RESEARCH ARTICLE

Divergence in an archipelago and its conservation consequences in Aleutian Island rock ptarmigan

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Abstract The identification and assessment of island endemics is a conservation priority. We genotyped 115 rock ptarmigan from five insular populations in the Aleutian-Commander archipelago and two Alaska mainland populations to identify conservation units, assess genetic diversity and gene flow, and to determine whether populations have declined over time. We found four distinct populations that appear to be completely isolated and which correspond closely to recognized subspecies. The most geographically isolated populations also have the lowest genetic diversity. Three populations (Attu Island, Rat Islands, and Adak Island), which each experienced historic introductions of an exotic predator, showed genetic signals of declines, but the timing did not correspond with the introduction. We recommend management of each endemic group as a unique conservation unit.

Keywords Aleutian Islands · Island endemic · Genetic diversity · *Lagopus muta* · Rock ptarmigan

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Introduction

Organisms found on oceanic islands are geographically isolated, often have small populations, and undergo different selection pressures than mainland organisms (Grant 1998). These aspects of island life can lead to endemic populations that are frequently of conservation concern, because they harbor much of the extant genetic variation in widespread species (Wilson et al. 2009) and are on independent evolutionary paths (Grant 1998; Van Dyke et al. 2008). In addition, island endemics are very susceptible to extinctions caused by human activities, such as the introduction of exotic predators (BirdLife International 2000; Frankham et al. 2002; Blackburn et al. 2004). Thus, the identification of island endemics and assessment of the genetic diversity of island populations are a priority for conservation biologists (Van Dyke et al. 2008).

The Aleutian Islands are a high-latitude archipelago that has many phenotypically based endemic populations of landbirds (Gibson and Byrd 2007; Fig. 1). The most geographically variable of these species is the rock ptarmigan (*Lagopus muta*), a holarctic grouse that exhibits limited movement behavior and high levels of subspecific diversity (Gibson and Kessel 1997; Montgomerie and Holder 2008). Researchers using mitochondrial (mt) and nuclear intron sequences have found concordance between these molecular markers and phenotype for some populations, implicating historical isolation in separate refugia during the last glacial maximum (∼20,000 ybp) as the likely cause of endemism (Holder et al. 1999, 2000, 2004; Pruett and Winker 2008a).

The Aleutian Islands are remote and have had little human habitation. However, the avifauna of the Aleutians was impacted by the introduction of arctic foxes (*Alopex lagopus*) during the 1700s (Croll et al. 2005). Native mammals are absent from the majority of the islands,
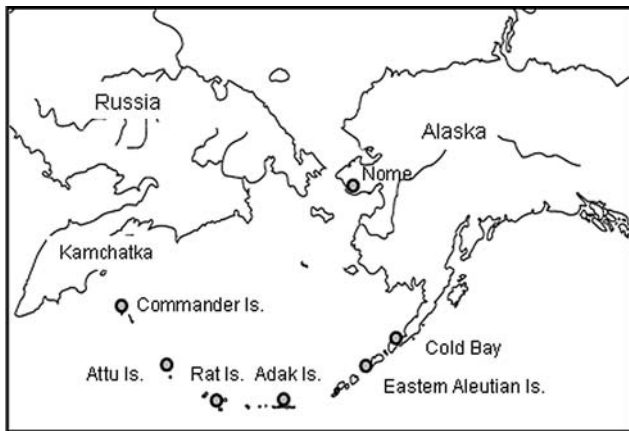
Fig. 1 Map of rock ptarmigan (*Lagopus muta*) populations sampled for this study (1995–2002)

occurring only in a few locations in the eastern Aleutians; thus, the effect of this introduction on a naïve avifauna was detrimental (Gibson and Byrd 2007). Rock ptarmigan populations on islands with foxes likely had population reductions and some localized extinction events (Bailey 1993; Holder et al. 2004). Thus, there were likely to have been several factors—both historic (late-Pleistocene glacial cycles) and more recent (introduction of arctic foxes)—that affected rock ptarmigan and could have caused restricted gene flow and losses in genetic diversity.

At least one population of rock ptarmigan is currently considered by the US Fish and Wildlife Service (USFWS) to be of conservation concern, the Attu Island rock ptarmigan (http://alaskamaritime.fws.gov/whatwedo/bioproject s/restorebiodiversity/ptarmigan.htm). Based on the studies of Holder et al. (1999, 2000), the Attu Island population (*L. m. evermanni*) was considered to be a priority for conservation, because it was found in only one location and appeared to represent an evolutionarily significant unit (Holder et al. 2004). In addition, this population is the most geographically isolated from mainland populations (Fig. 1). The USFWS has recently removed foxes from many Aleutian Islands and also reintroduced ptarmigan from Attu Island to a neighboring island (Agattu) so that more than one population of *L. m. evermanni* is now present in the Aleutians (Kaler 2007).

Previous studies of mtDNA have found low haplotype diversity in some Aleutian populations; however, other populations had higher diversity than mainland Alaska (Holder et al. 2004). Also, gene flow appeared to be restricted among some but not all populations. Whether these patterns were caused by the retention of ancestral polymorphisms or ongoing gene flow is difficult to discern using a single-locus approach, especially when populations have been bottlenecked (Johnson et al. 2007). Here we use multiple microsatellite loci to evaluate the conservation

status of Aleutian rock ptarmigan and to determine whether populations have experienced reductions in size. Specifically, we sought to (1) identify genetically differentiated populations and compare these results with other studies of Aleutian rock ptarmigan (Holder et al. 1999, 2000, 2004) to provide conservation recommendations; (2) assess population genetic diversity; (3) determine levels of contemporary gene flow among populations; and (4) evaluate whether populations have been bottlenecked either recently (e.g., through an introduced predator) or in the past (e.g., through presence in glacial refugia).

Methods

Whole genomic DNA from the tissues of 115 rock ptarmigan collected from seven breeding areas in the Aleutian Islands and neighboring locations (Fig. 1) was extracted using a QIAamp DNA Mini Kit (QIAGEN, Valencia, CA). Ptarmigan were collected and deposited in the University of Alaska Museum between April and November over several years. Collections on Attu Island occurred several years before some birds from that population were translocated to Agattu Island. Collections on the Commander Islands were from Bering Island (n = 4) and Medny Island (n = 10). Six microsatellite loci were amplified for all individuals using fluorescent dye-labeled primers developed for grouse using PCR conditions outlined in Piertney and Dallas (1997; LLSD4, LLST1), Caizergues et al. (2001; TTT1, TTT2, TTD6), and Segelbacher et al. (2000; TUT1). These amplifications were then genotyped using an ABI 3100 automated sequencer.

We performed tests for Hardy-Weinberg equilibrium for all individuals and for linkage disequilibrium between pairs of loci using Arlequin (version 3.11, Excoffier et al. 2005). We used the program MICROCHECKER (van Oosterhout et al. 2004) to test for the presence of null alleles using the methods of Chakraborty et al. (1992) and Brookfield (1996) and to determine whether there was evidence of stuttering and large-allele dropout. Measures of genetic diversity were examined for each population, including average observed heterozygosity (H_O), average unbiased expected heterozygosity (H_E), and allelic richness (A_R; Pruett and Winker 2008b), using Arlequin and FSTAT (Goudet 2002).

Genetic differences between populations (F_{ST}) were also determined using Arlequin. We constructed principal coordinates analysis (PCO) graphs using these pairwise F_{ST} estimates (GenAlEx6; Peakall and Smouse 2006). Principal coordinates analysis is a general ordination technique that can incorporate any distance metric (Gaugh 1982), including genetic ones (principal components analysis is a special case of PCO, in which distances are Euclidean). Our ordination graphs are meant only to provide a heuristic display

of relationships among sampled populations. Associations between $F_{ST}/(1 - F_{ST})$ and log-transformed geographic distances were assessed using simple Mantel tests. We constructed matrices of great-circle distances (http://mathworld.wolfram.com/GreatCircle.html) in kilometers between collection locations. A simple Mantel test was performed using the program zt (Bonnet and Van de Peer 2002), with significance of correlations assessed with 10,000 random permutations of the dependent matrix. Correlation between genetic diversity measures and geographic distance were also examined.

We used a Bayesian clustering approach as implemented in STRUCTURE version 2 (Pritchard et al. 2000; Falush et al. 2003) to examine how well predefined populations corresponded to genetic clusters (K). In this analysis, individual genotypes are assigned to clusters such that Hardy-Weinberg equilibrium and linkage equilibrium are achieved within each cluster. A Markov Chain Monte Carlo approach is used to determine the K that is most likely given the observed genotypes. We ran STRUCTURE three times for each user-defined K (from one to 10 clusters) with an initial burnin of 10^5, followed by 10^6 further iterations on the total dataset. No prior information was used on the population of origin of each individual. We used the admixture model, in which individuals may have mixed ancestry, and the correlations model, which takes into account that closely related populations may have correlated allele frequencies. When the K with the maximum likelihood value was found, the proportion of membership of each predefined population (e.g., Attu Island, Adak Island) within each genetic cluster was determined. To ensure that this was the correct number of clusters, we used the method of Evanno et al. (2005). We performed 10 runs for each K (2–10 clusters) with initial burn-in of 50,000 and 50,000 subsequent iterations for each analysis.

We used an assignment test to infer movement among populations (GENECLASS 2; Piry et al. 2004). When used conservatively, assignment tests have been shown to effectively measure dispersal among populations (Berry et al. 2004). We used the very conservative method outlined by Underwood et al. (2007) to exclude or assign individuals as immigrants using the methods of Rannala and Mountain (1997) and Paetkau et al. (2004). Individuals were excluded from their location of origin when the probability of exclusion was greater than 99% ($\alpha = 0.01$). Individuals excluded from their population of origin were marginally assigned to another sampled population when $P > 0.29$. This probability was chosen based on the lowest mean Bayesian probability for the populations examined and thus represents a very conservative method of identifying immigrants. Individuals not assigned to any population were assumed to be from an unsampled population, because we did not sample the entire distribution of rock ptarmigan.

We examined three populations of rock ptarmigan that were likely to have been affected by the introduction of arctic foxes: Attu Island, Rat Islands, and Adak Island. These three locations do not have native land mammals, unlike the eastern Aleutians, the Commander Islands, and the Alaska mainland. We assessed whether a recent bottleneck ($<4N_e$ generations ago, Cornuet and Luikart 1996) had occurred using the heterozygosity excess method in the program Bottleneck version 1.2.02 (Piry et al. 1999). As suggested by Piry et al. (1999), we simulated equilibrium conditions (1,000 replications) assuming a two-phase model of mutation with 30% multistep mutations and tested for significance using Wilcoxon signed-rank tests. We also examined whether populations had been reduced or had expanded in size using the Bayesian coalescent-based approach in the program MSVAR 1.3 (Beaumont 1999; Storz and Beaumont 2002). We performed three independent runs with different priors using the exponential model for each population. Using information available from long-term studies of rock ptarmigan (Montgomerie and Holder 2008), we used the formula of Sæther et al. (2005) to estimate a generation time of 5 years for the species. The Markov chain was run for 2×10^9 steps with values recorded every 10^5 steps for a total of 20,000 draws from the posterior distribution. If runs gave similar posterior distributions for each parameter, we combined the last 50% of each run for further analysis. The mode of the posterior distribution for current effective population size (N_0), ancestral effective population size (N_1), mutation rate (μ), and time (in years) when a population started to decline or expand (x_a) were determined using the function Locfit (Loader 1996) implemented in R (R Development Core Team, http://www.r-project.org/).

Results

Tests for Hardy-Weinberg equilibrium showed that all loci except for locus TTT2 for Adak Island were in equilibrium after adjustments for multiple comparisons. We found no evidence for the presence of genotyping artifacts such as null alleles, stuttering, or large-allele dropout at any locus. Thus, all loci were used in our analyses. All loci were in linkage equilibrium.

Aleutian and Commander island populations had lower genetic diversity than the mainland locations of Cold Bay and Nome (Table 1; t-test island versus mainland $P < 0.001$ for both H_O and H_E). Rock ptarmigan from Attu Island showed the lowest heterozygosity values, and the Commander Islands had the lowest allelic richness value (Table 1). Strong correlations between genetic diversity (for all three measures; $P < 0.05$) and distance-to-mainland were found when island populations were compared to

Table 1 Genetic diversity values of rock ptarmigan populations in the North Pacific, including average observed heterozygosity (H_O), average unbiased expected heterozygosity (H_E), and allelic richness (A_R)

Location	N	H_O	H_E	A_R
Island[a]	87	0.60 (0.12)	0.80 (0.11)	9.87
Mainland[b]	28	0.84 (0.07)	0.87 (0.05)	12.8
Nome	16	0.88 (0.04)	0.89 (0.04)	8.98
Cold Bay	12	0.79 (0.14)	0.81 (0.11)	7.92
Eastern Aleutians[c]	16	0.78 (0.12)	0.74 (0.09)	5.83
Adak Island	20	0.68 (0.16)	0.75 (0.13)	5.96
Rat Islands	17	0.54 (0.21)	0.62 (0.17)	3.83
Attu Island	20	0.43 (0.31)	0.45 (0.33)	3.29
Commander Islands	14	0.62 (0.23)	0.56 (0.20)	3.21

Standard deviation provided in parentheses

[a] Includes individuals from Eastern Aleutians, Adak Island, Rat Islands, Attu Island, and Commander Islands

[b] Includes individuals from Nome and Cold Bay

[c] Includes individuals from Unalaska Island (4), Islands of Four Mountains (8), and Shumagin Islands (4)

either side of the bracketing continental mainlands: (Kamchatka Peninsula H_O r = 0.59, H_E r = 0.77, A_R r = 0.83; Cold Bay H_O r = −0.66, H_E r = −0.77, A_R r = −0.82). Note that these relationships were positive with increasing distance from Kamchatka and negative with increasing distance from the Alaska Peninsula.

All pairwise F_{ST} estimates were significantly different from zero after Bonferroni correction ($\alpha = 0.0024$, 21 tests), except for Cold Bay and the eastern Aleutian Islands ($F_{ST} = 0.08$, $P = 0.0029$). Some of the highest pairwise estimates of F_{ST} were found between Attu Island and the Commander Islands (0.35) and Attu and the Rat Islands (0.34). This was an unexpected result, given that these populations are geographic neighbors (Fig. 1). This result matches well with the lack of association between geographic distance and genetic divergence (r = 0.063, $P = 0.39$) assessed using a Mantel test.

The most likely number of genetic clusters (K) identified in STRUCTURE analyses using the Evanno et al. (2005) method was seven. Four of the seven clusters corresponded to these sampling locations (clusters 1–4; Table 2): Commander Islands, Attu Island, Rat Islands, and Adak Island. Of the three remaining clusters, cluster 5 corresponded strongly to the eastern Aleutian Islands and marginally to Cold Bay, and clusters six and seven revealed admixture between the mainland locations of Cold Bay and Nome (Table 2). However, using assignment tests, we found that most birds (97%) correctly assigned to their population of origin with one ptarmigan from the eastern Aleutian Islands assigning with high probability to Cold Bay. Two individuals from Nome and one from Cold Bay could not

Table 2 Proportion of membership of individual rock ptarmigan from each predefined population in each genetic cluster from STRUCTURE (version 2; Pritchard et al. 2000; Falush et al. 2003)

Population	Cluster						
	1	2	3	4	5	6	7
Commander Islands	**0.95**	0.01	0.01	0.01	0.00	0.01	0.01
Attu Island	0.01	**0.96**	0.01	0.00	0.00	0.00	0.01
Rat Islands	0.01	0.01	**0.94**	0.01	0.01	0.01	0.01
Adak Island	0.03	0.03	0.00	**0.90**	0.01	0.01	0.02
E. Aleutian Islands	0.02	0.01	0.00	0.01	**0.84**	0.04	0.08
Cold Bay	0.01	0.00	0.02	0.01	**0.44**	0.15	0.37
Nome	0.01	0.01	0.02	0.02	0.06	**0.45**	**0.43**

Numbers in bold indicate the cluster that possesses the highest proportion of genetic membership for each location

be assigned to any sampled population. Thus, recent instances of gene flow appear to be limited even among geographically neighboring populations (Fig. 1).

There was no evidence for a recent population bottleneck ($P > 0.05$) for the three Aleutian Island populations most likely affected by arctic fox introductions in the 1700s (Attu Island, Rat Islands, and Adak Island). These populations appeared to be in mutation-drift equilibrium. We found that these populations did show evidence of past reductions in population size (Fig. 2), but differences among populations in degrees and timing of apparent reductions were pronounced. Attu Island had an ancestral effective size of approximately 25,000 individuals and a current size of approximately 5,000; however, this reduction in size probably began over 20,000 ybp (Fig. 3). Analyses suggested that Adak Island has a current effective population size (N_0) of ∼650 and an ancestral effective size (N_1) of 20,000 with a population reduction that began ∼2,000 ybp, and the Rat Islands had a population reduction that began ∼1,200 ybp with an ancestral effective size of approximately 8,000 and a current effective size of 900 (Figs. 2, 3). Thus, Adak suffered the largest population decline, and it began relatively recently. However, none of the populations had a high likelihood of population declines beginning at the time that foxes were introduced (∼300 ybp; Fig. 3). Attu Island showed the oldest population decrease, which appeared to occur during the last glacial maximum (∼10,000–30,000 ybp; Pielou 1991).
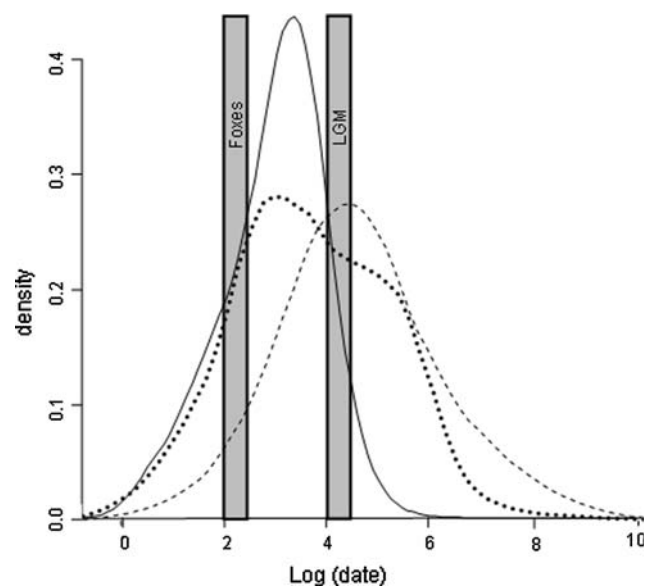
Discussion

Population structure and conservation status

Aleutian Island rock ptarmigan are genetically unique and are on independent evolutionary trajectories. The three most isolated populations, Attu Island, Rat Islands, and Adak
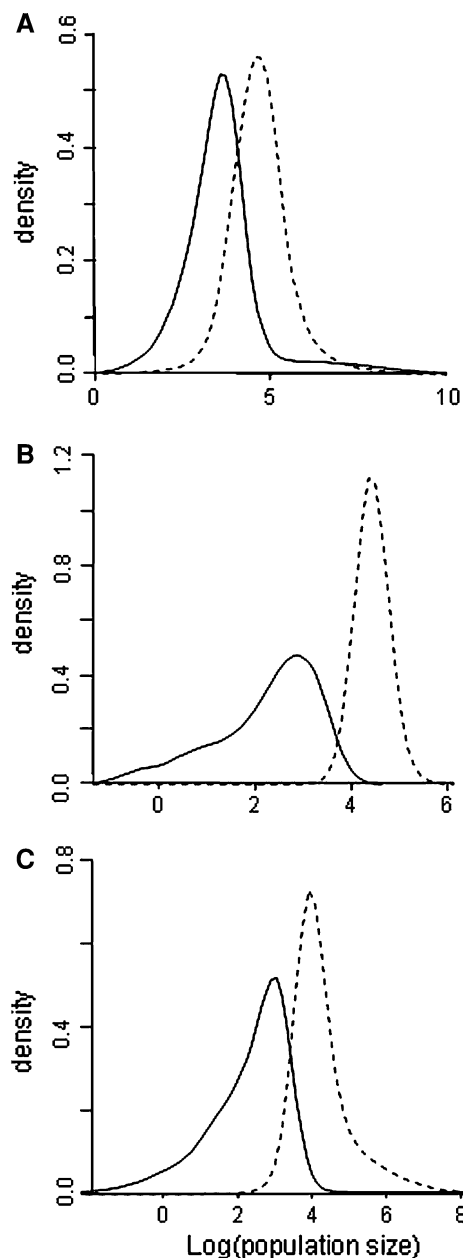
Fig. 2 Current (*solid line*) and ancestral (*dashed line*) effective population size for **a** Attu Island, **b** Adak Island, and **c** Rat Islands

Fig. 3 Time since populations began to decline for Attu Island (*dashed line*), Adak Island (*solid line*), and Rat Islands (*black dotted line*). *Gray areas* represent approximate years before present when arctic fox were introduced to these islands and the timing of the last glacial maximum (LGM)

Island, each form discrete genetic clusters and, based on assignment tests, appear to be completely isolated from other rock ptarmigan. The same appears to be the case with the Commander Island population; this is considered further below. Our findings fit well with the known limited movement behavior of this species (Montgomerie and Holder 2008) and correspond closely with the different phenotypes found on each Aleutian island (Gibson and Kessel 1997). Among the other populations, very limited or no gene flow is likely; however, the mainland locations shared two genetic clusters, and Cold Bay is genetically similar to the eastern Aleutian location (Fig. 1) based on STRUCTURE analyses

(Table 2). Thus, there is likely to be some limited gene flow among these latter three populations.

Holder et al. (1999, 2000, 2004) found concordance between mtDNA haplotypes and the divergent morphologies found on some of the island populations in their study. Our results support their conclusions and provide additional insight into more recent but complete isolation of Aleutian rock ptarmigan. Holder et al. (2004) concluded that Attu Island and Adak Island rock ptarmigan were distinctly different populations, and we concur with these findings. These locations are evolutionarily significant units (ESUs) and should be given high conservation priority; they are genetically differentiated, phenotypically unique (the subspecies *L. m. evermanni* and *atkhensis*; Gibson and Kessel 1997), and isolated from all other rock ptarmigan populations.

We also found that Rat and Commander islands populations (subspecies *L. m. townsendi* and *ridgwayi*, respectively) were distinctly different. This finding is at odds with other studies (Holder et al. 1999, 2000), which could not differentiate these locations from mainland Alaska birds. These different results are likely caused by incomplete lineage sorting in mtDNA. We do not have population-level samples from the Russia mainland and so could not assess the genetics of the Commander Islands population and the neighboring Kamchatka population using microsatellites, but the Commander Islands population is phenotypically distinct from the neighboring mainland form (Stejneger 1884). In a previous study, we sequenced the mtDNA cytochrome *b* gene from some (n = 4) birds from the Commander Islands and found a haplotype that was

different from those found on the Russia (n = 2) and Alaska mainlands (Pruett and Winker 2008a). Although sample sizes from Russia are low, preliminary evidence supports the Commander Islands as being genetically different from other rock ptarmigan. Based on the STRUCTURE analyses and assignment tests, the Rat Islands and Commander Islands are completely isolated from other sampled populations and deserve to be recognized as unique conservation units. The remaining three locations are genetically similar and share the same subspecies status (*L. m. nelsoni*; Gibson and Kessel 1997). However, moderate or high gene flow among these latter locations seems unlikely.

Colonization and isolation

Rock ptarmigan in the Aleutian Islands are not isolated by distance. A simple stepping-stone colonization of the Aleutians from North America after the last glacial maximum, as occurred for another Aleutian landbird, the song sparrow (*Melospiza melodia*; Pruett and Winker 2005), is unlikely. The relationships among populations are difficult to assess, except that mainland populations are closely related to the eastern Aleutian Islands (Fig. 4). In addition, recent colonization from Russia is unlikely. It is possible that dispersal across long distances from unsampled locations could have occurred after the last glacial maximum. However, for several populations this is unlikely because three different genetic marker systems (mtDNA, a nuclear intron, and microsatellite loci) and several phenotypic characters reveal that Attu and Adak islands are differentiated. These differences have not been observed in other rock ptarmigan populations (Holder et al. 1999; Montgomerie and Holder 2008). Rock ptarmigan are a terrestrial landbird and a short-distance disperser (Montgomerie and Holder 2008). Thus, many long-distance colonization events seem improbable.
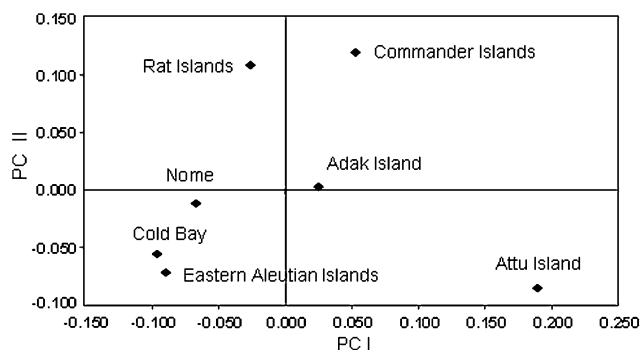
Fig. 4 Principal coordinates analysis calculated using pairwise F_{ST} estimates between populations of rock ptarmigan using the program GenAIEx (Peakall and Smouse 2006). The first two axes explained 89% of variation in the population comparison

By examining both relatively rapidly mutating (microsatellites) and rapidly coalescing markers (mtDNA), we can begin to understand genetic patterns in relation to historical events. Our data fit the prevailing hypothesis of Aleutian rock ptarmigan isolation and divergence: that some populations diverged during the late Pleistocene glacial cycles (Holder et al. 1999; Pruett and Winker 2008a). However, the exact colonization patterns of the Aleutians cannot be determined using either marker system (see also Holder et al. 1999). Isolation occurred long enough ago to limit the usefulness of rapidly mutating microsatellites in determining relatedness among populations, but among all of the sampled populations some have not been isolated long enough for complete lineage sorting within mtDNA (Holder et al. 2004; Pruett and Winker 2008a).

We found strong correlations between island-to-mainland geographic distance and genetic diversity. When genetic diversity was examined in relation to geographic distance from the Alaska Peninsula, the most distant locations had the lowest genetic diversity. The opposite pattern was found in relation to the Kamchatka Peninsula in Russia. Thus, populations that are the most isolated from Alaska have the lowest genetic diversity. This pattern could be associated with founder events wherein populations were colonized from an Alaska source (Pruett and Winker 2005) or subsequent population bottlenecks with less chance of replenishment by gene flow in the most isolated locations. Regardless of the cause, Aleutian and Commander island populations have similar or much lower genetic diversity than Pyrenees rock ptarmigan that are considered to have low diversity (Caizergues et al. 2003; Bech et al. 2009), and Attu Island has approximately one-half to one-third the genetic diversity found on the Alaska mainland. The recent translocation of birds from Attu Island to Agattu Island to increase the number of populations (Kaler 2007) was a sound management decision and will hopefully lead to a greater chance of long-term persistence.

Historic and contemporary effects on population size

Attu Island has a current effective population size of rock ptarmigan that is five times larger than that found on Adak Island or in the Rat Islands. The reason for this disparity is unknown, but it is not linked to island area (893 km², Attu Island; 711 km², Adak Island; 934 km², Rat Islands), and there are no known habitat differences among islands (Gibson and Byrd 2007).

We know of at least two historical events that might have led to population declines, the introduction of arctic foxes to the Aleutian Islands in 1700s and late-Pleistocene glaciations (Gibson and Byrd 2007). However, a signal of a recent population bottleneck was not found, and all of the populations appeared to begin declining before foxes were

introduced. Thus, at least genetically, the effects of arctic fox introductions on rock ptarmigan appear to have been small, which may not have been the case with some seabirds (Bailey 1993; Gibson and Byrd 2007). Rock ptarmigan extirpations that have been linked to foxes apparently occurred only on smaller islands with minimal nesting habitat (Bailey 1993).

The Adak Island and Rat Islands populations showed similar timing in the genetic signals of historic population declines (1,000–2,000 ybp; Fig. 3). Insofar as these populations are geographic neighbors, it is possible that population reductions on these islands were linked to the same event (Fig. 1). Volcanic eruptions and human predation provide two possible explanations. Humans are thought to have colonized the western Aleutians approximately 3,000 ybp, and increased hunting pressures might have negatively affected populations (West et al. 2007). The Aleutians form the northern portion of the "ring of fire" that surrounds the Pacific Ocean; thus, a large eruption could have affected both populations. It is likely that both humans and volcanic eruptions would have affected Attu Island birds; however, Attu rock ptarmigan began declining much earlier than when humans arrived.

We found an association between the Attu Island population decline and the last glacial maximum, but this decline was probably not severe or of long duration. Isolation in a glacial refugium has been suggested to account for differences among populations (Holder et al. 1999, 2004; Pruett and Winker 2008a), and this might have caused populations to decline. An equally plausible explanation is that the reduction in size is associated with the initial founding of the population. This is concordant with the limited genetic diversity of Attu Island rock ptarmigan, and reductions in diversity have been linked to founding events in another Aleutian landbird (Pruett and Winker 2005). In addition, pre-decline effective population sizes for both Adak and Attu islands were considerably larger than what would be expected based on the sizes of these islands and the population density of this species (Johnsgard 1972), implicating founder events from large mainland populations as causing population declines.

Attu and Adak islands had similar historical effective population sizes of ∼20,000 individuals, but Adak Island showed a much smaller current effective population size. Thus, Adak Island rock ptarmigan experienced a more severe population decline than did Attu rock ptarmigan. Ptarmigan populations on Adak and Rat islands showed similar current effective sizes of <1,000 birds. Although these sizes are much smaller than for Attu Island, these values are considered large enough (>500) to limit the chances of inbreeding depression, mutational meltdown, and reduced adaptive potential (Franklin 1980; Frankham et al. 2002; Keller and Waller 2002). Although all of these island populations have declined over time, current sizes seem large enough to be viable over the long term. However, these populations will require continued monitoring because they represent unique conservation units.

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