km per hour are common.

Plant communities on the two islands are similar. At coastal areas, the upper beach strand plant community forms a narrow fringe around each island, dominated by beach rye (*Leymus arenarius*), beach fleabane (*Senecio pseudo-arnica*), and beach greens (*Honckenya peploides*). Wet meadow communities in sheltered valley bottoms are dominated by grasses (*Poa eminens*, *Calamagrostis canadensis*) and sedges (*Carex* spp., *Eriophorum russeolum*). Sloping hillsides are dominated by two plant community types: tall forbs (*Geranium erianthum*, *Anemone narcissiflora*, *Geum calthifolium*) or dwarf shrub meadows with a mixture of crowberry (*Empetrum nigrum*) and lichens (*Cladina* spp.). Woody plants (*Salix* spp., *Sorbus sambucifolia*) are sparse but occur in protected low-lying areas where they may grow to 0.5–1.0 m in height. Higher elevations (>250 m) show a transition to upland dwarf shrub mats dominated by dwarf willow (*Salix arctica*), heaths (*Phyllodoce aleutica*,

Cassiope lycopodioides), and forbs (*Saxifaga* spp., *Geum calthifolium*). Glaucous-winged Gulls (*Larus glaucescens*) and Common Ravens (*Corvus corax*) were potential predators of eggs and chicks, whereas Peregrine Falcons (*Falco peregrinus*) and Snowy Owls (*Nyctea scandiaca*) were a threat to adult ptarmigan (Gibson and Byrd 2007). Agattu Island does not have introduced populations of rats (*Rattus* spp.), which are a problem elsewhere in the Aleutian Islands.

METHODS

Evermann's Rock Ptarmigan were captured with noose poles, noose carpets, and ground nets in the area of Massacre Bay, Attu Island. Five sets of translocations from Attu to Agattu Island were conducted: four between 27 May and 9 June of 2003–2006 and one during 4–8 September 2003 (Kaler et al. 2010). Ptarmigan were transported from Attu Island by ship and released at one of three coastal beach sites at Agattu Island: MacDonald Cove (2003), Karab Cove (2004–2005), or Binnacle Bay (2006; Fig. 22.1). During June–August of 2005 and 2006, we remained at Agattu during the breeding season to conduct an intensive radiotelemetry study of ptarmigan movements and behavior. We compared behavior between two groups of birds: ptarmigan that had been previously translocated or hatched at Agattu (hereafter, *established* birds) versus ptarmigan that were newly translocated and released at Agattu during 2005 or 2006 (hereafter, *translocated* birds).

All ptarmigan were uniquely color banded and each female was fitted with a bib-style radio collar (2005: 15 g, Telemetry Solutions, Concord, CA), or a necklace radio collar (2006: 6 g, Holohil Ltd., Carp, ON). Radios had an expected battery life of 12–18 months and were equipped with mortality switches to facilitate detection of mortality events and dropped collars. Radio-tracking began immediately after release using a three-element Yagi antenna and portable radio receivers (R2000, Advanced Telemetry Systems, Isanti, MN). For the first two weeks after release, we located each bird daily using standard triangulation techniques. A compass bearing was recorded in the direction of a radio-marked bird from each of 3–4 georeferenced points spaced ≥ 100 m apart. Positions of females attending nests or broods were triangulated from distances of 30–50 m to reduce location errors (Garrott et al. 1986). All locations

were recorded in Universal Transverse Mercator (UTM) coordinates using a handheld Global Positioning System receiver (Garmin GPSmap 76, Garmin International, Olathe, KS). Locations were downloaded using DNR Garmin version 5.1.1 software (Minnesota DNR, 2001) and entered into a Geographic Information System (GIS) using ArcView GIS 3.2a software (Environmental Systems Research Institute, Redlands, CA).

Nest site characteristics were measured after completion of each nesting attempt. Vegetation data were collected at each nest plot and four dependent non-nest plots placed at 50 m from the nest in each of the four cardinal directions. Using a 25-m-radius circular plot (0.2 ha) at each nest, or non-nest plot, percentage classes of each general vegetation type present were estimated using the classification system of Viereck et al. (1992), based on cover of exposed soil and rocks, and major plant functional groups such as lichens, mosses, grasses, forbs, and woody plants (Kaler 2007). Elevation, slope, aspect, and topography were also recorded for each 25-m plot. Using a 5-m-radius plot nested within the 25-m plot and centered at the nest site or middle of the non-nest plot center, we classified ground cover into 13 categories after Frederick and Gutiérrez (1992). Data were converted to the median point of each group. To maintain consistency among study plots, a single field observer conducted all measurements (RSAK).

Home Range and Habitat Use

We used the Animal Movement extension for ArcView GIS software to estimate movement rates and home range size based on minimum convex polygons (Hooge and Eichenlaub 1997). We quantified home range size of broods from locations collected during a five-week period (30 June–9 August). We excluded points collected within the first three days after hatching because most females remained close to the nest site. All locations receive equal weight in estimates of home range based on minimum convex polygons and thus our estimates of home range size may be biased low (Swihart and Slade 1985, Barg et al. 2005). We estimated an arithmetic center for home ranges of each brood and calculated linear distances between the nest site and the center of each home range. Change in elevation was calculated as the difference between the average

elevation of brood locations and the elevation of the nest.

Statistical Analysis

Statistical analyses were conducted with procedures of Program SAS (ver. 8, SAS Institute, Cary, NC). To determine habitat characteristics associated with the nest sites of Rock Ptarmigan, we used discriminant function analysis (DFA) to compare nest plots and non-nest plots. A stepwise discriminant analysis with 18 habitat characteristics (8 and 10 variables for 5-m and 25-m radius plots, respectively) was used to determine which variables best discriminated between nest sites and non-nest sites (Johnson 1998). A significance level of $\alpha = 0.5$ was used for parameter entry into the analysis while an $\alpha = 0.2$ significance level was used for parameter retention. We then conducted a DFA on the remaining subset of habitat characteristics to discriminate between the two groups. A cross-validation procedure was used to determine misclassification rates for nest and non-nest sites. DFA and cross-validation are usually conducted with a subset of the data to identify significant variables, and then tested on an independent set of the remaining data. Due to small sample sizes, we opted to use all data for both steps of the analysis. Analyses were conducted using Proc STEPDISC and Proc DSCRIM. Circular statistics and the Watson–Williams test were calculated with program Oriana (ver. 3.0, Kovach Computing Services, Anglesey, Wales). Prior to analysis, all non-normal data were log_e-transformed to meet the assumptions of normality. Differences in brood home range size between established and translocated ptarmigan were compared using t-tests (Proc TTEST). Fisher Exact tests were used for the analysis of 2×2 contingency tables. All means are presented with standard errors (SE) unless otherwise noted. All tests were two-tailed and considered significant at $\alpha \leq 0.05$.

RESULTS

During our two-year radiotelemetry study of Evermann's Rock Ptarmigan, we radio-tracked movements of 17 established females (6 in 2005, 11 in 2006) and 11 newly translocated females (9 in 2005, 2 in 2006). Nest failure ($n = 5$) and total brood loss ($n = 10$) reduced the number of broods available for monitoring, and our analyses of brood

home range and distances moved between nest sites and brood home ranges were based on six established and eight translocated females. Three females were followed in both years, of which two were followed as translocated birds during the first year of the radiotelemetry study. One established female was right-censored due to harness failure and loss of the radio transmitter.

Post-release Movements and Nest-site Selection

We calculated straight-line distances from release locations to nest sites for all 11 translocated females. Nest sites of translocated females averaged 4.2 km from their respective release location (SE = 0.7, range 0.7–7.6 km, $n = 11$). Average distance between the release location and the nest site was greater for the nine females released at the south side of the island in 2005 (mean = 5.1 km, SE = 1.9, range = 0.7–7.6 km, $n = 9$) than for two females released at the north side of the island in 2006 (mean = 2.7 km, SE = 1.6, range = 1.1–4.3 km, $n = 2$).

We detected no differences between nests of established and translocated females based on elevation, slope, aspect, and nest cover (Table 22.1), and we pooled information to characterize habitat requirements of the island population. Nests were simple 3–5-cm-deep scrapes with eggs usually laid on a thin layer of vegetation and a few ptarmigan contour feathers. Nests were well concealed; 50% (14 of 28 nests) were placed beneath a large rock or boulder (>30 cm diameter) and 46.4% (13 of 28 nests) were found among dense vegetation. Nest sites of established females were not more likely to be associated with either rocks or vegetation than those of translocated females (Fisher's Exact test: $P = 0.70$). Nest sites were

affected by slope aspect in the alpine nesting habitats, and had a nonrandom orientation with a preference for south-facing slopes (mean vector $\mu = 166^\circ$, SE = 12.4°, $r = 0.562$, SE = 0.08, $n = 28$, Rayleigh test: $z = 8.845$, $P < 0.001$).

We compared 28 nest sites with 112 non-nest plots in a discriminant function analysis (DFA) at two scales: eight variables in 5-m-radius plots to quantify ground cover composition, and 10 variables in 25-m-radius plots to describe general habitat types and topographic features. At the 5-m scale, 3 of 8 habitat characteristics were selected in the stepwise procedure that best discriminated between nest sites and non-nest sites. The significant parameters retained in the analysis ($P < 0.2$) included cover of rocks >20 cm ($F_{1,138} = 8.33$, $P = 0.005$), forbs ($F_{1,138} = 8.48$, $P = 0.058$), and rocks <20 cm ($F_{1,138} = 1.91$, $P = 0.169$). A DFA with all eight habitat characteristics correctly classified nest plots 46.4% (13 of 28) and non-nest plots 68.8% (77 of 112) of the time. When the three key habitat characteristics were used alone, the ability to discriminate between plot types increased marginally. A DFA based on the three significant variables correctly classified nest plots 67.9% (19 of 28) of the time; non-nest plots were correctly classified 65.2% (73 of 112) of the time. The proportion of rocks >20 cm in diameter ($F_{1,138} = 8.33$, $P = 0.005$) and forb cover ($F_{1,138} = 8.48$, $P = 0.058$) were the most important variables differentiating between nest and non-nest plots.

Nest plots could not be differentiated from non-nest plots at the 25-m-radius scale. The stepwise procedure selected two variables that best discriminated between nest plots and non-nest plots—open low scrub ($F_{1,138} = 20.2$, $P < 0.001$) and cover of mesic forbs ($F_{1,138} = 2.0$, $P = 0.17$)—but

TABLE 22.1
Topographic and nest cover measurements [means \pm SE (N)] for nests of established and translocated female Evermann's Rock Ptarmigan at Agattu Island, Alaska, 2005–2006.

| Parameter | Established | Translocated | Pooled | Test ^a | df | Statistic | P |
|-----------------|-------------------|---------------------|-------------------|-------------------|------|-----------|------|
| Elevation (m) | 237 \pm 28 (18) | 251 \pm 13.6 (10) | 242 \pm 14 (28) | <i>t</i> | 26 | −0.46 | 0.65 |
| Slope (degree) | 35 \pm 57 (18) | 27 \pm 10 (10) | 32 \pm 6 (28) | <i>t</i> | 25 | −0.55 | 0.59 |
| Aspect (degree) | 154 \pm 19 (18) | 179 \pm 16 (10) | 166 \pm 12 (28) | <i>F</i> | 1,26 | 1.04 | 0.32 |
| Nest cover (%) | 90 \pm 6 (18) | 82 \pm 12 (9) | 87 \pm 5 (27) | <i>t</i> | 25 | 0.8 | 0.46 |

^a*t* = *t*-test; *F* = Watson-Williams *F*-test.

the DFA procedure using the subset of variables did not improve classification results (21.4%, 6 of 28 nest plots were correctly classified). Female Rock Ptarmigan at Agattu Island may prefer certain habitat features during nest site selection, but these features had little to do with slope, aspect, or general habitat, and were instead influenced by percent cover of vegetation at the nest site, which determined concealment.

Home Range and Movements of Broods

Average number of locations for calculations of home range based on minimum convex polygons was 4.4 (SE = 0.3, range = 3–6, $n = 14$) and yielded one location per week during the first five weeks of the brood rearing period (30 June–9 August). Our analyses were conducted for established and translocated ptarmigan from a total of 52 and 40 locations, respectively. The home range size of females with broods aged 3–25 days did not differ between established (3.6 ha, SE = 1.6, range = 0.5–10.0 ha, $n = 5$ broods) and recently translocated females (6.7 ha, SE = 2.4, range = 0.5–16.6 ha, $n = 7$ broods, $t = -0.89$, $df = 10$, $P = 0.40$). After hatching, translocated females with broods moved greater distances from the nest site to the center of the brood home range (845 m, SE = 243, range = 171–2,185 m, $n = 8$) than established females attending broods (190 m, SE = 65.2, range = 47–394 m, $n = 6$, $t = -2.27$, $df = 12$, $P = 0.04$). Females with broods moved to higher elevations above the nest site, but the increase in elevation did not differ between established females (mean = +62 m, SE = 21.8, range = 15–157 m, $n = 6$) and translocated females (mean = +108 m, SE = 25, range = 34–233 m, $n = 9$, $t = -1.40$, $df = 13$, $P = 0.19$).

DISCUSSION

Our study provides the first data on the behavior and habitat requirements for a subspecies of Rock Ptarmigan endemic to the Aleutian Islands. We had three major findings, which should aid restoration efforts for other island populations impacted by introduced species of mammals. First, translocated females switched from using low-lying coastal areas of Attu Island to alpine habitats at higher elevations of Agattu Island. Second, newly translocated females selected nest sites in areas adjacent to established females and

their offspring. Ptarmigan nest sites were usually located on the lower third of south-facing slopes that provided sufficient cover from predators and inclement weather for nesting females. Last, brood movements and patterns of habitat use were similar between recently translocated and established females. Translocated females moved greater distances with broods than established females, but all females moved to higher elevations and had home ranges of similar size. Overall, our results indicate that translocated and established female ptarmigan had similar behavior and patterns of movement during early stages of establishment of a new island population.

Nest Site Selection

Translocated females were captured at low-lying tundra areas in the coastal area of Massacre Bay at Attu Island but settled and nested on mountain hillsides and rocky alpine areas at Agattu Island. The change in habitat use may imply a preference for upland habitats by Rock Ptarmigan, or could be due to island differences in environmental conditions, including competition for mates, availability of appropriate nesting sites or food resources, or predator communities (Herzog and Boag 1977, Gratson 1988, Martin et al. 1990). Timing of clutch initiation is normally synchronous in Rock Ptarmigan (Wilson and Martin 2010), but breeding attempts by translocated females were delayed one to two weeks due to capture and handling (Holder and Montgomerie 1993, Kaler et al. 2010). Thus, competition between translocated and established females for mates and nest sites may have been reduced at Agattu. Following onset of incubation by established female ptarmigan, pair bonds and territorial boundaries maintained by female–female aggression may have broken down, and males may have been unconstrained in acquiring second mates (Martin et al. 1990). Sex ratios can be male-biased in Rock Ptarmigan populations (Unander and Steen 1985, Cotter 1999, Holder and Montgomerie 1993), and unmated territorial males may have been available during settlement of translocated females at Agattu.

Our finding that translocated and established ptarmigan preferred higher elevations at Agattu is consistent with early reports of habitat associations of Evermann's Rock Ptarmigan at Attu (Bent 1932, Haflinger and Tobish 1977). Habitat preferences may have developed with exposure to high

densities of introduced foxes at lower-elevation coastal areas of Attu during the past century, and could explain why ptarmigan persisted at Attu but were extirpated from other islands (Ebbert and Byrd 2002). Unander and Steen (1985) argued that lowland coastal areas were not suited for nesting by ptarmigan at Svalbard Island because of late snowmelt and high predation risk. Snow accumulation at low elevations is limited in the Aleutian Islands because of the maritime climate. However, Glaucous-winged Gulls are potential egg and chick predators, and high densities of gulls at coastal areas could have influenced the preferences of female ptarmigan for alpine nesting sites.

If settlement was constrained by competition, we predicted that translocated and established females might select different nesting habitats, but we found no difference in topographic features or amount of nest cover between the two groups. Furthermore, recently translocated and established females sometimes nested in close proximity (<100 m) and used the same ecological factors for nest site selection. The results of our vegetation and habitat analysis at two scales (5-m and 25-m radius) suggested that after locating a larger area of suitable nest habitat, female ptarmigan appear to select nest sites based on microhabitat features of ground and nest cover. Nesting cover used by incubating females may provide concealment from avian predators and protection from inclement weather (Giesen et al. 1980, Wilson and Martin 2008), which can affect embryo development and thermoregulatory costs of incubating females (Webb 1987; Wiebe and Martin 1997, 2000).

In areas with mammalian predators, ptarmigan may select nest sites with cover that balances the trade-off between increasing nest survival while decreasing the risk of mortality for incubating females (Götmark et al. 1995, Wiebe and Martin 1998). Nests of ptarmigan at Agattu were well concealed and typically placed beneath rocks or among thick vegetation, which provided complete cover from visual predators above the nest but could have restricted a female's ability to detect and elude predators. Nest sites of Rock Ptarmigan at Svalbard Island, where arctic foxes are present, were placed in steep and rocky locations that provided a more open view of the surrounding areas (Pedersen et al. 2005). A lack of native terrestrial mammalian predators in the Aleutian

Islands may explain why female Evermann's Rock Ptarmigan select nest sites that provide concealment from avian predators and greater protection from adverse weather conditions. Wilson and Martin (2008) suggested that lateral cover was an important characteristic for nest sites of Rock Ptarmigan at an alpine site in the Yukon, but we found no evidence of selection for such features, possibly because selection criteria for nest sites vary among populations or because our sample of nests was small.

Nest placement could have been influenced by access to food resources determined by seasonal patterns of snow melt. Female ptarmigan at Agattu were sometimes observed feeding on ericaceous food plants <100 m from their nest sites in moist depressions created by late snowmelt. Gardarsson (1988) reported that Rock Ptarmigan in Iceland nested in sites with greater cover that were close to feeding areas with preferred food plants. If females synchronize clutch initiation with snow melt in areas near nests, they could minimize time off the nest by reducing travel time between foraging areas and nest sites, limiting their exposure to predators and increasing nest attendance during incubation (Wiebe and Martin 2000, Yoder et al. 2004). We lacked information on the quality of vegetation in foraging areas, but proximity of areas with good nest concealment to feeding locations may be important for nest site selection among translocated Rock Ptarmigan.

Brood Movements and Home Range Size

Female ptarmigan attending broods at Agattu departed their nesting territories and moved to higher elevations that were 60–100 m above their nesting site, where they remained in a relatively small home range. Translocated females moved greater distances and tended to have larger brood home ranges than established females. Movement of broods to higher elevations likely addresses the nutritional needs of ptarmigan chicks, which feed on arthropods initially but shift their diet to an increasing proportion of plant material as they mature (Spidsø 1980). Greater brood movements were associated with a 1–2-week delay in clutch initiation among translocated females (Kaler et al. 2010), which could have resulted in a phenological mismatch between the timing of hatching and the availability or nutritional quality of arthropods and plants along an elevational gradient. Alternatively,

translocated females may have been forced to select nest sites without regard to locations of brood-rearing habitats, and established females minimized brood movements by familiarity with local areas (Bergerud and Gratson 1988).

Females might be expected to minimize home range size if movements increase the mortality of young by exposing chicks to predators or to inclement weather before the chicks are able to thermoregulate. Our estimates of the size of brood home ranges at Agattu (5.5 ha) are comparable to values for Rock Ptarmigan in the Yukon (≤ 4 ha; Wilson 2008), but larger brood home ranges have been reported from other field studies of Rock Ptarmigan (24 ha, Favaron et al. 2006; 50 ha, Steen and Unander 1985), Willow Ptarmigan (*L. lagopus*; 14 ha, Erikstad 1985; 25–27 ha, Bergerud and Huxter 1969), and White-tailed Ptarmigan (*L. leucurus*; 70 ha, Schmidt 1988). Some variation could be due to estimation technique or number of locations per brood. However, variation could also be due to differences in patterns of space use or ecological conditions. Small home ranges are often associated with a high brood density, and minimal overlap among home ranges of different broods may be evidence of spacing behavior (Erikstad 1985), whereas large home ranges with a high degree of overlap may indicate that food availability is low or patchily distributed (Favaron et al. 2006). Small home ranges of female ptarmigan attending broods at Agattu Island were likely due to a combination of low breeding densities in a newly established population, minimal competition among broods, and high-quality habitats that have not been exploited by ptarmigan since the 1930s. Based on our understanding of ptarmigan distributions at Attu, we predict that low-elevation habitats at Agattu will become occupied in the next decade if the ptarmigan population continues to grow.

Our behavioral data for Evermann's Rock Ptarmigan indicate that translocated birds were able to settle quickly in preferred habitats and had performance similar to established birds. Subsequent population surveys have shown that population numbers have been stable during 2007–2009 after translocations were completed. Translocated birds may survive for several years before the population fails (Woolf et al. 1984), but our evidence for successful settlement, reproduction, and survival are encouraging for persistence of Evermann's Rock Ptarmigan at Agattu Island (Kaler et al. 2010).

A combination of eradication of introduced mammals and translocations should be useful tools for future restoration of island populations of terrestrial birds in the Aleutian Archipelago.

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