



Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna

Chris J. Conroy, John R. Demboski and Joseph A. Cook *University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska, 99775-6960, USA, e-mail: chris.conroy@stanford.edu*

Abstract

Aim A large number of studies have analysed the distribution of mammals within archipelagos, yet few have focused on islands that were heavily glaciated and subsequently colonized following deglaciation.

Location We explored the relative effects of island area and isolation on faunal composition based on twenty-three mammalian taxa of twenty-four islands of the Alexander Archipelago, Southeast Alaska.

Methods We used regression of log-transformed variables and several indices of nestedness.

Results These faunas showed significant nested structure using tests of nestedness and regression models. Unlike most landbridge and mainland archipelagos studied previously, isolation appears to be the primary factor determining patterns of species richness.

Main conclusions Colonization ability of particular taxa, rather than extinction, has determined this nested structure. We suggest that other higher latitude archipelagos may show similar historical patterns.

Keywords

Mammals, Alaska, nestedness, islands, colonization.

INTRODUCTION

Investigations of archipelagos have illuminated how communities are assembled (Patterson, 1990; Peck, 1991; Haydon, Radtkey & Pianka, 1993; Brown, 1995) and how factors such as competition, predation, and mutualism affect mammalian species richness (MacArthur & Wilson, 1967; Diamond, 1975). There is growing recognition that historical factors, such as extinction, dispersal events, and independent geographical origins, influence patterns of species richness on archipelagos (Brown & Gibson, 1983; Heaney & Patterson, 1986; Dudley, 1991; Ricklefs & Schluter, 1991).

One pattern, nestedness, is observed in oceanic and lacustrine archipelagos, and occurs when species making up relatively species-poor islands are subsets of the species present on richer islands. This pattern is often seen in continental communities as well and has been of particular interest to biogeographers (May, 1978; Brown & Gibson, 1983; Patterson & Brown, 1991; Lomolino, 1996). Nested subsets usually have a geographic component, such as distance or area, that principally contribute to the structure. For example, as one moves away from a species-rich mainland pool in a landbridge archipelago, fewer species are found on islands and these form smaller, nested

subsets of the mainland biota (Darlington, 1957). Three conditions considered essential in the development of nestedness are comparable biogeographic histories of species, contemporary environments, and hierarchical organization of niche relationships (Patterson & Brown, 1991). Alternatively, communities may be nested due to differences in colonization ability among species (Tilman, 1994; Lomolino, 1996). Nestedness is a common phenomenon (summarized by Cook, 1995), and several distinct mechanisms have been suggested as contributing to nestedness (Patterson & Atmar, 1986; Patterson, 1990; Cutler, 1994; Kadmon, 1995).

Few studies have examined historical processes in north temperate archipelagos that have experienced significant disturbance due to glaciation (but see Lomolino, 1993, 1994). Mammalian species richness in recently deglaciated archipelagos should be determined primarily by colonization events (including periglacial origin of colonizing species, time of arrival, and species-specific colonization abilities), rather than faunal relaxation (i.e. extinction; Patterson, 1990). In such cases, island isolation should be a better predictor than island area of both species richness and species occurrence. The Alexander Archipelago of Southeast Alaska may be classified as landbridge because of the relatively shallower ocean depths

(continental shelf) between islands (Lawlor, 1986). However, it may not be a 'classic' landbridge archipelago because during periods of lowered sea levels (e.g. Wisconsinan) extensive glaciation may have prevented direct connections between the archipelago and mainland populations. Thus, we predict that the archipelago might exhibit patterns commonly observed in oceanic archipelagos (e.g. lower species richness, lower z -value for species/area curve).

Geographic ranges of mammals in north temperate landscapes have fluctuated due to glacial advances and retreats (Hewitt, 1996). These landscapes provide opportunities to study range expansion and contraction within species (phylogeography *sensu* Avise, 1994) and to test models of community assemblage, or the order in which species accumulate. Island archipelagos are excellent candidates for such studies because area, isolation, species richness, and community composition can be measured, though their biological significance is debatable. A recent summary of the distributions of terrestrial mammals of the Alexander Archipelago, Southeast Alaska (MacDonald & Cook, 1996) allowed us to examine the relative and combined contributions of these factors to nestedness in this north temperate archipelago.

MATERIALS AND METHODS

Site Description

Southeast Alaska (54° and 60°N latitude, 130° and 140°W longitude) is a highly fragmented landscape at the northern extreme of the greater Pacific Northwest temperate rainforest belt (Alaback, 1991). More than 20,000 islands, ranging in size from less than one km² to nearly 6000 km² (Prince of Wales), form the Alexander Archipelago (Fig. 1). Inter-island distances in this archipelago range from less than one km to 26 km (from Dall to Forrester), and ocean depths between islands range from less than 50 m (between Kosciusko and Prince of Wales) to deeper than 180 m across major straits. The Coast and Saint Elias mountain ranges effectively isolate the region from interior British Columbia, Yukon Territory, and the remainder of Alaska.

The topography of Southeast Alaska has been shaped by extensive glaciation, the most recent occurring 22,000–17,000 BP (Heusser, 1960; Clague, 1989; Mann & Hamilton, 1995). Most of the region was ice-covered during the last glacial maximum by extensions of the Coast Range ice caps and piedmont glaciers which formed on islands with greater topographic relief (e.g. Admiralty, Baranof, and Prince of Wales—(Blaise, Clague & Mathewes, 1990; Mann & Hamilton, 1995). However, the full extent of glaciation in Southeast Alaska is unclear. Ice-free regions have been documented in some areas of northwestern Southeast Alaska (Mann, 1986), but their role in post-glacial colonization is controversial (MacDonald & Cook, 1996). The extent of isostatic rebound after deglaciation is also unclear (Mann & Hamilton, 1995). Therefore, whether a given species had access to now submerged landbridges during early stages of deglaciation and before major changes in sea levels is speculative (MacDonald & Cook,

1996; but see Byun, Koop & Reimchen, 1997; Heaton, Talbot & Shields, 1996).

Deglaciation of the archipelago began approximately 16,000 years BP, and the region may have achieved its present glacial limits by 13,500–10,000 BP. From the maximum glaciation until approximately 15,000 BP, the region was thought to be devoid of most flora and fauna. Lodgepole pine and alder reached northern Southeast Alaska by 12,500 BP (Cwynar, 1990). Forest similar to the present may have been established by 4000 BP (Peteet, 1986; Cwynar, 1990). River corridors and mountain passes that traverse the Coast and Saint Elias mountain ranges (east-west orientation), and coastal corridors (north-south orientation) allowed floral and faunal recolonization of Southeast Alaska (Fig. 1). The late opening of river corridors has fluctuated due to smaller, localized advances of ice during periods of colder temperatures at 10,300, 5500, 3000 and 100 years BP (Mann, 1986).

Terrestrial mammals of Southeast Alaska may have come from northern refugia (e.g. Beringia) and refugia south of the Laurentide ice sheets (Youngman, 1975; MacDonald & Cook, 1996), including western montane, western coastal, and eastern boreal refugia (Hoffmann, 1981). Swarth (1936) reviewed the origins of the vertebrate fauna of Southeast Alaska and concluded that the assemblage was of recent origin (Holocene), with most species originating from the southern refugia and arriving from the east. Notable exceptions include *Ursus arctos* and *Microtus oeconomus* from Beringia. All taxonomy and nomenclature in this paper follows Wilson & Reeder (1993). The biogeographic history of mammals has been further synthesized by Klein (1965), Heaton *et al.* (1996) and MacDonald & Cook (1996).

Analysis

The terrestrial mammalian fauna of Southeast Alaska consists of fifty-four species (MacDonald & Cook, 1996), but only thirty of these are found on islands of the Alexander Archipelago. Several taxa that are present on islands (*Lontra canadensis*, *Castor canadensis*, and all Chiroptera) were excluded from the analysis because they are volant, or semi-aquatic, or poorly documented. *Ondatra zibethicus* was included because it occurs on relatively few islands and does not appear to disperse as readily as other semi-aquatic mammals (MacDonald & Cook, 1996). A presence/absence matrix for twenty-three species was constructed to determine species richness and test structure among those species in the Alexander Archipelago (Table 1). Species richness, island area (km², Alaska Geographical Society, 1993) and isolation (minimum shore to shore distance (km) from island to mainland, calculated from USGS 1:250,000 quadrangle maps) were tabulated for twenty-four islands. Island isolation is the shortest island to mainland distance, or sum of island to island distances, excluding the distance across islands (e.g. eastern Forrester to western Dall, eastern Dall to western Prince of Wales, eastern Prince of Wales to mainland).

Several statistics were used to test the relationship among independent variables and species occurrence. Because log transformation reduced heteroscedasticity, all analyses used log

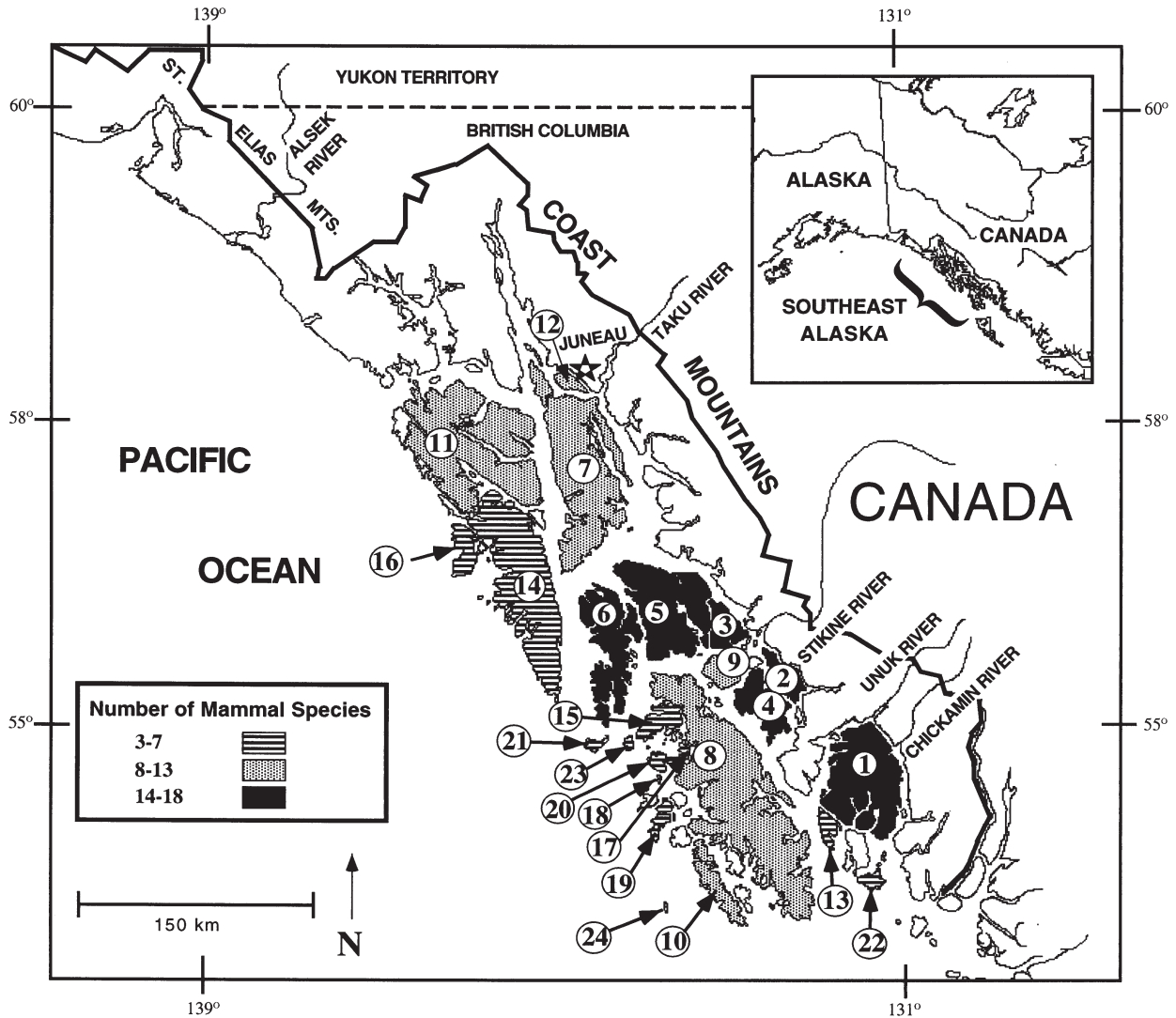


Figure 1 Islands, mainland areas, and major river drainages of Southeast Alaska used in the analysis and discussed in the text. Patterns on islands indicates number of mammal species. The mainland has ≥ 54 species. Unshaded areas were not included in this study. Island numbers refer to Table 1.

transformed variables. A least squares linear regression model was constructed using island area and isolation regressed against species richness (Connor & McCoy, 1979). A least squares regression model with both variables assessed the relative contribution of island area and isolation to species richness. The Mann-Whitney test (Zar, 1974) tested whether islands on which a species is present differ from islands on which it is absent (Patterson, 1984), according to three different rankings. Islands were ranked from: (1) most species to most depauperate, (2) largest to smallest, and (3) closest to mainland to most remote. Different ranking of islands specifically tests which variable contributes most to presence and absence (Kadmon, 1995; Lomolino, 1996). Ranks for equivalent values of species richness (equal numbers of taxa per island) and isolation (rounded to nearest 0.25 km) were averaged (Zar, 1974). Because the distributions of species were not necessarily

independent (e.g. predator/prey interactions), the Mann-Whitney scores for each species were not pooled for an inclusive test of nestedness for the archipelago (Patterson, 1984).

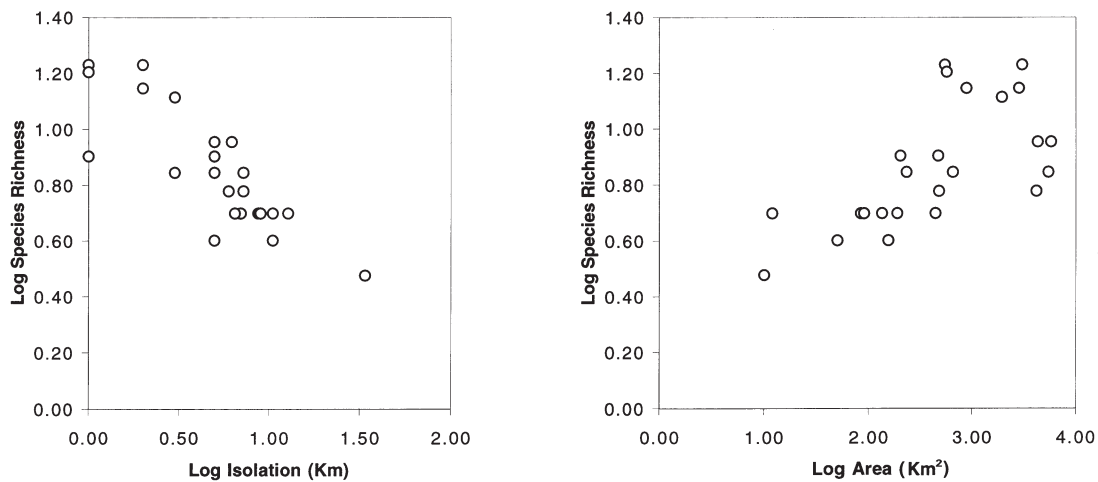
The programs RANDOM0, RANDOM1 (Patterson & Atmar, 1986), and Nestedness 'Temperature' Calculator (Atmar & Patterson, 1995) were used to test the assumption that the presence of species across islands was random. For the RANDOM programs, we used a presence/absence matrix with species ranked in decreasing order of occurrence on islands and islands ranked in decreasing order of species occurrence (Table 1). Extent of departure from perfect nestedness (N index) was calculated by: (1) determining the island having lowest species richness in which species i occurs; (2) examining all richer islands for the presence of species i ; (3) counting the number of absences of species i on richer islands; and (4) summing the counts across all species (Patterson & Atmar,

Table 1 Data matrix used for calculation of nestedness index (N) and raw data for regressions. Species abbreviations are as follows: O. b., *Odocoileus hemionus*; P. k., *Peromyscus keenii*; S. m., *Sorex monticolus*; M. l., *Microtus longicaudus*; M. v., *Mustela vison*; U. am., *Ursus americanus*; C. lu., *Canis lupus*; S. c., *Sorex cinereus*; T. b., *Tamiasciurus bairdianus*; M. a., *Martes americana*; G. s., *Glaucomys sabrinus*; A. a., *Alces alces*; E. d., *Erethizon dorsatum*; G. g., *Gulo gulo*; O. z., *Ondatra zibethicus*; U. ar., *Ursus arctos*; C. g., *Clethrionomys gapperi*; M. o., *Microtus oeconomus*; M. p., *Microtus pennsylvanicus*; S. b., *Symplocorys borealis*; C. la., *Canis latrans*; C. r., *Clethrionomys rutilus*; Z. b., *Zapus hudsonius*. The last three rows are z scores from Mann-Whitney U tests. Boldface values are significant at P<0.05.

| Island Name | No. of species | Iso-lation (km) | Area (km ²) | O. b. | P. k. | S. m. | M. l. | M. v. | U. am. | C. l. | S. c. | T. b. | M. a. | G. s. | A. a. | E. d. | G. g. | O. z. | U. ar. | C. g. | M. o. | M. p. | S. b. | C. la. | C. r. | Z. b. |
|-------------------|----------------|-----------------|-------------------------|--------|-------|--------|--------|--------|--------|--------|--------|---------|--------|--------|--------|--------|--------|--------|--------|---------|--------|---------|--------|--------|--------|--------|
| 1 Revillagigedo | 17 | 2.00 | 3024.2 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 2 Mitkof | 17 | 1.00 | 547.1 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 3 Wrangell | 16 | 1.00 | 569.0 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 4 Etolin | 14 | 2.00 | 889.3 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 5 Kupreanof | 14 | 2.00 | 2822.0 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 6 Kuiu | 13 | 3.00 | 1933.1 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 7 Admiralty | 9 | 5.00 | 4309.7 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 8 Prince of Wales | 9 | 6.25 | 5777.5 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 9 Zarembo | 8 | 5.00 | 472.3 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 10 Dall | 7 | 7.25 | 658.2 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 11 Chichagof | 7 | 5.00 | 5448.9 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 12 Douglas | 8 | 1.00 | 202.6 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 13 Gravina | 7 | 3.00 | 232.9 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 14 Baranof | 6 | 6.00 | 4162.6 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 15 Kosciusko | 6 | 7.25 | 482.2 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 16 Kruzof | 5 | 7.00 | 446.5 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 17 Tuxekan | 5 | 6.50 | 85.2 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 18 Anguilla | 5 | 9.00 | 12.1 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 19 Baker | 5 | 12.75 | 135.0 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 20 Heeeta | 5 | 8.75 | 189.0 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 21 Coronation | 5 | 10.50 | 91.1 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 22 Duke | 4 | 5.00 | 155.3 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 23 Warren | 4 | 10.50 | 50.6 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| 24 Forrester | 3 | 33.75 | 10.1 | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| Occurrence | | | | 0.0485 | — | 0.2546 | 0.0162 | 0.0013 | 0.0037 | 0.0102 | 0.0025 | 0.0002 | 0.0002 | 0.0094 | 0.0001 | 0.0006 | 0.0006 | 0.0018 | 0.4522 | 0.00057 | 0.4801 | 0.0475 | 0.0643 | 0.3336 | 0.0643 | |
| Distance | | | | 0.0485 | — | 0.2946 | 0.3557 | 0.0505 | 0.0183 | 0.0823 | 0.0002 | <0.0001 | 0.0003 | 0.0436 | 0.0014 | 0.0002 | 0.0018 | 0.0104 | 0.5 | 0.00129 | 0.4364 | 0.0951 | 0.0643 | 0.0643 | 0.1401 | |
| Area | | | | 0.0485 | — | 0.0823 | 0.0708 | 0.0091 | 0.1492 | 0.0618 | 0.0110 | 0.1003 | 0.0162 | 0.1075 | 0.0060 | 0.1020 | 0.0475 | 0.0150 | 0.0183 | 0.102 | 0.0239 | 0.11251 | 0.3594 | 0.4129 | 0.3050 | 0.1401 |

Table 2 Results from linear regressions between variables. Statistically significant results (*) are at $P < 0.05$.

| Variables regressed | P | R^2 | Adjusted R^2 | Slope | SE of model |
|------------------------------------|------------------------|-------|----------------|-------|-------------|
| Log distance <i>v.</i> log species | 193×10^{-7} * | 0.716 | 0.703 | -0.49 | 0.12 |
| Log area <i>v.</i> log species | 5×10^{-4} * | 0.43 | 0.426 | 0.18 | 0.17 |
| Log distance <i>v.</i> log area | 0.020* | 0.221 | 0.186 | -0.23 | 0.11 |

**Figure 2** Log transformed plots of species richness against island isolation and island area.

1986). For example, *Sorex monticolus* is present on all the depauperate islands from Forrester to Tuxecan, but is absent from Kruszof, Kosciuszko, and Baranof (Table 1). The N index was also calculated after reordering islands with respect to isolation and area.

RANDOM0 and RANDOM1 calculated values of N for random archipelagos (500 iterations) with the same levels of richness using Monte Carlo simulations (Patterson & Atmar, 1986). RANDOM0 assigns equal probabilities to all taxa, whereas RANDOM1 assigns weighted probabilities to each taxon relative to its proportion in the data set. RANDOM1 is more rigorous and will produce random N scores closer to the observed value than RANDOM0 (Patterson, 1990).

Nestedness 'Temperature' Calculator was also used because its statistic, T , is normalized for the size and shape of the matrix, thus making it comparable to other systems of varying size and shape. A temperature scale (0° – 100°) is used with 0° representing perfect nestedness and 100° representing complete randomness. The program optimally packs the presence/absence matrix, regardless of species or island ranking, and calculates the statistic T . As with the RANDOM programs, random matrices are generated (250 iterations) with the same richness level and a variance is calculated for T . This software also identifies islands and species which detract from nestedness. These idiosyncratic islands and species represent departures from general trends in occurrence and might indicate separate histories for some taxa or islands.

RESULTS

Log transformed regressions (Table 2, Fig. 2) indicated that isolation is a better predictor of mammalian species diversity

($P = 1.93 \times 10^{-7}$, adjusted $R^2 = 0.70$) than island area ($P = 0.0005$, adjusted $R^2 = 0.426$, $z = 0.18$). Island area and isolation were significantly correlated. Both variables were significant in a combined least squares model ($R^2 = 0.80$, $F = 41.59$, $P < 0.001$).

The Mann–Whitney tests provided significant values ($P < 0.05$) for species ranked by occurrence, island area, and island isolation (Table 1). More species displayed significant structure when ordered by isolation (48%, $n = 12$) than by area (39%, $n = 10$). Some taxa, regardless of island ranking, had significant Mann–Whitney results. For example, the occurrence of *Odocoileus hemionus*, *Sorex cinereus*, *Martes americana*, *Ondatra zibethicus*, and *Clethrionomys gapperi* was predicted significantly when islands were ranked by island area and isolation. However, the occurrence of *Peromyscus keeni*, *Synaptomys borealis*, *Canis latrans*, *Clethrionomys rutilus*, and *Zapus hudsonius* was not predicted significantly when islands were ranked with respect to area or isolation. Widespread taxa (e.g. *O. hemionus*, *P. keeni*) or extremely rare taxa (e.g. *C. gapperi*, *Z. hudsonius*) may bias the test. When consistently ranked or unranked taxa were removed, the occurrence of 45% of the species ($n = 5$) was predicted by isolation, and 27% ($n = 3$) by area.

Calculated N for the Alexander Archipelago was 110. Estimated nestedness scores for 1000 random archipelagos from RANDOM0 and RANDOM1 were $N_0 = 371.5$ and $N_1 = 300.0$, respectively (Table 3). Both values were significantly different from the calculated N at $P < 10^{-16}$ and $P = 3 \times 10^{-5}$ for RANDOM0 and RANDOM1, respectively (Table 3). The N index calculated for the archipelago was greater when the matrix was ordered by isolation ($N_I = 111$) or area ($N_A = 156$) than when ordered by richness ($N = 110$). The isolation and area

Table 3 Results from RANDOM0, RANDOM1, and Nestedness Temperature Calculator programs. Calculated N and T do not have associated variances (NA). In the third column are probabilities that a matrix created randomly by RANDOM0, RANDOM1, or Nestedness 'Temperature' Calculator could be more nested than that calculated from the data.

| | Calculated or estimated value | Variance | Probability of finding a more nested system |
|--------------------------------|-------------------------------|----------|---|
| Calculated N (by occurrence) | 110 | NA | |
| Calculated N (by isolation) | 111 | NA | |
| Calculated N (by area) | 156 | NA | |
| RANDOM0 | 371.5 | 192.5 | $P < 10^{-16}$ |
| RANDOM1 | 300.0 | 503.9 | $P = 3 \times 10^{-5}$ |
| Nestedness Temperature (T) | 13.67° | NA | |
| Randomly generated T | 61.76° | 25.3° | 6.79×10^{-22} |

values were significantly different from random ($P < 0.0005$), but cannot be compared to each other because they lack associated variances. The Nestedness 'Temperature' Calculator (Atmar & Patterson, 1995) calculated a temperature of 13.67° (Table 3). The estimated temperature for a random archipelago with the same species diversity was 61.76° ($SD = 5.03^\circ$) and the probability of obtaining a 'colder' matrix was 6.79×10^{-22} . The maximally packed matrix order for islands was significantly correlated with ordering of islands both by area and by isolation ($P < 0.001$). Of the five most idiosyncratic species, two were common (*M. longicaudus* and *S. monticolus*), two were carnivores (*Gulo gulo* and *Canis lupus*), and one colonized from Beringia (*M. oconomus*). Of the six most idiosyncratic islands, four (Baker, Duke, Warren, Forrester) were among the most depauperate islands (occurred at the bottom of the matrix), one was a nearshore island (Zaremba), and one was a distant, medium sized island (Kruzof).

DISCUSSION

Nested structure in archipelagos generally has been attributed to differential extinction and colonization, or a combination of these processes (Patterson, 1990; Kadmon, 1995). Nestedness may also be derived from the nested nature of ecological communities and species niches (Patterson & Brown, 1991; Wright & Reeves, 1992), or may be an artefact of passive sampling from abundant and rare species (Cutler, 1994). Patterson & Atmar (1986) and Patterson (1987, 1990) suggested that differential extinction (i.e. faunal relaxation) was the principal factor determining nestedness on archipelagos in post-glacial assemblages of mammals. Structure due to colonization is thought to be less likely because it requires correlation between colonization probabilities of species and degree of isolation (Patterson, 1987, 1990). Alternatively, colonization or dispersal ability has been suggested to be more important for nestedness under some situations (e.g. woody plants on small islands, Kadmon, 1995; birds on oceanic islands, Ryti & Gilpin, 1987; Patterson, 1990). This overview of the Alexander Archipelago suggests that higher latitude archipelagos (i.e. those subject to glaciation during the Pleistocene) may be nested due to differential colonization. However, other factors need to be tested. For example, increased island area may promote ecological complexity, thus producing nestedness.

More species showed significant occurrence (Mann–Whitney test) by isolation (48%) than by area (39%). Though correlated with island area, island isolation is a better predictor of nestedness. Other landbridge archipelagos influenced by glaciation, either by direct glaciation or loss of habitat from climate related effects (e.g. Japanese, Kuril) may show structure similarly related to isolation and area. Isolation should be the primary predictor in recently colonized systems, and area should be more important in communities that are approaching saturation (Caswell & Cohen, 1993).

The superior performance of isolation as a predictor of species richness is noteworthy. MacArthur & Wilson (1967) suggested that species richness was positively correlated with area and negatively with island isolation; a relationship long recognized (Hesse, Allee & Schmidt, 1937, p. 517; Darlington, 1957, p. 485) and repeatedly corroborated (e.g. Brown & Kodric-Brown, 1977; Lomolino, 1993, 1994; this study). Area affects the probability of persistence for a resident fauna (e.g. by providing more habitat, MacArthur & Wilson, 1967; Cox & Moore, 1993), and the likelihood of colonization (e.g. the 'target area' hypothesis, Lomolino, 1990). Isolation, on the other hand, may be closely tied to colonization abilities of individual species and zoogeographic history of the regional fauna (e.g. differential arrival of species in the region). The isolation index in our study explained more variation in species richness than did area (Table 2). This highly significant relationship between isolation and species richness is consistent with a Late Pleistocene/Holocene arrival of mammals in the Alexander Archipelago.

Archipelagos traditionally are defined as oceanic (e.g. Heaney, 1986; Adler, Austin, & Dudley, 1995), landbridge (e.g. Crowell, 1986; Lomolino, 1994), or mainland (e.g. Brown, 1971; Patterson & Atmar, 1986) based on geologic and/or geographic history. Lawlor (1986) defined islands separated from the mainland by ocean depths greater than 120m as oceanic due to continuous isolation throughout Pleistocene glaciations. However, these categories may overlap. Differences among archipelagos have been identified with characteristic z scores and nestedness statistics (Lawlor, 1986; Cook, 1995). The Alexander Archipelago appears to be closer to the end of the scale (relatively low z score = 0.18) typical for oceanic archipelagos (Lawlor, 1986). Cook (1995) provided data that suggest that mammalian communities on landbridge

archipelagos have lower Nestedness 'Temperature' Calculator temperatures (mean = 17.7°, $n=5$) than oceanic archipelagos (mean = 23.3°, $n=5$). The Alexander Archipelago temperature (13.7°) indicates a landbridge archipelago structure.

Mainland and low latitude landbridge archipelagos are more likely nested than oceanic archipelagos and are often structured by faunal relaxation (Patterson, 1987, 1990). Full complement communities on coastlines became island populations when Late Pleistocene warming induced a rise in sea level. Heaney (1986) demonstrated this effect for mammals on the Philippine Archipelago on the Sunda Shelf. Species richness diminished on these islands due to extinctions. Conversely, the faunas of oceanic archipelagos are often derived from highly vagile mammals from multiple sources. The likelihood that a particular taxon will occur on an oceanic island may differ from those on landbridge islands. That is, as vagility increases, the relationship between area and presence decreases (Lomolino, 1994). Nearshore islands may be colonized by species with low vagility and in the Alexander Archipelago species such as *Zapus hudsonius*, *Clethrionomys gapperi*, *Microtus pennsylvanicus* are found on islands close to the mainland. Throughout their entire range, these species are found on few islands.

Although most of the fauna of the Alexander Archipelago is probably derived from post-glacial colonization, its history has been dynamic since the mid-Pleistocene (Heaton & Grady, 1993; Heaton, 1995; MacDonald & Cook, 1996). Fossils found before and following the last glacial maximum indicate several taxon-island associations that no longer exist (e.g. *U. arctos*, *Marmota caligata* and *Vulpes vulpes* on Prince of Wales; Heaton & Grady, 1993; Heaton, 1995). Brown and black bears may have been sympatric on Prince of Wales in the past, but do not commonly co-occur on any island in the archipelago now. Heaton *et al.* (1996) suggested that brown bears may have persisted in the archipelago throughout the last glacial maximum, though the fossil evidence does not support this conclusion.

The possible persistence of taxa in glacial refugia on or near the Alexander Archipelago warrants further investigation. A refugium to the south has been postulated for eastern Graham Island in the Queen Charlotte Islands (Heusser, 1989) and recently supported by genetic analysis of the three-spined stickleback, *Gasterosteus aculeatus* (O'Reilly *et al.*, 1993). Sea levels greater than 100 m below the current level exposed large areas of sea shore, united the Queen Charlotte Islands, and nearly doubled the area of these islands about 12,000 years ago (Josenhans *et al.*, 1995). Endemic birds and mammals (Foster, 1965; Cowan, 1989), crustaceans (Bousfield, 1958), insects (Kavanaugh, 1980, 1989), and flora (Ogilvie, 1989) are also known from the Queen Charlotte Islands. In the Alexander Archipelago, subalpine fir (*Abies lasiocarpa*) on Dall and Prince of Wales suggests a possible refugium from Late Wisconsin glaciation (Harris, 1965; Heusser, 1989; but see Worley & Jacques, 1973). The large number of endemic taxa in the Alexander Archipelago (MacDonald & Cook, 1996), particularly on outer islands, might be indicative of refugia. However, many of these endemics possess classic 'island effect' characteristics such as larger body size for small mammals (Adler & Levins, 1994). Whether these endemics represent

neoendemics or paleoendemics (*sensu* Myers & Giller, 1988) is currently under investigation.

We have focused on the role of history; however, the contribution of proximate factors, or interactions between species, cannot be dismissed (Patterson & Brown, 1991). Tilman (1994) suggested that community organization after *tabula rasa* conditions may be the result of differences in colonization, competition, and longevity among species. The three largest carnivores in Southeast Alaska, *Ursus americanus*, *U. arctos* and *Canis lupus*, co-occur throughout northwestern North America. Yet, in the Alexander Archipelago, *Ursus arctos* occurs on islands north of Frederick Sound, while *U. americanus* and *C. lupus* occur only on islands south of Frederick Sound. All three species are found on the mainland (MacDonald & Cook, 1996). These disjunct distributions suggest that competition may play a role in species sorting on some islands. Similarly, the two most common shrews in Southeast Alaska, *S. cinereus* and *S. monticolus*, co-occur on the mainland and several near-shore islands, but not on large islands such as Admiralty, Baranof, Chichagof and Prince of Wales (MacDonald & Cook, 1996). Both species are similar in body size and may competitively exclude each other on islands (Hanski, 1994). Species of *Microtus* are also largely exclusive and agonistic behaviour may play a role in such spatial segregation (Colvin, 1973). *Microtus longicaudus* is the most common species of *Microtus* on the mainland and the only species on most islands, with the apparent exception of Baranof Island (*M. oeconomus*) and Kadin (*M. pennsylvanicus*). Whether these disjunct distributions are due to historical or recent ecological interactions is unclear. In contrast, *M. longicaudus* and *M. oeconomus* are known from Chichagof, while *M. longicaudus* and *M. pennsylvanicus* co-exist on Mitkof and Admiralty islands.

Heterogeneous distributions, complex colonization history, and potential for refugia in Southeast Alaska suggest readily testable hypotheses of the history and relationships among populations. DNA sequence data from the mitochondrial cytb gene (Demboski, Jacobsen & Cook, 1998; CJC, JRD, JAC, K. Stone unpublished) indicate different phylogeographic histories for individual species. For example, though *M. longicaudus* is widespread across the archipelago and mainland, a genetic break exists between an island (and north coast) clade and a clade consisting of most mainland populations, including interior British Columbia and Alaska. This break suggests at least two waves of colonization into the region. Other species (e.g. *S. monticolus*, *Martes americana*, *U. arctos*) show large phylogeographic breaks, but along different geographic lines. Recent molecular work (Byun *et al.*, 1997; Wooding & Ward, 1997) has supported the distinction of northwest coast black bear (*U. americanus*), though the precise location of a refugium is unclear.

CONCLUSIONS

The Alexander Archipelago displays a nested structure primarily due to differential colonization following glacial retreat, not faunal relaxation. The relationship between species richness, island area, and island isolation reflects post-glacial

movement of taxa onto nearshore islands, regardless of area. This result differentiates the archipelago from many commonly studied mainland and landbridge archipelagos structured primarily by faunal relaxation. The region provides a promising opportunity to examine the different colonization histories of taxa and to examine both evolutionary and ecological aspects of a developing fauna. Phylogeographic research into the colonization history of individual species with differing origins should shed light upon the histories of subsets of islands. Although we have begun to identify the historical contribution to species richness, additional work remains to illuminate proximate influences such as competition, predation, and parasitism in ecologically similar taxa. A combination of ecological and phylogeographic studies will help build a cohesive explanation for both community and species specific patterns in this and other recently colonized archipelagos.

ACKNOWLEDGMENTS

We thank S. O. MacDonald for his contributions to fieldwork and for his encouragement in this project. Several agencies (USDA Forest Service, US Fish & Wildlife Service, National Park Service, and Alaska Department of Fish & Game) assisted fieldwork with logistical and financial support. E. Rexstad provided advice on the statistical methods. Special thanks to R. Dial, B. Patterson and M. Lomolino for constructive criticism and suggestions.

REFERENCES

- Adler, G.H. & Levins, R. (1994) The island syndrome in rodent populations. *Quart. Rev. Biol.* **69**, 473–490.
- Adler, G.H., Austin, C.C. & Dudley, R. (1995) Dispersal and speciation of skinks among archipelagos in the tropical Pacific Ocean. *Ecol. Ecol.* **9**, 529–541.
- Alaback, P. (1991) Comparative ecology of temperate rainforests of the Americas along analogous climatic gradients. *Rev. Chil. Hist. Nat.* **64**, 399–412.
- Alaska Geographic Society (1993) *Southeast Alaska* (ed. by P. Remick). Volume 20, No. 2. Alaska Geographical Society, Anchorage, Alaska.
- Atmar, J.W. & Patterson, B.D. (1995) *The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices*. AICS Research, Inc., University Park, NM, and The Field Museum, Chicago.
- Avise, J.C. (1994) *Molecular markers, natural history and evolution*. Chapman & Hall, New York.
- Blaise, B., Clague, J.J. & Mathewes, R.W. (1990) Time of the late Wisconsin glaciation, west coast of Canada. *Quat. Res.* **34**, 282–295.
- Bousfield, E.L. (1958) Fresh-water amphipod crustaceans of glaciated North America. *Can. Field-Nat.* **72**, 55–113.
- Brown, J.H. (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *Am. Nat.* **105**, 467–478.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H. & Gibson, A.C. (1983) *Biogeography*. C.V. Mosby Company, St. Louis.
- Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.
- Byun, S.A., Koop, B.F. & Reimchen, T.E. (1997) North American black bear mtDNA phylogeography: implications for morphology and the Haida Gwaii glacial refugium controversy. *Evolution*, **51**, 1647–1653.
- Caswell, H. & Cohen, J.E. (1993) Local and regional regulation of species-area relations: a patch-occupancy model. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R. E. Ricklefs and D. Schluter), pp. 99–107. University of Chicago Press, Chicago.
- Clague, J.J. (1989) Cordilleran ice sheet. *Quaternary Geology of Canada and Greenland, No. 1* (ed. by R.J. Fulton), pp. 40–42. Geological Survey of Canada, Geology of Canada.
- Colvin, D.V. (1973) Agonistic behaviour in males of five species of voles *Microtus*. *Anim. Behav.* **21**, 471–480.
- Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species-area relationship. *Am. Nat.* **113**, 791–833.
- Cook, R.R. (1995) The relationship between nested subsets, habitat subdivision, and species diversity. *Oecologia*, **101**, 204–210.
- Cowan, I.M. (1989) Birds and mammals on the Queen Charlotte Islands. *The outer shores* (ed. by G.G.E. Scudder and N. Gessler), pp. 175–186. Queen Charlotte Islands Museum Press, Skidgate, British Columbia.
- Cox, C.B. & Moore, P.D. (1993) *Biogeography: an ecological and evolutionary approach*, 5th edn. Blackwell Scientific Publications, Oxford.
- Crowell, K.L. (1986) A comparison of relict versus equilibrium models for insular mammals of the Gulf of Maine. *Biol. J. Linn. Soc.* **28**, 37–64.
- Cutler, A.H. (1994) Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. *Landscape Urban Plann.* **28**, 73–82.
- Cwynar, L.C. (1990) A late Quaternary vegetation history from Lily Lake, Chilkat Peninsula, southeast Alaska. *Can. J. Bot.* **68**, 1106–1112.
- Darlington, P.J. (1957) *Zoogeography, the geographical distribution of animals*. Wiley, New York.
- Demboski, J.R., Jacobsen, B.K. & Cook, J.A. (1998) Implications of cytochrome b sequence variation for biogeography and conservation of northern flying squirrels (*Claucomus sabrinus*) of the Alexander Archipelago. *Canadian Journal of Zoology* **76**, 1771–1777.
- Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 316–331. Harvard University Press, Cambridge.
- Dudley, E.C. (1991) *The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology, Vol. 1*. Dioscorides Press, Portland, Oregon.
- Foster, J.B. (1965) *The evolution of the mammals of the Queen Charlotte Islands, British Columbia*. British Columbia Provincial Museum Occasional Papers, **14**, 1–130.
- Hanski, I. (1994) Population biological consequences of body size in *Sorex*. *Advances in the biology of shrew* (ed. by J.F. Merritt, G.L. Kirkland, Jr and R.K. Rose) pp. 15–26. Carnegie Museum of Natural History Special Publication No. 18, Pittsburgh.
- Harris, A.S. (1965) Subalpine Fir on Harris Ridge near Hollis, Prince of Wales Island, Alaska. *Northwest Sci* **39**, 123–128.
- Haydon, D., Radtkey, R.R. & Pianka, E.R. (1993) Experimental biogeography: interactions between stochastic, historical, and ecological processes in a model archipelago. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 117–133. University of Chicago Press, Chicago.
- Heaney, L.R. (1986) Biogeography of mammals in Southeast Asia: estimates of rates of colonization, extinction and speciation. *Biol. J. Linn. Soc.* **28**, 127–165.
- Heaney, L.R. & Patterson, B.D. (1986) *Island biogeography of mammals*. Academic Press, Inc., London.

- Heaton, T.H. (1995) Middle Wisconsin bear and rodent remains discovered on Prince of Wales Island, Alaska. *Curr. Res. Pleist.* **12**, 92–94.
- Heaton, T.H. & Grady, F. (1993) Fossil grizzly bears (*Ursus arctos*) from Prince of Wales Island, Alaska, offer new insights into animal dispersal, interspecific competition, and age of deglaciation. *Curr. Res. Pleist.* **10**, 98–100.
- Heaton, T.H., Talbot, S. & Shields, G.F. (1996) An Ice Age refugium for large mammals in the Alexander Archipelago, southeastern Alaska. *Quat. Res.* **46**, 1–8.
- Hesse, R., Allee, W.C. & Schmidt, K.P. (1937) *Ecological animal geography*. John Wiley & Sons, New York.
- Heusser, C.J. (1960) Late-Pleistocene environments of North Pacific North America. *American Geographical Society, Miscellaneous Publication*, **35**, 1–308.
- Heusser, C.J. (1989) North Pacific coastal refugia—the Queen Charlotte Islands in perspective. *The outer shores*, pp. 91–106. Queen Charlotte Islands Museum Press, Skidgate, British Columbia.
- Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* **58**, 247–276.
- Hoffmann, R.S. (1981) Different voles for different holes: environmental restrictions on refugial survival of mammals. *Evolution today, Proceedings of the second international congress of systematic and evolutionary biology*, (ed. by G.G.E. Scudder and J.L. Reveal) pp. 25–45. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pennsylvania.
- Josenhans, H.W., Fedje, D.W., Conway, K.W. & Barrie, J.V. (1995) Post glacial sea levels on the Western Canadian continental shelf: evidence for rapid change, extensive subaerial exposure, and early human habitation. *Mar. Geol.* **125**, 73–94.
- Kadmon, R.N. (1995) Nested species subsets and geographic isolation: a case study. *Ecology*, **76**, 458–465.
- Kavanaugh, D.H. (1980) Insects of Western Canada, with special reference to certain Carabidae (Coleoptera): present distribution patterns and their origins. *Can Entomol.* **112**, 1129–1144.
- Kavanaugh, D.H. (1989) The ground-beetle (Coleoptera: Carabidae) fauna of the Queen Charlotte Islands. *The outer shores* (ed. by G.G.E. Scudder and N. Gessler), pp. 131–146. Queen Charlotte Islands Museum Press, Skidgate, British Columbia.
- Klein, D.R. (1965) Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. *Arctic*, **18**, 7–20.
- Lawlor, T.E. (1986) Comparative biogeography of mammals. *Biol. J. Linn. Soc.* **28**, 99–125.
- Lomolino, M.V. (1990) The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos*, **57**, 297–300.
- Lomolino, M.V. (1993) Winter filtering, immigrant selection and species composition of insular mammals of Lake Huron. *Ecography*, **16**, 24–30.
- Lomolino, M.V. (1994) Species richness of mammals inhabiting near-shore archipelagoes: area, isolation, and immigration filters. *J. Mammal.* **75**, 39–49.
- Lomolino, M.V. (1996) Investigating the causality of nestedness of insular communities: selective immigrations or extinctions. *J. Biogeogr.* **23**, 699–703.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Monographs in Population Biology, Princeton University Press, New Jersey.
- MacDonald, S.O. & Cook, J.A. (1996) The land mammal fauna of southeast Alaska. *Can Field-Nat.* **110**, 571–599.
- Mann, D.H. (1986) Wisconsin and holocene glaciation of southeast Alaska. *Glaciation in Alaska: the geologic record* (ed. by T.D. Hamilton, K.M. Reeder and R.M. Thorson). Alaska Geologic Society Report.
- Mann, D.H. & Hamilton, T.D. (1995) Late Pleistocene and Holocene paleoenvironments of the North Pacific Coast. *Quat. Sci. Rev.* **14**, 449–471.
- May, R.M. (1978) The evolution of ecological systems. *Sci. Am.* **239**, 160–175.
- Myers, A.A. & Giller, P.S. (1988) Biogeographic patterns. *Analytical biogeography: an integrated approach to the study of animal and plant distributions* (ed. by A.A. Myers and P.S. Giller), pp. 15–22. Chapman and Hall, New York.
- Ogilvie, R.T. (1989) Disjunct vascular flora of Northwestern Vancouver Island in relation to the Queen Charlotte Islands. *The outer shores* (ed. by G.G.E. Scudder and N. Gessler), pp. 127–130. Queen Charlotte Islands Museum Press, Skidgate, British Columbia.
- O'Reilly, P., Reimchen, T.E., Beech, R. & Strobeck, C. (1993) Mitochondrial DNA in *Gasterosteus* and Pleistocene glacial refugium on the Queen Charlotte Islands, British Columbia. *Evolution*, **47**, 678–684.
- Patterson, B.D. (1984) Mammalian extinction and biogeography in the southern Rocky Mountains. *Extinctions* (ed. by M.H. Nitecki), pp. 247–293. University of Chicago Press, Chicago.
- Patterson, B.D. (1987) The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* **1**, 323–334.
- Patterson, B.D. (1990) On the temporal development of nested subset patterns of species composition. *Oikos*, **59**, 330–342.
- Patterson, B.D. & Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.* **28**, 65–82.
- Patterson, B.D. & Brown, J.H. (1991) Regionally nested patterns of species composition in granivorous rodent assemblages. *J. Biogeogr.* **18**, 395–402.
- Peck, S.B. (1991) The Galapagos archipelago, Ecuador: with an emphasis on terrestrial invertebrates, especially insects; and an outline for research. *The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology, Vol. 1*. (ed. by E.C. Dudley), pp. 319–336. Dioscorides Press, Portland, Oregon.
- Petee, D.M. (1986) Vegetational history of the Malaspina Glacier District. *Quat. Res.* **25**, 100–120.
- Ricklefs, R.E. & Schluter, D. (1991) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.
- Ryti, R.T. & Gilpin M.E. (1987) The comparative analysis of species occurrence patterns on archipelagos. *Oecologia*, **73**, 282–287.
- Swarth, H.S. (1936) Origins of the fauna of the Sitkan District, Alaska. *Proc. Calif. Acad. Sci.* **23**, 59–78.
- Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.
- Wilson, D.E. & Reeder, D.M. (1993) *Mammal species of the world: a taxonomic and geographical reference*, 2nd edn. Smithsonian Institution Press, Washington.
- Wooding, S. & Ward, R. (1997) Phylogeography and Pleistocene evolution in the North American black bear. *Mol. Biol. Evol.* **14**, 1096–1105.
- Worley, I.A. & Jacques, D. (1973) Subalpine Fir (*Abies lasiocarpa*) in coastal Western North America. *Northwest Sci.* **47**, 265–273.
- Wright, D.H. & Reeves, J.H. (1982) On the meaning and measurement of nestedness of species assemblages. *Oecologia*, **92**, 416–428.
- Youngman, P.M. (1975) *Mammals of the Yukon Territory*. National Museums of Canada, Ottawa, Publications in Zoology, **10**, 1–92.
- Zar, J.H. (1974) *Biostatistical analysis*, pp. 109–114. Prentice-Hall, Inc, Englewood Cliffs, New Jersey.

BIOSKETCHES

This paper is an extension of the authors' ongoing molecular research interests in the evolution, historical biogeography and conservation biology of mammals. **Chris Conroy** is currently a postdoctoral associate at Stanford University. He investigated phylogeography and speciation of arvicoline rodents at the University of Alaska. **John Demboski** is a Ph.D candidate in the Biochemistry and Molecular Biology Program, researching phylogeography and evolution of leporids, soricids, and sciurids. **Joseph Cook** is an associate professor in the Biology and Wildlife Department at UAF and Curator of Mammals at the University of Alaska Museum. His research interests include zoogeography and conservation biology of Alaska mammals. He also studies speciation and chromosomal evolution in subterranean rodents. Other investigators in our laboratory are studying molecular systematics of various arctic and subarctic vertebrates.