Great Basin Naturalist

Volume 49 | Number 3 Article 13

7-31-1989

Role of post-Pleistocene dispersal in determining the modern distribution of Abert's squirrel

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ROLE OF POST-PLEISTOCENE DISPERSAL IN DETERMINING THE MODERN DISTRIBUTION OF ABERT'S SQUIRREL

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ABSTRACT.—Abert's squirrel is a forest-dwelling mammal, dependent upon ponderosa pine, that now ranges from southern Wyoming to northern Mexico. During the late Pleistocene, ponderosa pine and this squirrel occurred no further north than central Arizona and New Mexico. In consequence, the present range of the squirrel north of the 36th parallel must have been the result of post-Pleistocene (Holocene) dispersal. If such dispersal took place after the fragmentation of the northern montane conifer forest, at least some leakage across barriers of unsuitable (non-ponderosa pine) habitat must have occurred. Dispersal following transplanting "experiments" has shown that such barriers can be crossed; other evidence is provided that suggests this may occur sufficiently often to produce significant changes in distribution within short periods of time. Thus, explanations for the distribution of Abert's squirrel, based only on historical legacy and local extinctions, are found to be insufficient. An alternative explanation is proposed in which post-Pleistocene dispersal also plays an important role.

The present distribution of the Abert's squirrel, *Sciurus aberti*, extends discontinuously from northern Mexico to southern Wyoming (Fig. 1). These disjunct populations have been thought to be Pleistocene relicts (McKee 1941). Presumably, during the late Pleistocene Abert's squirrel was widely distributed throughout a vast coniferous forest. With Holocene aridity, this forest, with its Abert's squirrel component, fragmented and retreated to higher elevations. Supposedly, since this arboreal squirrel is restricted to coniferous forests, dispersal across the resulting woodland gaps was impossible. In consequence, the squirrel was thought to be a helpless prisoner of geography (Goldman 1928, Turbak 1987a) and of a fragmented post-Pleistocene forest (McKee 1941); the distribution since the Pleistocene could only be influenced by local extinction.

However, a study of presence and absence showed a distributional pattern for Abert's squirrel that was consistent with one influenced strongly by dispersal (Fig. 2). In consequence, the traditional historical legacy explanation for the present distribution of Abert's squirrel now requires reexamination.

SQUIRREL DEPENDENCE ON PONDEROSA PINE

While individual Abert's squirrels are occasionally observed in pinyon pine (*Pinus edulis*) woodland, Douglas-fir (*Pseudotsuga menziesii*) and spruce-fir (*Picea-Abies*) habitats (Nash and Seaman 1977, Brown 1984, Hoffmeister 1986), numerous studies have shown that reproducing populations are restricted to forests dominated by ponderosa pine (*Pinus ponderosa*) (Rasmussen 1941, Keith 1965, Patton and Green 1970, Patton 1975, Rasmussen et al. 1975, Stephenson 1975, Pederson et al. 1976, Stephenson and Brown 1980, Hall 1981, Brown 1984, Pederson and Welch 1985). Dependence on a base of ponderosa pine is a characteristic trait of the species and occurs in each of the now geographically isolated populations (compare Figs. 1 and 3).

With the reasonable assumption (Wettstein and States 1986) that there have never been any unique populations of Abert's squirrel capable of reproduction and continued survival in the absence of ponderosa pine (and which later independently developed the ponderosa pine dependency now characteristic of the entire species), we can be confident that this squirrel has never ranged beyond the geographical limits of the distribution of ponderosa pine.

HISTORY OF THE DISTRIBUTION OF PONDEROSA PINE AND ABERT'S SQUIRREL IN THE SOUTHWESTERN UNITED STATES

Ponderosa pine has had a long and complex

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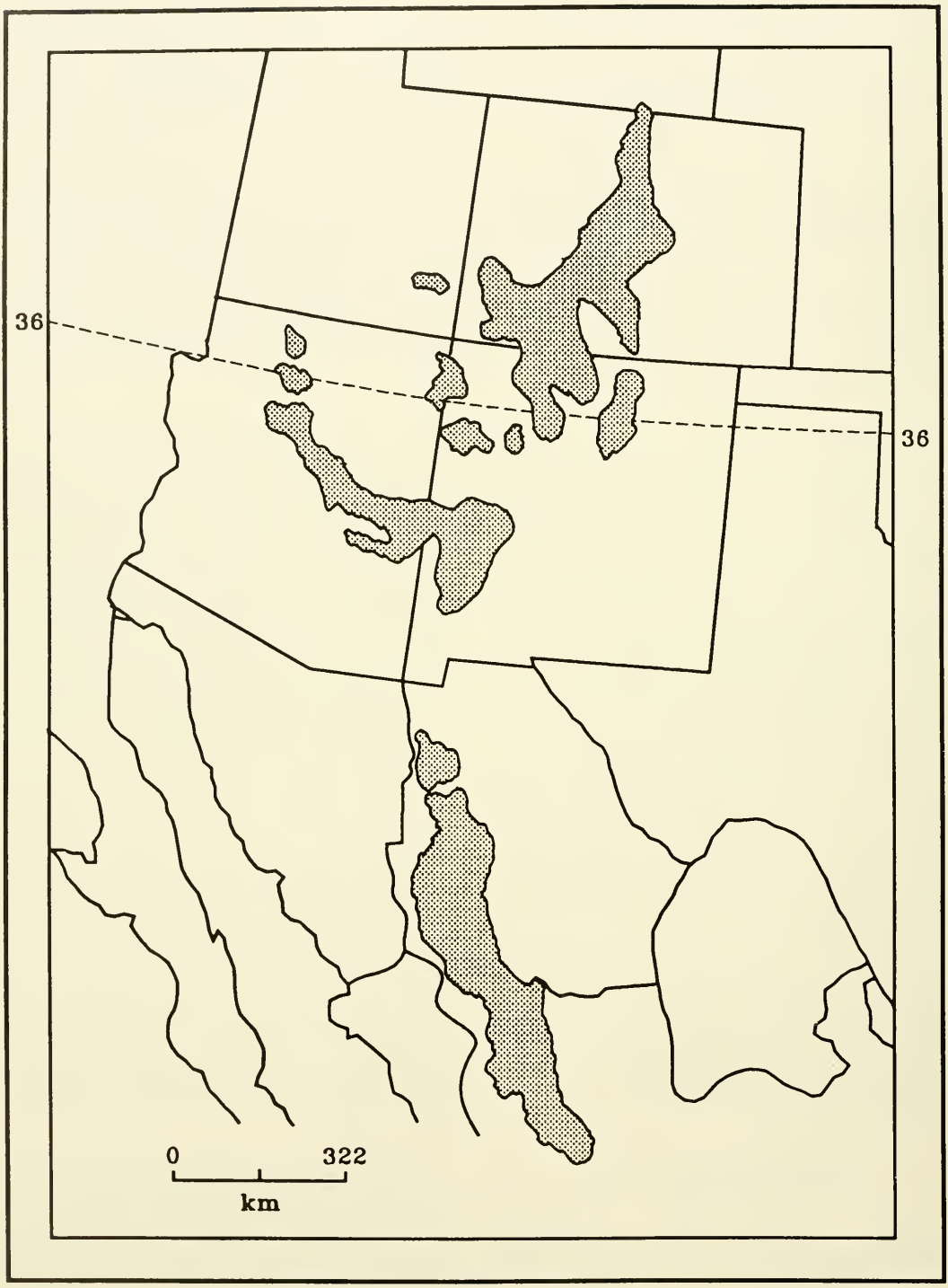

Fig. 1. The modern distribution of Abert's squirrel (modified from Hoffmeister and Diersing 1978, Brown 1984, and Davis and Bissell 1989). The dashed line for 36° North latitude designates the northern limit of ponderosa pine in late Pleistocene. Introductions are not included.

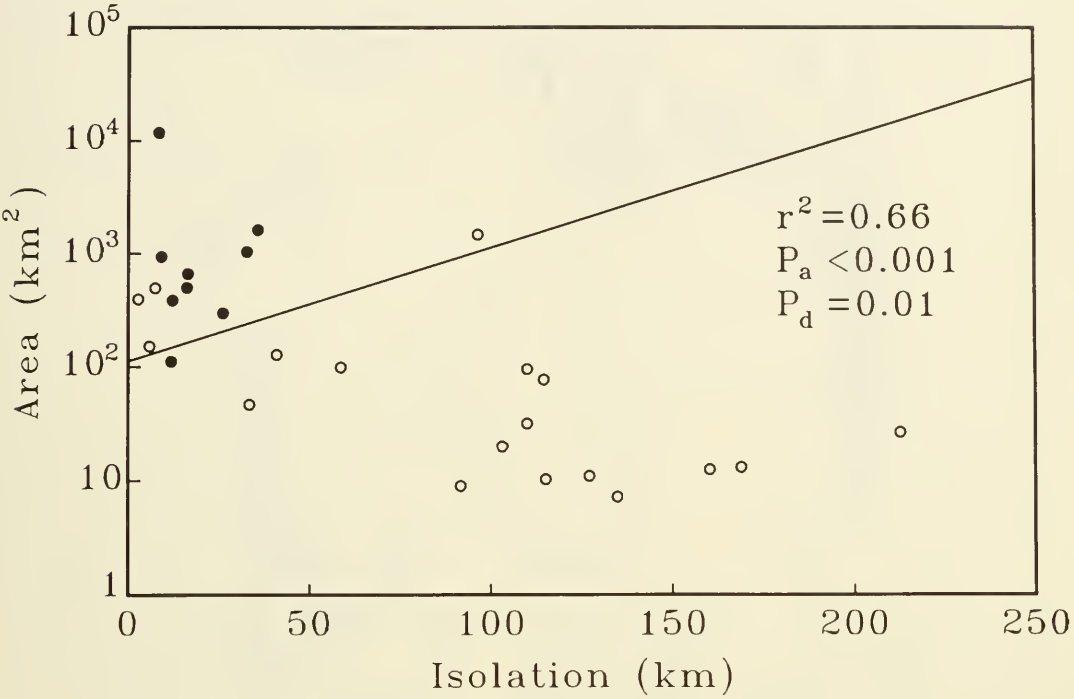

Fig. 2. Effects of area and isolation on the presence and absence of Abert's squirrel on 27 forest islands in the American Southwest (Lomolino et al. 1989; see also Lomolino 1986). Darkened circles indicate presence; open circles indicate absence. Probabilities that insular occurrence is not influenced by area (extinction) = P_a, and not influenced by distance (dispersal) = P_d.

history in western North America. Fossil plant parts similar to those of this species have been recorded from middle- and late-Miocene deposits in Nevada (Axelrod 1986). In the Pleistocene, these trees apparently occurred as far north as southern Wyoming during the Sangamonian interglacial (Baker 1986), but during the late Wisconsin glacial they were restricted in the United States to refugia in southern Arizona and New Mexico. During late Pleistocene, ponderosa pine is known no further north than 36 degrees North latitude (Betancourt and Van Devender 1981, Cole 1982, Thompson and Van Devender 1982, Wells 1983, Betancourt 1984, Spaulding 1984, Van Devender et al. 1987). In consequence, Abert's squirrel would not have been further north in late Pleistocene than north central Arizona and New Mexico (Fig. 1).

Beginning in early Holocene, climatic changes again favored dispersal of ponderosa pine northward beyond the 36th parallel into northern Arizona–New Mexico, and from there into Utah, Colorado, and Wyoming. Eventually, the vast northern conifer forest of the late Pleistocene (Lomolino et al. 1989) contracted into the isolated montane patches that exist today, now dominated at middle elevations by ponderosa pine. The rapid expansion of ponderosa pine into the huge, modern range it now occupies (Fig. 3) represents one of the most remarkable dispersal events of the Holocene (Van Devender et al. 1984).

The northward movement of ponderosa pine allowed a corresponding movement of Abert's squirrel. Populations of these squirrels now present in northern Arizona, New Mexico, Colorado, Utah, and Wyoming must have had their origin from populations that had previously been present in ponderosa pine forests south of the 36th parallel.

In northwestern Arizona, the squirrel somehow reached the north Kaibab (Fig. 1). Contrary to both traditional and popular opinion (Goldman 1928, Turbak 1987a, 1987b), the population now in the north Kaibab apparently

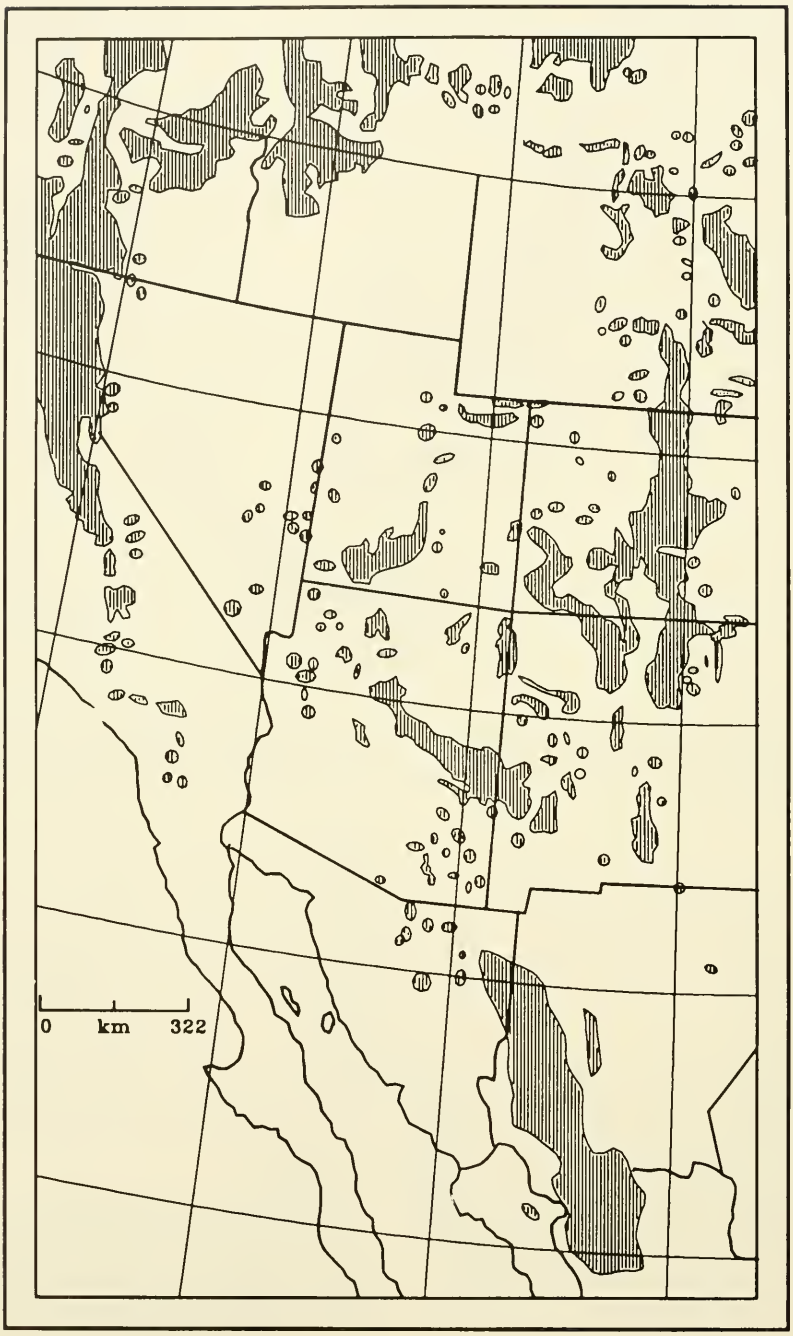

Fig. 3. Distribution of ponderosa pine in Mexico and a selected portion of the United States (Little 1971). While individual Abert's squirrels occasionally occur in habitats other than those dominated by ponderosa pine, at this scale any suggestion of the occurrence of populations of these squirrels (Fig. 1) outside the range of ponderosa pine is an artifact resulting from errors in the estimations of the distributions of one or the other of these two species.

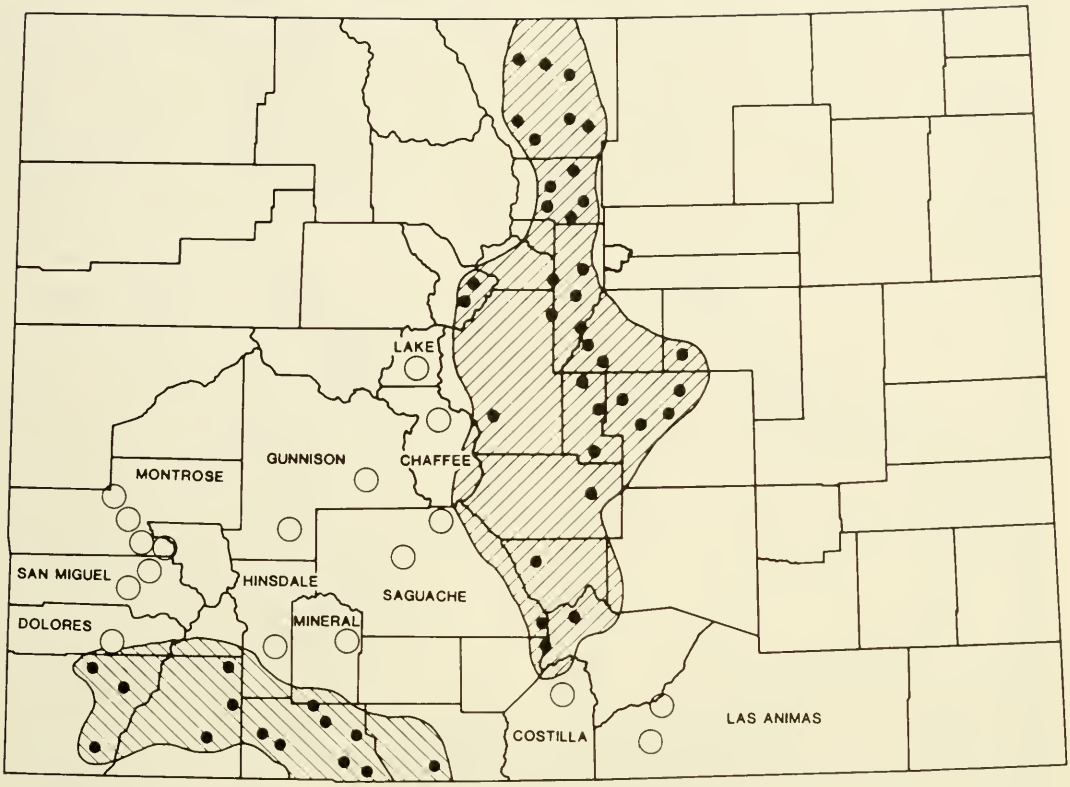

Fig. 4. Distribution of Abert's squirrel in Colorado (Davis and Bissell 1989). Cross-hatched area is Armstrong's estimate (1972), and black dots represent records he compiled. Localities indicated by open circles are the sites of post–1972 records; several sites close together are shown by a single open circle.

could not be a Pleistocene relict; there is no evidence of the existence of ponderosa pine forests north of the Colorado River until after the end of the Pleistocene.

In the absence of fossil evidence (Harris 1985), there is no way of knowing when the northward post-Pleistocene dispersal of Abert's squirrel began nor when the distribution of this species reached its modern extent. Forests dominated by ponderosa pine probably developed on the Colorado Plateau in the early or middle Holocene (Betancourt and Van Devender 1981), when the squirrel may or may not have been present. The chronology of certain records over the past 100 years, however, suggests that Abert's squirrel may not have reached parts of its present range north of the 36th parallel (Fig. 1) until quite recently.

For example, even though first recorded in southern Colorado in 1875 (Armstrong 1972), it was not reported in southeastern Utah until 1947 (Durrant 1952) nor in Wyoming until 1963 (Brown 1965). Based on observational records, a recent expansion of range has been reported in the southern and southwestern portions of Colorado (Fig. 4). Given its high visibility, it is unlikely that this squirrel could have escaped detection in all of these localities throughout historic time until its recent, fortuitous discovery. A hypothesis suggesting the relatively recent arrival of the squirrel in at least portions of its present northern range is certainly as well supported by available evidence as any to the contrary.

Dispersal Across Non-Ponderosa Pine Habitat

Weighing against any hypothesis involving a role of post-Pleistocene dispersal is the present disjunct distribution of isolated montane patches of ponderosa pine forest in which

this squirrel now occurs (Fig. 1; Lomolino et al. 1989). Northward post-Pleistocene dispersal by this squirrel beyond the 36th parallel could have taken place through continuous ponderosa pine habitat only if ponderosa pine arrived in the north prior to the disjunction of the massive late-Pleistocene forest. If dispersal occurred when vegetational conditions were similar to those existing today, then much of this must have taken place across apparent barriers of "unsuitable" (non-ponderosa pine) habitat. The presence of such apparent barriers is especially critical to our suggestion of the possibility of recent range expansion into Utah and into the southwestern portions of Colorado. The Abajo Mountains in southeastern Utah, the only Utah locality in which these squirrels occur, are separated by a gap of about 30 km of non-ponderosa–pine habitat from the nearest forests of southwestern Colorado (Lomolino et al. 1989). Likewise, the ponderosa pine forests in southwestern Colorado, north of the San Juan Mountains, are small and disjunct (Armstrong 1972) and comparably isolated. It is logical, then, to postulate that at least some gaps of non-ponderosa–pine habitat were likely to have been present whenever the northward, post-Pleistocene dispersal of Abert's squirrel occurred. To be plausible, a dispersal hypothesis such as this requires verification that these squirrels are capable of crossing such apparent barriers. Evidence for this comes from several sources.

First, even though reproducing populations of Abert's squirrel are restricted to ponderosa pine forests, Hoffmeister (1986) indicates that 20% of the locality records in Arizona are within pinyon-juniper woodlands. Consequently, there is no question that individuals can exist at least temporarily in pinyon-juniper habitat (Pederson et al. 1976) and should be capable of dispersal through this habitat at least for short distances from one ponderosa pine forest to another.

In addition, in central Arizona there is an example of a natural range expansion (not assisted by transplanting; Davis and Brown 1989) that must have occurred through intervening habitats of chaparral and woodland. In the Mazatzal Mountains there are a few small patches of ponderosa pine. These had been examined previously by personnel of the Arizona Game and Fish Department and visited by many hikers and hunters. Those who knew this mountain and its game mammals had been confident of the absence of these distinctive and obvious squirrels prior to the first record of their occurrence (in 1969 and 1970) in three of the forest patches (Brown 1984). About 10 years later their presence was reported about 32 km further south in this same range in another patch of ponderosa pine where there had been no previous sign of them. The ponderosa pine forest nearest to the Mazatzal Mountains is at least 50 km to the north.

Other evidence is provided from a reconstruction of the distribution of vegetation occurring in late Pleistocene (Lomolino et al. 1989). If this reconstruction is valid, then even in late Pleistocene the distribution of Abert's squirrel could not have been continuous and unfragmented. There apparently was never a continuous, late-Pleistocene connection between the extensive boreal conifer forest of central and northern Arizona–New Mexico and the austral conifer forest of northern Mexico. The closest approximation of such a connection occurred in southeastern Arizona where forests were present on montane islands surrounded by woodlands. These forests were only slightly less isolated then than they are today (Lomolino et al. 1989). Consequently, if dispersal through this region occurred at any time during the past 30,000 years, it could only have taken place because the squirrel was able to cross non-ponderosa–pine habitat barriers and island-hop from one montane island of ponderosa pine to another. It is interesting to note that while populations of this squirrel must have occurred on the mountains in southeastern Arizona at some time or another, these eventually became extinct. It occurs now only on a few of these mountains as the result of transplanting (Davis and Brown 1989). Such local extinction is not unexpected; these habitat islands are small.

Even stronger evidence for the ability of this squirrel to disperse through non-ponderosa–pine habitat was provided by biogeographical experiments resulting from a transplanting program conducted by the Arizona Game and Fish Department, beginning in 1940–41. Abert's squirrel was known to be absent from several isolated mountain ranges containing ponderosa pine, and it was thought

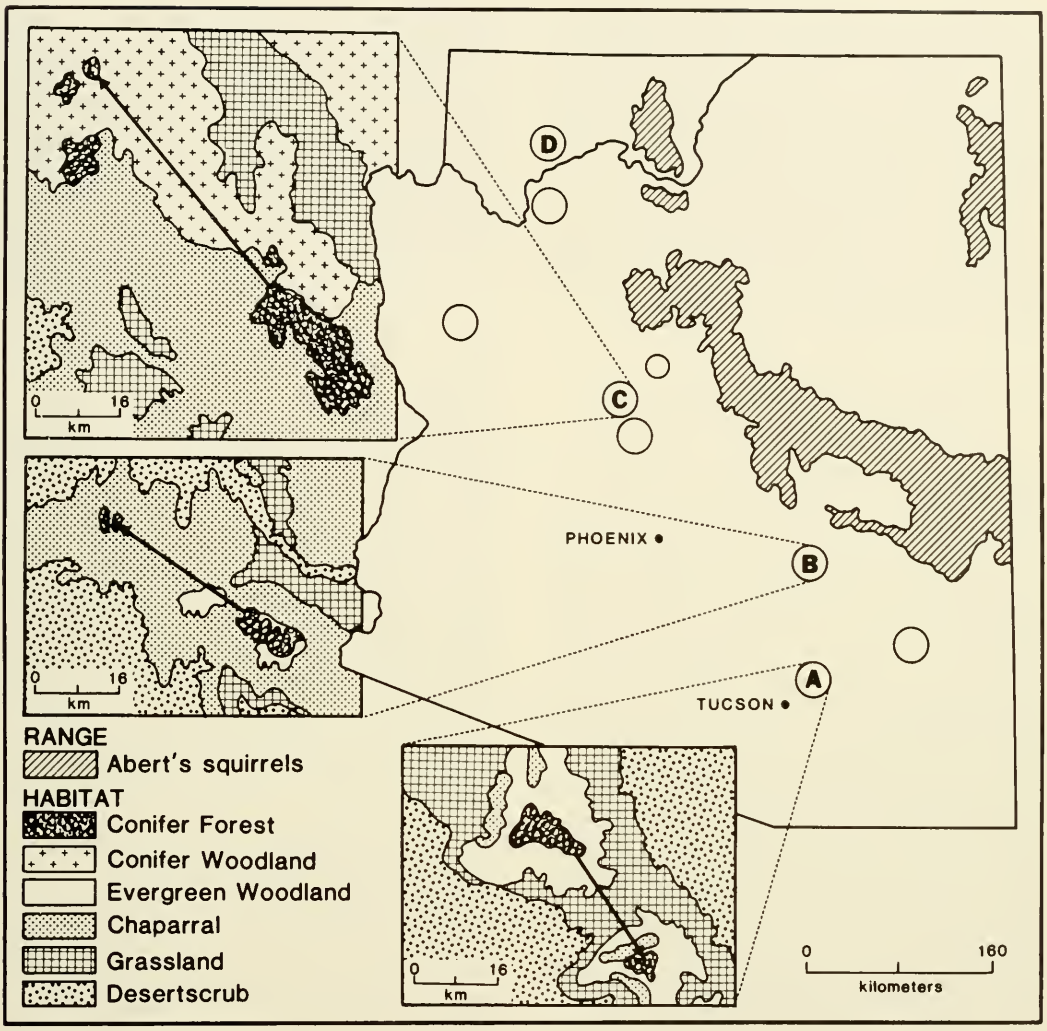

Fig. 5. The distribution of Abert's squirrel in Arizona (modified from Brown 1984), with examples of dispersal and colonization. Circles indicate sites of transplants (Davis and Brown 1989). A–D are transplants that were followed by colonization of nearby, isolated forests; and the straight lines with arrows for A–C are the shortest possible routes of dispersal; intervening habitats are indicated (from Brown and Lowe 1983). At D, the site of transplant was Mt. Logan, with subsequent dispersal through pinyon-juniper woodland to three nearby, isolated forests 8–12 km distant.

appropriate to transplant this squirrel into the larger of these. In several instances following release, the squirrel then dispersed through intervening nonforest habitats to colonize other smaller, adjacent forests from which it was also known to have been absent previously (Fig. 5). In these experiments, the time at which colonization was detected following transplanting increased with the distances between the isolated forests: 8 to 12 km in about 10 years (D in Fig. 5), 23 km in about 20 years (A), 29 km in 30 years (B), 57 km in 40 years (C). The intervening habitats include oak and pinyon-juniper woodlands, interior chaparral, and even semidesert grassland (Fig. 5). In each case, the sources of dispersing squirrels could have been from elsewhere than the sites of transplanting as indicated in Figure 5; if this were the case, however, the distances involved would then be even greater and the intervening habitats no less harsh (Fig. 5, and Brown and Lowe 1983). These are examples of natural dispersal and subsequent colonization; additional transplanting was not involved (Davis and Brown 1989).

Observations of individuals of any species dispersing through unsuitable habitat are rare. However, Cooper (1987) observed an Abert's squirrel crossing alpine tundra, 350 m elevation above treeline and at least 1,250 m above the ponderosa pine forest. Alpine tundra on mountain tops would seem to be even less suitable habitat for a tree squirrel than the woodlands at lower elevations in which individuals occasionally occur and through which much of the dispersal shown in Figure 5 must have taken place.

SUMMARY, CONCLUSION, AND DISCUSSION

Because all reproducing populations of *Sciurus aberti* are restricted to ponderosa pine forests, and since ponderosa pine is not known north of the 36th parallel in the late Pleistocene, two conclusions emerge: (1) this squirrel could not have been north of the 36th parallel prior to the arrival of ponderosa pine, and (2) post-Pleistocene dispersal must have played a major role in determining the modern distribution of the squirrel north of this latitude. While much of such dispersal may have occurred prior to the fragmentation of the vast northern forest of the late Pleistocene (but after the arrival of ponderosa pine), there remains the possibility that some dispersal of Abert's squirrel may have taken place considerably later when modern fragmented conditions existed. In fact, although unproven (and though alternate possibilities exist), there is evidence suggesting that this squirrel may have arrived rather recently in certain isolated portions of the northern part of its range.

In any case, once habitat conditions reached today's norms, no matter how much later dispersal may have occurred, at least some must have taken place across gaps in the distribution of ponderosa pine. Evidence from several sources clearly demonstrates that such gaps would not have prevented dispersal and that these squirrels are presently capable of colonizing isolated forests.

Historical legacy may have been involved in the distribution of this species south of the 36th parallel, and local extinction has apparently occurred at least on the montane islands in southeastern Arizona. All of the current range of this squirrel north of the 36th parallel, however, must have resulted from post-Pleistocene dispersal unimpeded by habitat barriers.

Abert's squirrel is absent from most of the ponderosa pine forests of North America (compare Figs. 1 and 3). In some cases this absence can be explained as the result of local extinction in small forests (as in the mountains of southeastern Arizona) or as a result of excessively low dispersal rates to the more isolated forests (Fig. 2). In addition, there is always the typical enigma of dispersal; some habitat and distance barriers are crossed while other barriers, apparently with higher probabilities of dispersal, are not (Fig. 2).

In any case, the lack of complete overlap of the distributions of these two species should come as no surprise. Abert's squirrel is dependent upon ponderosa pine, but the reverse relationship does not exist. These two species have very different characteristics. Abert's squirrels have poorer dispersal ability and a lower probability of successful colonization following dispersal. Also, reproducing populations of these mammals have much greater resource-area requirements.

In addition, their absence north of southern Wyoming suggests the possibility that these squirrels may be unable to exist in more northern climates and thus may have a narrower range of ecological tolerance. On the other hand, if the distribution of Abert's squirrel is as dynamic as we have proposed, and if they have reached both southern Wyoming and southeastern Utah only quite recently (as the chronology of records suggests), then we have no way yet of knowing what their potential may be for future expansion to either the north or west (compare Figs. 1 and 3).

This study involves only a single species of mammal, but the phenomenon demonstrated may have broad implications. If post-Pleistocene dispersal can so significantly influence the current distribution of *Sciurus aberti,* a species with an obligatory relationship with montane forests dominated by ponderosa pine, it could have a comparable influence on the distribution of other small, mountain-dwelling, nonflying mammals—especially those less restricted to montane habitats. The yellow-nosed cotton rat (*Sigmodon ochrognathus*) is such a species, and it has been shown to have recently expanded its range (Davis and Dunford 1987, Davis and Ward 1988). If this phenomenon should occur

widely, then post-Pleistocene dispersal has played a major role in determining the modern patterns of distribution of montane forest mammals of the American Southwest. Analyses of both community- and species-level patterns and evidence that many forest-dwelling species occasionally occur in woodlands and other low-elevation habitats have provided strong support for this hypothesis (Davis et al. 1988, Lomolino et al. 1989).

ACKNOWLEDGMENTS

Several people reviewed preliminary versions of this paper and provided helpful suggestions: D. Armstrong, J. Betancourt, E. L. Cockrum, S. Cross, M. Lomolino, J. Mead, B. Patterson, R. Sheehy, R. Sidner, and T. Van Devender. C. Dunford and P. S. Martin helped with a major revision that eventually resulted in the present version. Discussions with J. Betancourt, J. Mead, and T. Van Devender, regarding ponderosa pine distribution during the late Pleistocene, were invaluable. Figures 1–3 were prepared by J. Abbott; Figures 4 and 5 were prepared by C. Ernstein.

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