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The Great Basin is a vast region of western North America characterized by island-like mountain ranges surrounded by desert basins. Boreal mammals (mammals found only in the mountains and/or far north) living on Great Basin mountaintops have long been portrayed as isolated relicts from the last ice age, ~10,000 years ago, when boreal habitats extended into the basins. We tested whether boreal mammals in the Great Basin are truly isolated by studying patterns of genetic variation in ten populations of a representative species, the yellow-bellied marmot (*Marmota flaviventris*). Our results indicate that marmots move and exchange genes among Great Basin ranges.

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**MARMOTS ON GREAT BASIN MOUNTAINTOPS: USING GENETICS TO TEST A BIOGEOGRAPHIC PARADIGM**

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**Abstract.** Boreal mammals in the Great Basin have long been viewed as island-bound Pleistocene relicts because they occupy island-like patches of montane habitat separated by desert lowlands that presumably are impermeable to dispersal. Recent work, however, raised the possibility that dispersal among mountain ranges is an important process in the biogeography of boreal mammals in the Great Basin. We test this proposition using genetic variation in a representative species, the yellow-bellied marmot (*Marmota flaviventris*). A total of 332 marmots was sampled from 10 ranges and genotyped at six microsatellite loci. If the intervening desert lowlands are impermeable barriers to dispersal, then there should be no relationship between genetic distance and geographic distance among mountaintop populations, and genetic diversity should be diminished because gene flow would not be available to replace alleles lost over thousands of generations of isolation. Our results did not support these predictions. There was a strong correlation between genetic and geographic distance, demonstrating an isolation-by-distance pattern, and genetic diversity was high. Our results suggest that marmot populations in the Great Basin may be linked by dispersal, providing a mechanism to replenish genetic variation lost by drift. However, global climate change over the next several decades could make the desert lowlands more difficult to traverse, eventually transforming the boreal faunas of Great Basin mountaintops into the isolated relicts they were originally portrayed to be.

**Key words:** biogeography; boreal; dispersal; gene flow; Great Basin USA; habitat islands; *Marmota flaviventris*; microsatellites.

**INTRODUCTION**

The equilibrium theory of island biogeography (MacArthur and Wilson 1967) has been one of the most influential models in ecology. Originally developed to explain species richness on oceanic archipelagos, the model subsequently was extended to "habitat islands" (habitat fragmented into patches) and has provided an important conceptual basis for species conservation and reserve design (Shafer 1990, Cornelius et al. 2000).

One of the first applications of the model to habitat islands was Brown's (1971) study of boreal mammal distributions in the Great Basin of western North America, where island-like mountain ranges are surrounded by "seas" of desert scrublands (see Plate 1). These habitat islands are the remnants of a once contiguous network of montane life zones present during the late Pleistocene; because of climatic warming during the Holocene, desert scrublands spread throughout the lowlands, montane habitats contracted, and mountaintop populations of boreal mammals began to dwindle and go extinct, resulting in the relatively impoverished (i.e.,

relaxed) fauna that exists now (Grayson 1993). Brown (1971) found that distributions of boreal mammals on Great Basin mountain ranges were incongruent with MacArthur and Wilson's model, in which a balance between immigration and extinction produces an equilibrium level of species richness. For example, geographic isolation (distance to nearest colonization source) was not related to species richness, which Brown attributed to a lack of between-range immigration. Hence Brown (1971) proposed a "nonequilibrium" model, in which the arid scrublands separating mountaintop habitats pose an insurmountable barrier to immigration in boreal mammals, resulting in extinction without recolonization since the end of the Pleistocene.

Subsequent research, however, showed that some mammals thought to be extinct on certain mountain ranges were indeed present, suggesting that extinction was overestimated or between-range dispersal (i.e., recolonization) has occurred (Lawlor 1998, Grayson and Madsen 2000). Furthermore, using updated data on species distributions, Lawlor (1998) found a much weaker relationship between mountaintop area and species richness than did Brown, suggesting that mammalian distributions cannot be explained by extinction alone, without recolonization.

Thus, the question of whether dispersal plays a significant role in the biogeography of boreal mammals

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