

BIOGEOGRAPHIC IMPLICATIONS OF RECENT LOW-ELEVATION RECOLONIZATION BY *NEOTOMA CINEREA* IN THE GREAT BASIN

DONALD K. GRAYSON* AND DAVID B. MADSEN

*Burke Museum of Natural History and Culture and Department of Anthropology, Box 353010,
University of Washington, Seattle, WA 98195 (DKG)
Utah Geological Survey, 1594 West North Temple, Suite 3410,
Salt Lake City, UT 84114-6100 (DBM)*

Homestead Cave, a paleontological site located in a low-elevation arid setting in the northern Bonneville Basin of northcentral Utah, documents the local extinction of *Neotoma cinerea* during the Middle Holocene. *N. cinerea* is present there today, and the Homestead Cave record suggests that recolonization likely occurred sometime prior to 1,000 years ago. This history supports the view (forwarded by T. E. Lawlor) that cross-valley dispersal by mammals that generally are most abundant in cooler and moister (and therefore higher elevation) parts of the Great Basin is still occurring, showing that Brown's model of Great Basin montane mammalian biogeography is incorrect. These dispersal patterns suggest that conservation efforts directed toward montane mammals in the Great Basin must include low-elevation access corridors to mountain masses.

Key words: biogeography, climate change, conservation biology, Great Basin, *Neotoma cinerea*

Nearly 3 decades ago, J. H. Brown's analysis of the discontinuous distribution of a set of montane mammals across mountains within the Great Basin of the western United States led him to hypothesize that this distribution reflects initial Pleistocene colonization by the mammals followed by Holocene isolation and differential extinction across mountains (e.g., Brown 1971, 1978; Brown and Gibson 1983; Kodric-Brown and Brown 1993; cf. Lawlor 1998; Skaggs and Boecklen 1996). Two conceptually and empirically distinct sets of critiques have been directed toward this argument. The earliest critiques, spurred largely by paleontological analyses, occurred as it became clear that the model was insufficiently dynamic to reflect effects of spatial variability in Great Basin environments, variability in small-mammal adaptations to those environments, and variability in responses of particular species to cli-

mate change during the past 11,000 years. Those critiques were explicitly offered as fine tuning of an explanation that seemed to be in substantial accord with the Pleistocene and Holocene paleontological record of the Great Basin (Grayson 1987, 1993).

More recent critiques have been based largely on knowledge of the present rather than knowledge of the past. Beginning in 1993 (Grayson and Livingston 1993; Grayson et al. 1996; cf. Kodric-Brown and Brown 1993; Skaggs and Boecklen 1996), those critiques suggested that basic distributional data on which Brown (1971, 1978) based his model reflected search time of mammalogists as well as the actual distribution of the mammals at issue. The most comprehensive and significant of those critiques, presented by Lawlor (1998), has now falsified both the basis for the model and the model itself. Here, we present paleontological data that amplifies some of the issues raised by Lawlor (1998).

* Correspondent: grayson@u.washington.edu

To test Brown's model against the actual history of Great Basin mammals, Grayson (1981, 1987, 1993) derived a series of paleontological expectations of varying power from that model (for a complete exposition of these expectations, see Grayson 1993): 1) montane mammals currently isolated on Great Basin mountains must once have occupied the intervening lowlands, because those lowlands are hypothesized to have provided corridors of access to mountains; 2) montane mammals found on only some Great Basin mountains today should have been present on other mountains in the past, because the model hypothesizes that mountains were occupied by a common pool of species that was differentially reduced across mountains by local extinctions; and 3) there may have been species of montane mammals on Great Basin mountains in the past that no longer exist in the region today; i.e., because some mammal species are now missing from some ranges, others may be missing from all of them.

The model also requires that there has been no colonization of Great Basin mountains by montane mammals during the Holocene or, in the more dynamic version of the model suggested in Grayson (1987, 1993), since those mountains became biogeographically isolated during the late Pleistocene or Holocene. This prediction follows from the requirement that the differential presence of montane species on Great Basin mountains is due to extinction, not colonization. Confirmation of the lack of colonization would suggest that dispersal processes cannot account for positive outcomes of the first 3 predictions.

It is impossible to document that no montane mammal has colonized any Great Basin mountain range since the time that these ranges, according to the model, should have been isolated. Among other things, paleontological sites that would provide this documentation are not likely to exist. It is, however, possible to document the likely absence of late colonization of a particular range for which detailed paleonto-

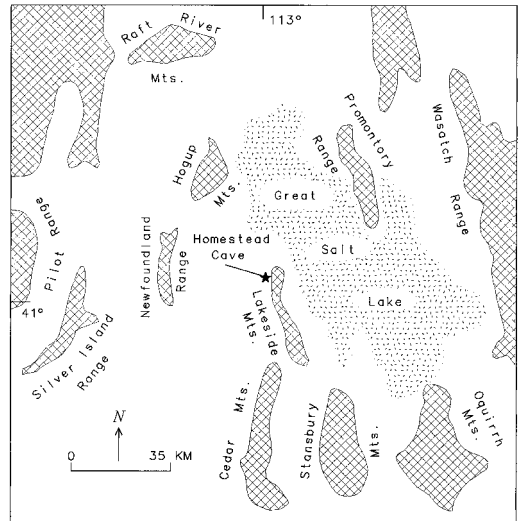


FIG. 1.—Location of Homestead Cave within the northern Bonneville Basin, Utah.

logical sequences are available. Insofar as we have appropriate sequences (e.g., the Toiyama Range of central Nevada; Grayson 1983), they have failed to show such colonization.

It is also possible to detect the unexpectedly late presence of montane mammals in valley settings. Although Brown's (1971) model has passed this test in certain areas (Grayson 1987, 1993), it does not pass it everywhere.

MATERIALS AND METHODS

Homestead Cave (1,406 m above mean sea level) is located on Homestead Knoll, the most northwestern spur of the Lakeside Mountains, a few kilometers west of Great Salt Lake in north-central Utah and immediately east and southeast of the barren playa of Pleistocene Lake Bonneville (Fig. 1). The area receives about 23 cm of precipitation per year under conditions of high summer temperatures (average August temperature is 33°C) and thus has high evaporation rates (National Climatic Data Center 1997), and it lacks active springs and permanent streams. Vegetation in the vicinity of the site is dominated by such shrubs as shadscale (*Atriplex confertifolia*) and horsebrush (*Tetradymia*) and by grasses. The valley floor beneath the site is dominated by greasewood (*Sarcobatus vermicula-*

TABLE 1.—Numbers of identified mammal specimens and estimated radiocarbon ages for the Homestead Cave strata.

Stratum	No. specimens	Approximate age (years) ^a
XVIII	1,047	
XVII	15,548	1,000
XVI	6,296	1,200
XII	22,860	3,500
XI	10,096	
X	6,601 ^b	5,300
IX	22,088	
VIII	8,289	
VII	13,905	6,200
VI	24,330	7,100
V	5,109	8,200
IV	26,615	8,200
III	2,884	
II	7,855	8,500–8,900
I	10,275	10,200–11,300

^a Ages provided only for strata with radiocarbon dates.

^b Only kangaroo rats (*Dipodomys*) have been identified for this stratum.

tus), shadscale, and introduced Eurasian cheat-grasses (*Bromus*). The knoll reaches a maximum elevation of 1,625 m and, with the exception of a few scattered Utah junipers (*Juniperus osteosperma*), is treeless. Although the Lakeside Mountains reach a maximum elevation of 2,019 m, Homestead Knoll is separated from the main mass of those mountains by a 2.5-km pass <1,500 m in elevation that is marked by the same xerophytic vegetation found in the area of Homestead Cave. The cave is about 6 km from the base of that main mass.

In 1993, we excavated a 1- by 1-m column sample to bedrock (encountered at a depth of about 2.7 m) toward the center of the cave. Deposits were removed according to 18 well-defined strata and were passed through 0.64-cm, 0.32-cm, and 0.16-cm mesh screens, and organic remains were removed from screen residues. The chronology for the site is based on 21 radiocarbon determinations (Madsen, in press); all ages reported here are in radiocarbon years. The fish, bird, and mammal remains retrieved from the column were identified by different specialists. Results reported here are based on the identification of about 184,000 mammal bones and teeth to at least the genus level from the 0.64-cm and 0.32-cm sample fractions from 15 of the 18 Homestead Cave strata (Table 1; no plans

exist to identify the mammals from strata XIII, XIV, and XV, or from the 0.16-cm sample fraction). The extraordinary organic richness of the deposits in Homestead Cave is accounted for by the excellent preservation provided by the arid and sheltered setting and by the cave having served as a roosting site for owls throughout its depositional history.

Data on which these analyses are based and criteria used to achieve identifications are available elsewhere (Madsen, in press). Two other aspects of the Homestead Cave mammals have been discussed elsewhere. Grayson (1998) examined the implications of the Homestead Cave fauna for developing an understanding of the richness of small-mammal communities in arid settings, and Grayson (2000) examined the impact of Middle Holocene aridity on those communities. Accordingly, the discussion presented here focuses only on the significance of the Homestead faunal assemblages in light of Brown's (1971) model.

RESULTS AND DISCUSSION

Of the approximately 15 species of mammals that Brown (1971, 1978) treated as members of his montane assemblage, 5 occurred in Homestead Cave: *Mustela erminea*, *Lepus townsendii*, *Sylvilagus nuttallii*, *Marmota flaviventris*, and *Neotoma cinerea*. *S. nuttallii* was represented sporadically throughout the deposits, but reliably identifiable specimens were present in such low numbers that little light has been shed on its local history. *M. flaviventris*, however, was reasonably well represented in the deepest stratum of the cave, and its subsequent history shows that it became locally extinct during the arid Middle Holocene, along with a series of other small mammals that did not play a role in Brown's (1971, 1978) analyses (Grayson, 2000). This sequence is consistent with the history of *M. flaviventris* in more northern parts of the Great Basin, including the far western edge of the Bonneville Basin (Grayson 1988, 1993).

Mustela erminea appears only in stratum I (11,300–10,200 years ago), and *L. townsendii* appears only in strata I and II

(11,300–8,500 years ago). Although *Thomomys talpoides* was not included in Brown's (1971, 1978) analysis, it also is largely confined to cooler parts of the Great Basin and was present only in the stratum I assemblage. None of these species is known to occur in this area presently.

Local histories of *M. erminea*, *L. townsendii*, and *M. flaviventris* and similar histories from other parts of the Great Basin (Grayson 1993) provide support for the 1st prediction drawn from Brown's model: "montane" mammals were once present in lowland settings in which they do not now exist. The situation for *N. cinerea*, however, is distinctly different.

Initial analyses of the Homestead Cave fauna revealed that *N. cinerea* was abundant in the late Pleistocene and Early Holocene (11,300–8,500 years ago) in this area and that its abundance declined as the Middle Holocene approached. Other northern Great Basin sequences have provided similar results (Grayson 1988, 1993). In 1995, however, we livetrapped *N. cinerea* within Homestead Cave itself. Subsequent research revealed prior (unpublished) records for this species in nearby low-elevation settings (Grayson et al. 1996).

Given what was then known about the faunal sequence in Homestead Cave, we hypothesized that either *N. cinerea* had managed to survive the hyperarid Middle Holocene in this area and had thus maintained a continuous presence since the Pleistocene, or it had become locally extinct during this climatic episode and subsequently had recolonized the area. The latter possibility was considered more likely, and we suggested that such recolonization probably occurred during the Late Holocene and perhaps even during the 1980s (Grayson et al. 1996), a time of extremely high precipitation in the northern Great Basin. We concluded that populations of *N. cinerea* can either find sufficient refuge in low-elevation xeric habitats to survive for many thousands of years or that this species can move across xeric lowlands far more readily than

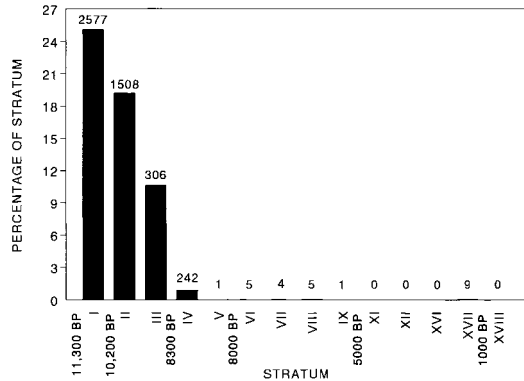


FIG. 2.—Percentages of identified *Neotoma cinerea* specimens in the Homestead Cave strata. Figures above the bars provide numbers of skeletal specimens identified as *N. cinerea*.

had been suspected, or both. Given the nature of Homestead Knoll and its isolation from the main mass of the Lakeside Mountains, neither possibility is consistent with Brown's (1971, 1978) model, or at least with the inclusion of this particular species within that model.

The more complete sequence now available from Homestead Cave shows a dramatic decline in *N. cinerea* after about 8,300 years ago and strongly suggests that this species was extirpated from the area during or towards the end of the Middle Holocene (Fig. 2). This decline is paralleled by the *Neotoma* fecal pellet record in Homestead Cave (Madsen, in press). The species of *Neotoma* that deposited these pellets is unknown, but the pellets are present and often abundant in all strata except Middle Holocene strata VI–XI. Skeletal and fecal pellet data together leave little doubt that *N. cinerea* became locally extinct in the cave area during the Middle Holocene.

Neotoma cinerea appears to have recolonized the area sometime before 1,000 years ago (Fig. 2; its absence from stratum XVIII has little meaning, given the very small sample available from this stratum). It is possible that the 9 specimens of *N. cinerea* in stratum XVII reflect long-distance transport by a carnivore or raptor. If

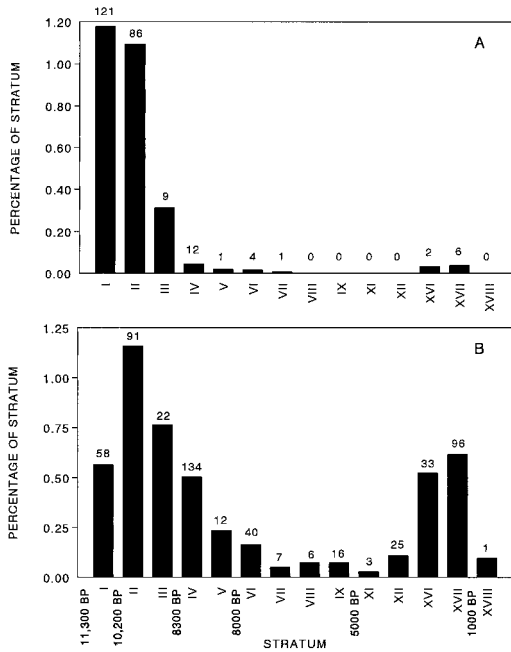


FIG. 3.—Percentages of identified specimens from Homestead Cave strata of A) *Perognathus parvus* and B) *Reithrodontomys megalotis*. Figures above the bars provide the numbers of skeletal specimens identified as each species (because all *Reithrodontomys* specimens that could be identified to species are *R. megalotis*, specimens that could be identified only as *Reithrodontomys* are included in the counts).

so, recolonization of this area by *N. cinerea* would postdate the period of time documented by the deposits at this site. However, reappearance of this species in the Homestead record is matched by reappearance of other small mammals at about the same time, including *Perognathus parvus* (Fig. 3A) and *Lemmiscus curtatus*, and an increase in abundance of *Reithrodontomys megalotis* (Fig. 3B) and other species. It is most likely that *N. cinerea* recolonized the Homestead Cave area prior to about 1,000 years ago after an absence of several thousand years and during a climatic episode favorable to a set of species that required more mesic habitats than those that had existed since the end of the Early Holocene. Perhaps most importantly, the complete ab-

sence of *N. cinerea* specimens during much of the Middle Holocene here documents that recolonization has occurred, even if our inference that it occurred sometime before 1,000 years ago is incorrect.

CONCLUSIONS

The Homestead Cave faunal sequence thus documents local extinction and recolonization of *N. cinerea*, 1 of the species included as part of Brown’s (1971) set of montane mammals, in a low-elevation arid area within the Great Basin. It also documents local extinctions of *M. erminea*, *L. townsendii*, and *M. flaviventris* in the same area; these extinctions have not been followed by recolonization. These discoveries have multiple implications for understanding the histories, current distributions, and futures of small mammals in the Great Basin.

First, the local history of *N. cinerea* provides direct empirical evidence of the process inferred from modern distributional data by Lawlor (1998): cross-valley dispersal by some montane mammals in the Great Basin in the very recent past. Second, it is possible, as Lawlor (1998) argued, that recent discoveries of “missing species” on mountains in the Great Basin reflect recent dispersal events (cf. Grayson and Livingston 1993) as well as inadequate knowledge of modern distributions. Third, the distinct histories of *M. erminea*, *L. townsendii*, *M. flaviventris*, and *N. cinerea* (and a wide variety of other species not included in Brown’s model; Grayson, 2000) demonstrate that species-level and not assemblage-level analyses of small mammals in the Great Basin are needed to understand the present distribution and to predict the futures of these animals, attending to, as Lawlor (1998:1126) put it in a slightly different context, the “ecological peculiarities” of each. Fourth, the fact that at least some of these mammals can disperse across low-elevation settings in the Great Basin under either current conditions (e.g., *S. nuttallii*—Grayson and Livingston 1993) or

those very close to modern conditions (e.g., *N. cinerea* in the Homestead Cave area) implies that conservation efforts directed toward such species must include low-elevation corridors as part of those efforts.

Brown's (1971, 1978) model has had a long and productive life. However, as Lawlor (1998) noted, it is now clear that the model is incorrect and that predictions based on it, such as those involving the magnitude and nature of extinction under conditions of global warming (e.g., McDonald and Brown 1992; Murphy and Weiss 1992; cf. Skaggs and Boecklen 1996), are also likely to be incorrect.

ACKNOWLEDGMENTS

We thank K. M. Bovy, J. M. Broughton, M. D. Cannon, M. A. Etnier, J. Hunt, L. Nagaoka, and S. S. Hughes for critical laboratory assistance, E. Rickart for assistance at the Utah Museum of Natural History, and the Zoology Division of the Burke Museum of Natural History and Culture for access to modern comparative specimens. The analyses reported here were supported by the Legacy Project, Department of Defense, and Hill Air Force Base, Utah.

LITERATURE CITED

- BROWN, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. *The American Naturalist* 105:467–478.
- BROWN, J. H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs* 2:209–227.
- BROWN, J. H., AND A. C. GIBSON. 1983. *Biogeography*. C. V. Mosby, St. Louis, Missouri.
- GRAYSON, D. K. 1981. A mid-Holocene record for the heather vole, *Phenacomys intermedius*, in the central Great Basin and its biogeographic significance. *Journal of Mammalogy* 62:115–121.
- GRAYSON, D. K. 1983. The paleontology of Gatecliff Shelter: small mammals. *American Museum of Natural History Anthropological Papers* 59:99–126.
- GRAYSON, D. K. 1987. The biogeographic history of Great Basin small mammals: observations on the last 20,000 years. *Journal of Mammalogy* 68:359–375.
- GRAYSON, D. K. 1988. Danger Cave, Last Supper Cave, Hanging Rock Shelter: the faunas. *American Museum of Natural History Anthropological Papers* 66:1–130.
- GRAYSON, D. K. 1993. The desert's past: a natural prehistory of the Great Basin. Smithsonian Institution Press, Washington, D.C.
- GRAYSON, D. K. 1998. Moisture history and small mammal community richness during the latest Pleistocene and Holocene, northern Bonneville Basin, Utah. *Quaternary Research* 49:330–334.
- GRAYSON, D. K. 2000. Mammalian responses to Middle Holocene climatic change in the Great Basin of the western United States. *Journal of Biogeography* 27:181–192.
- GRAYSON, D. K., AND S. D. LIVINGSTON. 1993. Missing mammals on Great Basin mountains: Holocene extinctions and inadequate knowledge. *Conservation Biology* 7:527–532.
- GRAYSON, D. K., S. D. LIVINGSTON, E. RICKART, AND M. W. SHAVER, III. 1996. Biogeographic significance of low elevation records for *Neotoma cinerea* from the northern Bonneville Basin, Utah. *The Great Basin Naturalist* 56:191–196.
- KODRIC-BROWN, A., AND J. H. BROWN. 1993. Incomplete data sets and geographic isolation: a case study. *Ecology* 76:458–465.
- LAWLOR, T. E. 1998. Biogeography of Great Basin mammals: paradigm lost? *Journal of Mammalogy* 79:1111–1130.
- MADSEN, D. B. In press. Late Quaternary paleoecology in the Bonneville Basin. *Utah Geological Survey Bulletin* 130.
- MCDONALD, K. A., AND J. H. BROWN. 1992. Using montane mammals to model extinctions due to global change. *Conservation Biology* 6:409–415.
- MURPHY, D. F., AND S. B. WEISS. 1992. The effects of climate change on biological diversity in western North America: species losses and mechanisms. Pp. 355–368 in *Global warming and biological diversity* (R. L. Peters and T. E. Lovejoy, eds.). Yale University Press, New Haven, Connecticut.
- NATIONAL CLIMATIC DATA CENTER. 1997. Utah. 1997 Climatological data annual summary. Vol. 99 (13). National Atmospheric and Oceanographic Institute, Asheville, North Carolina.
- SKAGGS, R. W., AND W. J. BOECKLEN. 1996. Extinctions of montane mammals reconsidered: putting a global-warming scenario on ice. *Biodiversity and Conservation* 5:759–778.

Submitted 22 October 1999. Accepted 31 March 2000.

Associate Editor was Ronald E. Barry.