

Figure 3a shows a chromatogram of the saturate hydrocarbon fraction of the gilsonite. The chromatogram shows depletion of the *n*-alkanes, which is typical for degraded hydrocarbons. The occurrence of authigenic magnetite in apparently biodegraded hydrocarbons has been discussed previously^{12,14}.

The dark bands in the speleothems possess up to an order of magnitude stronger magnetization (average $8 \times 10^{-4} \text{ A m}^{-1}$) than the lighter bands (average $6 \times 10^{-5} \text{ A m}^{-1}$). Specimens of the dark calcite exhibit stable linear decay to the origin during both alternating field and thermal demagnetization. Commonly, over 95% of the magnetization was removed by 125 mT and maximum unblocking temperatures were below 580 °C. The dark calcites contain a CRM with a south-easterly and shallow 'Kiaman' or Permian direction of magnetization (declination = 159° E, inclination = 3°, $k = 29$, $\alpha_{95} = 5^\circ$, $n = 25$). The magnetization in the light bands, which do not contain as many hydrocarbon inclusions as the dark bands, was too weak to yield stable results during demagnetization.

IRM acquisition curves (Fig. 1b) for all specimens show that the magnetization is dominated by a low coercivity phase such as magnetite. Thermal demagnetization of the IRM shows that maximum unblocking temperatures are below 580 °C. These data, in conjunction with the demagnetization results, suggest that the magnetization mainly resides in magnetite.

The hydrocarbons extracted from the calcites are at most only slightly degraded (Fig. 3b). Magnetic extracts from the dark calcites contain spherical, botryoidal, and other authigenic forms which, based on EDA, contain iron as the only detectable element. The XRD patterns of extracts from the calcites also indicate the presence of magnetite. The botryoidal and spherical forms are similar to authigenic magnetite reported in the literature and found in the gilsonite.

The magnetization in the speleothems was acquired in the Permian, resides in authigenic magnetite, and is interpreted as a CRM. The fact that cave deposits form at relatively shallow depths and that the Arbuckle Group speleothems were never deeply buried probably eliminates the possibility of a thermoviscous origin for the magnetization. Stable carbon and oxygen isotope values for the light ($\delta^{13}\text{C}_{\text{PDB}} -6.7\%$; $\delta^{18}\text{O}_{\text{PDB}} -4.2\%$) and dark ($\delta^{13}\text{C}_{\text{PDB}} -6.2\%$; $\delta^{18}\text{O}_{\text{PDB}} -4.7\%$) speleothems are consistent with a shallow depth of formation from fresh water¹⁵. The similarity of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for the adjacent dark and light calcites favours a common origin.

The presence of authigenic magnetite in the gilsonite indicates a relationship between hydrocarbons and magnetite. The results from the light and dark speleothems also suggest that there is a relationship between hydrocarbons and authigenic magnetite; the stronger magnetization invariably resides in the dark calcites, where the hydrocarbons became concentrated. The occurrence of hydrocarbon inclusions along growth planes suggests that hydrocarbons seeped into the caves during the precipitation of the speleothems and were trapped in the calcite crystals. This relationship between intensity of magnetization and abundance of hydrocarbons leads us to propose that chemical conditions created by the hydrocarbons could have caused precipitation of authigenic magnetite and acquisition of the associated CRM. The fact that the time of acquisition of remanence is consistent with the age of the speleothems also provides a test that hydrocarbons can cause acquisition of a stable secondary magnetization residing in magnetite.

Although the results from the Arbuckle Group indicate a spatial and temporal relationship between authigenic magnetite and hydrocarbons, the mechanism for magnetite formation is not yet known. The fact that the gilsonite is degraded and contains magnetite suggests that microbial attack of hydrocarbons is one possible diagenetic pathway that might contribute to the formation of authigenic magnetite. This connection, however, is only tentative at best; almost all gilsonite or similar bitumen found at the Earth's surface is degraded. The magnetite may have formed during biodegradation, but an origin related

to other diagenetic processes cannot be ruled out. The fact that the hydrocarbons in the speleothems are not extensively degraded also argues against biodegradation as the only mechanism for precipitation of authigenic magnetite. We are now investigating this problem by conducting laboratory simulation experiments.

Support for this research was provided by the donors of the Petroleum Research Fund, administered by the American Chemical Society (PRF # 18484-AC2) and a grant from ARCO to R.D.E., and by the NSF (EAR-8352055) to M.H.E. The Energy Resources Institute at the University of Oklahoma also provided partial support.

Note added in proof: Analyses of the speleothems in a newly constructed magnetically shielded room confirm the results described above, although stable linear decay to $\sim 620^\circ\text{C}$ in some specimens indicates the presence of a weak component residing in haematite. Haematite has also been found in the magnetic extracts from the speleothems.

Received 31 July; accepted 4 November 1986.

1. Bagin, V. I. & Malumgan, L. M. *Izv. Akad. Nauk. SSSR, Fiz zeml.* 4, 73-79 (1976).
2. Donovan, T. J., Forgy, R. L., & Roberts, A. A. *Bull. Am. Ass. Petrol. Geol.* 63, 245-248 (1979).
3. Reynolds, R. L., Fishman, N. S., Hudson, N. R., Karachewski, J. A. & Goldhaber, M. B. *Eos* 66, 867 (1985).
4. Reynolds, R. L., Fishman, N. S., Grauch, R. I. & Karachewski, J. A. *Eos* 65, 866 (1984).
5. McCabe, C., Van der Voo, R., Peacor, D. R., Scotese, R. & Freeman, R. *Geology* 11, 221-223 (1983).
6. Wisniowiecke, M. J., Van der Voo, R., McCabe, C. & Kelly, W. C. *J. geophys. Res.* 88, 6540-6548 (1983).
7. Kent, D. V. *Geophys. Res. Lett.* 12, 805-808 (1985).
8. Middleton, M. F. & Schmidt, P. W. *J. geophys. Res.* 87, 5351-5359 (1982).
9. Oliver, J. *Geology* 14, 99-102 (1986).
10. Elmore, R. D., Dunn, W. & Peck, C. *Geology* 13, 558-561 (1985).
11. Cochran, K. A. & Elmore, R. D. *J. sedim. Petrol.* (in the press).
12. Elmore, R. D., Cochran, K. A. & Nick, K. E. *Eos* 67, 265 (1986).
13. Zijdeveld, J. D. A. in *Methods in Paleomagnetism* (eds Collinson, D. W., Creer, K. M. & Runcorn, S. K.) 254-286 (Elsevier, New York, 1967).
14. McCabe, C. *Eos* 67, 265 (1986).
15. Allan, J. R. & Mathews, R. K. *Geology* 5, 16-20 (1977).

A land-bridge island perspective on mammalian extinctions in western North American parks

William D. Newmark

School of Natural Resources, University of Michigan, Ann Arbor, Michigan 48109, USA

In recent years, a number of authors¹⁻³ have suggested several geometric principles for the design of nature reserves based upon the hypothesis that nature reserves are analogous to land-bridge islands. Land-bridge islands are islands that were formerly connected to the mainland and were created by a rise in the level of the ocean. Land-bridge islands are considered supersaturated with species in that the ratio of island to mainland species numbers is higher than expected from the area of the island. As a result, the rate of extinction should exceed the rate of colonization on a land-bridge island, resulting in a loss of species that is suggested to be related to the size and degree of isolation of the island⁴. If nature reserves are considered to be similar to land-bridge islands, because most are slowly becoming isolated from their surroundings by habitat disturbance outside the reserves⁴⁻⁸, several predictions follow. First, the total number of extinctions should exceed the total number of colonizations within a reserve; second, the number of extinctions should be inversely related to reserve size; and third, the number of extinctions should be directly related to reserve age. I report here that the natural post-establishment loss of mammalian species in 14 western North American national parks is consistent with these predictions of the land-bridge island hypothesis and that all but the largest western North American national parks are too small to retain an intact mammalian fauna.

I tested the land-bridge island predictions by examining the change in mammalian species number in 14 western North American national parks and park assemblages (Table 1) located

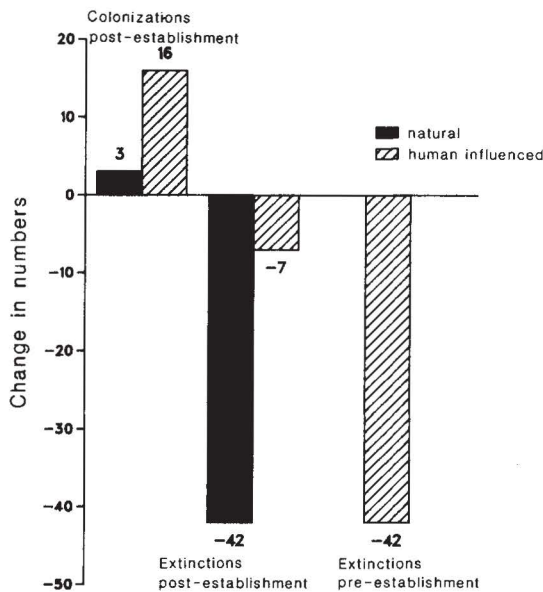


Fig. 1 Comparison of number of post-establishment colonizations with number of post-establishment and pre-establishment extinctions in 14 western North American national parks. Colonizations and extinctions are classified as either natural (solid bars) or human-influenced (hatched bars).

within the Rocky Mountains, Sierra-Cascades and Colorado Plateau. A park assemblage is defined as two or more contiguous parks. The age of a park is defined as time since park establishment; the age of a park assemblage is defined as the mean time since park establishment for the individual parks. Analysis was limited to the orders Lagomorpha, Carnivora and Artiodactyla, because these orders had the most complete park sighting records. Species of these orders tend to be more frequently reported because of their relatively large body size, non-fossorial nature and 'popularity'.

I recorded for every species in each park, based upon park sighting records and the literature, the date of last sighting as of 1983/84 and the total number of sightings for the species if it had been sighted less than five times since establishment of the park. Species which had been sighted less than three times since the establishment of the park were excluded in the analysis of post-establishment colonizations and extinctions. Biases may exist in the sighting records because of their non-standardized nature, potential misidentification of species by observers, and a lack of equivalent sampling effort between parks. I have attempted to minimize these biases by using conservative methods (see below) for classifying a sighting as valid and determining the number of post-establishment extinctions.

With the exception of sightings made by biologists or park employees, a sighting was considered valid only if it was accompanied by an accurate description of the species. The number of post-establishment extinctions was determined by assuming that all species that had not been sighted for a minimum of 10 years by 1983 were extinct. In a few cases, there was solid evidence that several species had become extinct in a park since 1973. This method for determining the number of post-establishment extinctions excludes any species that have become extinct and subsequently recolonized the park naturally since park establishment. The number of post-establishment colonizations was determined by assuming a colonization had occurred if a species had not been reported within a park near time of establishment but was subsequently sighted at least three times since park establishment. The number of pre-establishment extinctions, considered hypothetical, was determined using three criteria. First, a species must have a historic range, as described in the literature, overlapping a park. Second, the park must

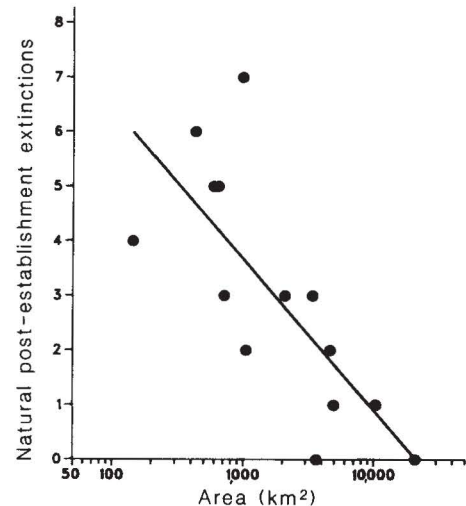


Fig. 2 Relationship between number of natural post-establishment extinctions and park area in 14 western North American national parks. Area is plotted on a logarithmic scale. The straight line shows the relationship $y = 11.95 - 2.76 \times (\log \text{ area})$.

currently meet known habitat requirements for a species. Third, a species must be documented as occurring either within a park or its vicinity before park establishment by a specimen, skeletal remains, pre-establishment sighting(s), post-establishment sighting(s) fewer than three times, or a post-establishment reintroduction by a park manager.

Colonizations and extinctions were classified as being natural or human-influenced. A natural extinction or colonization was an extinction or colonization that could not be related directly to human disturbance within a park. Conversely, a human-influenced extinction or colonization was one that could be potentially or directly related to human activities within a park (see below). Data are summarized in Table 1.

The number of cases (Fig. 1) of natural post-establishment extinctions of mammals ($n = 42$) has exceeded the number of post-establishment colonizations ($n = 3$). This result is consistent with the first prediction of the land-bridge island hypothesis. The natural colonizations resulted from range expansions by the raccoon (*Procyon lotor*) and the moose (*Alces alces*). Park managers have reintroduced 12 species that were found historically in the parks and four exotic species have colonized the parks from lands adjacent to the parks. I attribute the post-establishment human-influenced extinction of six species to predator control and one species to accidental poisoning. A large number of species ($n = 42$) were also lost before the establishment of most western North American national parks (Fig. 1). However, it is quite likely that many of the species that became extinct in the smaller parks before park establishment were transient populations. The pre-establishment loss of species is most probably attributable to human disturbance in the form of hunting, logging, grazing and mining which occurred in many of the western North American parks before their establishment⁹. Combining both pre- and post-establishment extinctions, up to 43% of all species of lagomorph, carnivore and artiodactyl (12 species) found historically within 14 western North American national parks have been lost within a given park (Table 1). Only the largest western North American park assemblage, the Kootenay-Banff-Jasper-Yoho park assemblage (20,736 km²), still contains an intact historical mammalian faunal assemblage.

The number of natural post-establishment mammalian extinctions (Fig. 2) is significantly and inversely related to log park area ($r^2 = 0.56$, $P < 0.01$). The number of natural post-establishment mammalian extinctions is insignificantly correlated with log park age ($r^2 = 0.00$, $P > 0.97$). However, if the effects of park

Table 1 Summary of pre- and post-establishment extinctions and colonizations, area and age for 14 western North American national parks

Park/Park assemblage	Proportional loss of total species found historically (%)	No. of pre-establishment human-influenced extinctions	No. of post-establishment natural extinctions	No. of post-establishment human-influenced extinctions	No. of post-establishment natural colonizations	No. of post-establishment human-influenced colonizations	Area (km ²)	Age (years)
Bryce Canyon	36	4	4	1	0	1	144	61
Lassen Volcanic	43	6	6	0	0	0	426	77
Zion	36	5	5	0	0	2	588	75
Crater Lake	31	5	5	0	0	2	641	82
Manning Provincial	26	4	3	0	1	1	712	43
Mount Rainier	32	1	7	0	0	1	976	85
Rocky Mountain	31	10	2	0	0	3	1,049	69
Yosemite	25	2	3	1	0	0	2,083	94
Sequoia-Kings Canyon	23	1	3	3	0	1	3,389	94
Olympic	6	0	0	1	0	2	3,628	75
Glacier-Waterton Lakes	7	1	2	0	1	1	4,627	81.5
Grand Canyon	18	2	1	1	0	0	4,931	76
Grand Teton-Yellowstone	4	0	1	0	1	1	10,328	83.5
Kootenay-Banff-Jasper-Yoho	0	1	0	0	0	1	20,736	84.5

Data from ref. 13.

area are held constant, the number of natural post-establishment extinctions is significantly and positively partially correlated with log park age ($r=0.57$, $P<0.05$). Log park area (a) and log park age (g) when combined in a multiple linear regression model account for 71% of the total variation in numbers of natural post-establishment extinctions (e). The multiple regression model is: $e = -6.04 - 3.49(a) + 10.82(g)$ ($n=14$, $F=13.15$, $P<0.002$). The results of the simple linear regression and the partial correlation are consistent with the second and third predictions of the land-bridge island hypothesis. In addition, the results of the simple and multiple linear regression indicate that park area is a more important determinant than park age of number of natural post-establishment mammalian extinctions in western North American parks.

The natural post-establishment loss of mammalian species is most probably attributable to the loss of habitat and the active elimination of fauna on adjacent lands or what has been described as short-term insularization effects¹⁰. This loss of habitat and the active elimination of fauna on lands adjacent to the parks have had a twofold effect. First, they have increased the probability of local extinction of species within the reserves because smaller parks tend to have smaller populations which in turn have a higher probability of extinction^{11,12}. Further support for this hypothesis is provided by the fact that population size is the most consistent predictor in a multivariate statistical analysis of life history characteristics of the probability of post-establishment persistence for populations of lagomorphs, carnivores and artiodactyls within 24 western North American national parks¹³. Second, this disturbance has reduced the potential for colonization from lands adjacent to the parks by increasing the distance or isolation of the parks from potential source areas. Openings as narrow as a road, open field, or clearcut have been shown to inhibit the movement of both large and small mammals¹⁴⁻¹⁷.

Without active intervention by park managers, it is quite likely that a loss of mammalian species will continue as western North American national parks become increasingly insularized. Yet it is possible that even without further insularization, mammalian species may continue to be lost in these parks because of a lag between past disturbance and subsequent extinction. Augmentation of existing mammalian park populations by natural colonization, or what has been described as the rescue effect¹⁸, probably will be limited to the most common species. The enhancement of populations for rare species will be largely dependent upon the active introduction of individuals by park managers.

A final factor that could explain the natural post-establishment loss of mammalian species in western North American parks is habitat change. It is widely acknowledged that fire suppression since the early 1900s has affected the vegetative structure of

western North American national parks¹⁹⁻²². However if this vegetative change has had an influence on post-establishment mammalian extinctions, one would expect that species that are dependent upon early successional vegetation should be most prone to extinction. Of the 42 populations of species that have become extinct in 14 parks since park establishment, only 10 may be classified as being dependent upon early successional vegetation. Thus for most species, it appears that successional change is not the principal determinant of post-establishment local extinction of species.

The natural post-establishment loss of mammalian species in western North American national parks indicates that virtually all western North American national parks were too small to maintain the mammalian faunal assemblage found at time of park establishment. To reduce the potential loss of mammalian fauna in the future will most probably require that the mammalian fauna within the parks be more actively managed and that the parks be 'enlarged' either through the acquisition or the cooperative management of lands adjacent to the parks.

I thank G. E. Belovsky, K. R. Miller, M. E. Soulé, B. J. Rathcke and B. S. Low for their advice and H. L. Gibbs for comments. I also thank the many National Park Service and Environment Canada, Parks employees who graciously reviewed species checklists and provided requested information. Support was provided by two Rackham Dissertation Improvement grants and four School of Natural Resources Thesis grants.

Received 23 July; accepted 24 November 1986.

1. Diamond, J. M. *Biol. Conserv.* 7, 129-146 (1975).
2. Terborgh, J. in *Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research* (eds Golley, F. B. & Medina, E.) 369-380 (Springer, New York, 1975).
3. Wilson, E. O. & Willis, E. O. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 522-534 (Harvard University Press, Cambridge, 1975).
4. Diamond, J. M. *Proc. natn. Acad. Sci. U.S.A.* 69, 3199-3203 (1972).
5. Wright, G. M., Dixon, J. S. & Thompson, B. H. *Fauna Series No. 1, Vol. 1* (US Govt Printing Office, Washington DC, 1932).
6. Soulé, M. E., Wilcox, B. A. & Holtby, C. *Biol. Conserv.* 15, 259-272 (1979).
7. National Park Service, *State of the Parks - 1980; A Report to the Congress* (US Dept of the Interior, Washington DC, 1980).
8. Newmark, W. D. *Biol. Conserv.* 33, 197-208 (1985).
9. Runte, A. *National Parks: The American Experience* (University of Nebraska, Lincoln, 1979).
10. Wilcox, B. A. in *Conservation Biology: An Evolutionary-Ecological Perspective* (eds Soulé, M. E. & Wilcox, B. A.) 95-117 (Sinauer, Sunderland, 1980).
11. Terborgh, J. & Winter, B. in *Conservation Biology: An Evolutionary-Ecological Perspective* (eds Soulé, M. E. & Wilcox, B. A.) 119-133 (Sinauer, Sunderland, 1980).
12. Diamond, J. M. in *Extinctions* (ed. Nitecki, M. H.) 191-246 (University of Chicago Press, Chicago, 1984).
13. Newmark, W. D. Ph.D., thesis, Univ. Michigan (1986).
14. Mader, H. J. *Biol. Conserv.* 29, 81-96 (1984).
15. Oxley, D. J., Fenton, M. D. & Carmondy, G. R. *J. appl. Ecol.* 11, 51-59 (1974).
16. Pedersen, R. J. in *Conf. Proc. Recreational Impact of Wildlands* (eds Ittner, R., Potter, D. R., Agee, J. K. & Anshell, S.) 169-173 (US Forest Service, 1979).
17. Wegner, J. F. & Merriam, G. *J. appl. Ecol.* 16, 349-357 (1979).
18. Brown, J. H. & Kodrick-Brown, A. *Ecology* 58, 445-449 (1977).
19. Kilgore, B. M. & Taylor, D. *Ecology* 60, 129-142 (1979).
20. Loope, L. L. & Gruell, G. E. *Quat. Res.* 3, 425-443 (1973).
21. McNeil, R. C. & Zobel, D. B. *NW Sci.* 54, 30-46 (1980).
22. Vankat, J. L. & Major, J. *J. Biogeogr.* 5, 377-402 (1978).