References and Notes

1. W. Lawlor, in *Impact of Global Climatic Changes on Photosynthesis and Plant Productivity*, Y. P. Abrol *et al.*, Eds. (Oxford & IBB Publishing, New Delhi, India, 1991), p. 431.
2. P. S. Curtis, X. Wang, *Oecologia* **113**, 299 (1998).
3. S. P. Hubbell *et al.*, *Science* **283**, 554 (1999).
4. E. Ribbens, J. A. Silander, S. W. Pacala, *Ecology* **75**, 1794 (1994).
5. J. S. Clark, E. Macklin, L. Wood, *Ecol. Monogr.* **68**, 213 (1998).
6. J. S. Clark, M. Silman, R. Kern, E. Macklin, J. HilleRisLambers, *Am. J. Bot.* **86**, 1 (1999).
7. E. Zamski, in *Seed Development and Germination*, J. Kigel, E. G. Galili, Eds. (Dekker, New York, 1995), p. 25.
8. E. J. Farnsworth, F. A. Bazzaz, *Oecologia* **104**, 454 (1995).
9. B. Schappi, *Oecologia* **106**, 93 (1996).
10. J. K. Ward, B. R. Strain, *Plant Cell Environ.* **20**, 254 (1997).
11. M. Fischer, D. Matthies, B. Schmid, *J. Ecol.* **85**, 681 (1997).
12. C. E. Lovelock, A. Virgo, M. Popp, K. Winter, *Plant Cell Environ.* **22**, 49 (1999).
13. E. L. Fiscus *et al.*, *J. Exp. Bot.* **48**, 307 (1997).
14. J. M. Grünzweig, C. H. Körner, *Global Change Biol.* **6**, 631 (2000).
15. K. Garbutt, F. A. Bazzaz, *New Phytol.* **98**, 433 (1984).
16. S. B. Idso, B. A. Kimball, *Agric. For. Meteorol.* **60**, 145 (1992).
17. H. S. Lee, P. G. Jarvis, *J. Biogeogr.* **22**, 323 (1995).
18. K. F. Conner, T. C Prewitt, F. T. Bonner, W. W. Elam, R. C. Parker, in *The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment (Ecological Studies)*, R. A. Mickler, S. Fox, Eds. (Springer, New York, 1998), vol. 128, p. 103.
19. E. H. Delucia *et al.*, *Science* **284**, 1177 (1999).
20. E. Naumberg, D. Ellsworth, *Oecologia* **122**, 163 (2000).
21. G. R. Hendrey, D. Ellsworth, K. Lewin, J. Nagy, *Global Change Biol.* **5**, 293 (1999).
22. For a complete description of the Duke Forest FACE system, including fumigation efficiency, see (*19*).
23. R. P. Schultz, *Loblolly Pine* (U.S. Department of Agriculture, Forest Service, Washington, DC, 1997).
24. S. C. Thomas, *Evol. Ecol.* **10**, 517 (1996). Using only one individual to count all cones minimized sampling error. Schultz (*23*) also found visual estimates of pinecone production to be comparable to harvested cone counts.
25. A. Shmida, S. Ellner, *Vegetatio* **58**, 29 (1984).
26. J. S. Clark, Y. Ji, *Am. Nat.* **146**, 72 (1995).
27. G. C. Hurtt, S. W. Pacala, *J. Theor. Biol.* **176**, 1 (1995).
28. C. Loehle, *Can. J. For. Res.* **18**, 209 (1988).
29. D. T. Tissue, R. B. Thomas, B. R. Strain, *Tree Physiol.* **16**, 49 (1996).
30. C. D. Reid, E. L. Fiscus, *J. Exp. Bot.* **49**, 885 (1998).
31. R. Ceulemans, M. Mosseau, *New Phytol.* **127**, 425 (1994).
32. D. T. Tissue, R. B. Thomas, B. R. Strain, *Plant Cell Environ.* **20**, 1123 (1997).
33. We thank I. Ibanez, M. Lavine, C. D. Reid, W. H. Schlesinger, and C. Williams for comments on the manuscript, or discussion. Supported by an NSF Graduate Fellowship; NSF grant DEB 9453498; and U.S. Department of Energy, Office of Energy Research, grant DE-FG0595ER62083.

17 November 2000; accepted 27 February 2001

Ecological Degradation in Protected Areas: The Case of Wolong Nature Reserve for Giant Pandas

Jianguo Liu,[1]* Marc Linderman,[1] Zhiyun Ouyang,[2] Li An,[1] Jian Yang,[3] Hemin Zhang[3]

It is generally perceived that biodiversity is better protected from human activities after an area is designated as a protected area. However, we found that this common perception was not true in Wolong Nature Reserve (southwestern China), which was established in 1975 as a "flagship" protected area for the world-renowned endangered giant pandas. Analyses of remote sensing data from pre- and post-establishment periods indicate that the reserve has become more fragmented and less suitable for giant panda habitation. The rate of loss of high-quality habitat after the reserve's establishment was much higher than before the reserve was created, and the fragmentation of high-quality habitat became far more severe. After the creation of the reserve, rates of habitat loss and fragmentation inside the reserve unexpectedly increased to levels that were similar to or higher than those outside the reserve, in contrast to the situation before the reserve was created.

More than 12,700 protected areas have been established around the world, accounting for 13.2 million km^2 (an area greater than the United States or China), or 8.81% of Earth's land surface (*1*). Although protected areas are generally believed to be the cornerstones of biodiversity conservation (*2–4*) and the safest strongholds of wilderness (*2*, *5*, *6*), human encroachments and threats are still very common in many protected areas (*7*, *8*). The problems of mismanagement and conservation politics have been widely publicized (*7*, *9*), but quantitative information about the deterioration of protected areas is scant (*10*). It is not clear whether all protected areas are effectively protected because there is little research comparing ecological degradation before and after the protected areas were established.

Is the rate of ecological degradation lower after the establishment of a protected area? To answer this question, we performed a case study of Wolong Nature Reserve, Sichuan Province, southwestern China (102°52′ to 103°24′E, 30°45′ to 31°25′N). We chose Wolong for three main reasons. First, it is the largest protected area designated for conserving the endangered giant pandas [*Ailuropoda melanoleuca* (*11*)] and contains approximately 10% of the wild panda population (*12*); created in 1975, the reserve covers an area of approximately 200,000 ha (*12*). Second, as in many other protected areas, there are local people residing in Wolong. Third, Wolong is a "flagship" nature reserve and has received exceptional financial and technical support from the Chinese government and many international organizations, such as the World Wildlife Fund (WWF) (*9*). To a large extent, Wolong's ecological fate represents the success or failure of tremendous conservation efforts made by the Chinese government and many international organizations (*9*).

We assessed the rates of change in forest cover and giant panda habitat before and after Wolong was established as a nature reserve. Forest cover, slope, and elevation are important factors affecting pandas (*11*, *12*). We incorporated these factors to estimate habitat suitability for pandas. In a process similar to hurricane damage assessment examining pre- and post-hurricane conditions (*13*, *14*), we quantified forest cover before and after the reserve's establishment, using remotely sensed data obtained at three different time points (*15*). The different sources of data used in our study are typical of many studies of land use and land cover change (*16–18*), because it is unrealistic to obtain remote sensing data on the same characteristics over a long period of time because of changes in the sensors. Neither aerial photography nor multispectral data were available for the entire time span of this study. Although cloud-free images with consistent phenology were not available, leaf-off [Corona data and Landsat Multispectral Scanner (MSS) data] versus leaf-on [Landsat Thematic Mapper (TM) data] conditions did not contribute significantly to the forest and panda habitat analyses

[1]Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, MI 48824, USA. [2]Department of Systems Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China. [3]China's Center for Giant Panda Research and Conservation, Wolong Nature Reserve, Wenchuan County, Sichuan Province, China.

*To whom correspondence should be addressed. E-mail: jliu@panda.msu.edu

for two reasons. First, our classifications were simple and consisted of only forest and nonforest categories. Second, because the 1997 image was acquired during leaf-on conditions, the analyses would give a more conservative estimate of forest loss. The images taken at different times were classified by means of photo interpretation, and the classifications were validated using several methods to ensure high quality (*19*).

In the reserve, elevation ranges from 1200 to 6250 m above sea level. Pandas' preferred areas are between 2250 and 2750 m above sea level (*11*, *12*). [Because of the limitations of abiotic factors such as elevation, even without human impacts less than half of the reserve is suitable for the panda (*12*).] Data on forest cover were obtained from the remote sensing analyses discussed above, whereas the slope and elevation values for each pixel were calculated from a digital elevation model that we developed using the topographic maps provided by the reserve. Using previously established habitat analysis procedures (*12*) and previous studies on pandas' biological requirements (*11*), panda habitat suitability was defined and divided into four categories: highly suitable, suitable, marginally suitable, and unsuitable (*12*). (Unsuitable habitat would be underestimated, because information regarding several factors affecting panda habitat, such as bamboo distribution, was not available for the entire reserve and was thus not considered in this study.) We then calculated the numbers and sizes of habitat patches as measures of the degree of habitat fragmentation (*20*) at each time point, using the FRAGSTATS program (*21*).

The average rates of change per year (in the amount of panda habitat, the number of habitat patches, and mean patch sizes) before and after the reserve's establishment were calculated in order to make appropriate comparisons, because the lengths of the pre-establishment period (1965–1974) and post-establishment period (1974–1997) were different. [When calculating rates of changes during pre- and post-establishment periods, we substituted the 1974 data for the data from 1975 (March), when the reserve was officially established, because of a lack of cloud-free remote sensing imagery from 1975. This data substitution should not generate a significant bias, because according to our interviews with local residents and reserve managers, human disturbance to the panda habitat in 1974 was not much greater than that during the previous years.] We also compared rates of change in panda habitat inside the reserve to those outside (where habitat is not protected), a method similar to the methods of spatial comparisons used in past studies (*4*, *22*, *23*). The "outside" was defined as a surrounding area (62,656 ha) within 3 km around the reserve boundary, because it shared similar biophysical characteristics (such as elevation) with the reserve.

The quantity and quality of panda habitat inside the reserve continued to decrease after the reserve was created (Fig. 1). More surprising, the rates of panda habitat change demonstrated that high-quality habitats were more severely affected after the reserve was established (Table 1). The rates of change (the loss of the total habitat area, decrease in the number of habitat patches, and reduction in the mean patch size) in highly suitable habitats were much higher after the reserve was set up than before the reserve's establishment (Table 1). For suitable habitats, the rate of loss of the total area after the reserve's establishment was lower than that before the reserve was established, but the rate of reduction in mean patch size was higher after the reserve was created. The number of habitat patches actually increased after the reserve was established. For marginally suitable habitats, the rates of loss and reduction in the number of patches were lower after the reserve was established, whereas mean patch sizes increased slightly. Rates of change (the increase in the total area, reduction in the number of patches, and increase in mean patch sizes) in unsuitable habitats were lower after the reserve was established.

Although the rates of habitat loss inside the reserve were lower than those outside the reserve before the reserve was created, after the designation of reserve status, the rates of habitat loss and fragmentation inside the reserve unexpectedly and dramatically increased to levels that were similar to or higher than those outside the reserve (Table 2). Furthermore, the differences in the rates of loss and fragmentation between inside and outside the reserve were particularly large for highly suitable habitats. For suitable habitats, the rate of habitat loss inside the reserve reached the same level as that in the surrounding area after the reserve was established. The rate of reduction in the mean patch size inside the reserve became even higher than that outside the reserve after the reserve's establishment. The amount of marginally suitable habitats increased outside the reserve but decreased inside the reserve after the reserve was established. The mean patch sizes of marginally suitable habitats continued to increase both inside and outside the reserve after the reserve was created. Both the amounts and mean patch sizes of unsuitable habitats inside and outside the reserve increased over time. The gap between the rates of increase in the amount of unsuitable hab-

Table 1. Ratios of mean annual rates of change (the amount of panda habitat, number of habitat patches, and mean patch size) after the reserve's establishment to those before the reserve was created. A ratio of >1 indicates that the absolute rate of change after the reserve's establishment was higher than that before the reserve was established. The signs within parentheses represent the directions of change ("+" indicates an increase and "−" indicates a decrease) before and after the reserve was established, respectively.

Habitat type	Amount of habitat	Number of patches	Mean patch size
Highly suitable	4.54 (−,−)	1.85 (−,−)	22.30 (−,−)
Suitable	0.56 (−,−)	0.78 (−,+)	1.11 (−,−)
Marginally suitable	0.07 (−,−)	0.25 (−,−)	0.07 (−,+)
Unsuitable	0.46 (+,+)	0.36 (−,−)	0.52 (+,+)

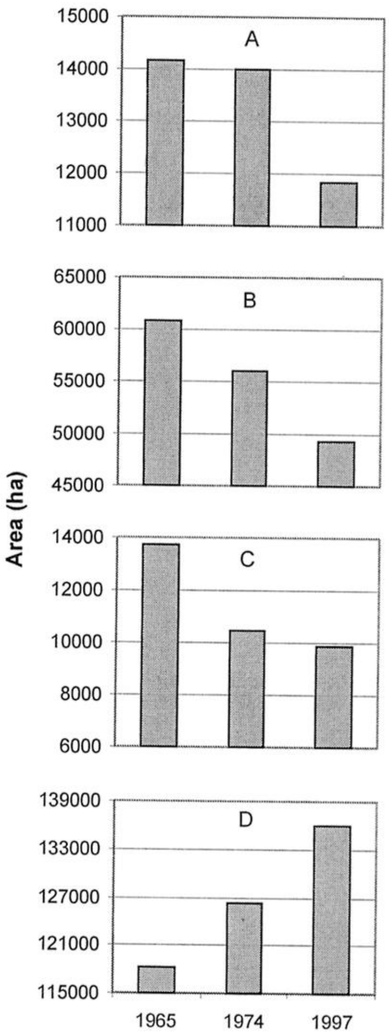

Fig. 1. Change in the amount of panda habitat in Wolong Nature Reserve before and after the reserve was established in March 1975. (**A**) Highly suitable habitat, (**B**) suitable habitat, (**C**) marginally suitable habitat, and (**D**) unsuitable habitat.

itats inside and outside the reserve has almost doubled since the reserve's establishment. Although the ratios of rates of increase in the mean patch sizes of unsuitable habitats inside the reserve to those outside the reserve slightly decreased after the reserve was created, the rate of increase in the mean patch sizes was still higher inside the reserve than outside.

The loss and fragmentation of panda habitats in Wolong were directly due to forest loss and fragmentation, which took two major forms (Fig. 2). First, forest fragments next to nonforest land continued to shrink and disappear. Second, large tracts of forest were divided into smaller tracts. The loss and fragmentation of the forest and of high-quality habitats were at least partially responsible for the dramatic decrease in the number of wild pandas in the reserve, from 145 in 1974 (*11*, *24*) to 72 in 1986 (*25*). Based on wildlife-habitat relationships (*26*) and the decreasing frequency of finding pandas in the wild (as indicated by our personal observations and by interviews with reserve biologists and local residents), the current number of wild pandas in Wolong is likely to be even smaller.

By examining the human population and activities in the reserve, it is not difficult to explain the much higher rates of loss and fragmentation of high-quality panda habitat after Wolong was designated as a protected area. There were 4260 local residents and 904 households inside the reserve in 1995, whereas there were only 2560 people and 421 households in 1975 when the reserve was established (*12*). This rapid increase in the local population was mainly due to the high birth rate (about 2.5 children per woman in 1997) in the reserve (*12*), because China's one-child policy does not apply to the members of the minority ethnic groups who account for approximately 75% of the local residents (*27*). The rate of increase in the number of households was even higher than the rate of the population increase because more young people established new households rather than staying with their parents and grandparents to live a traditional lifestyle, in which several generations live under one roof. In addition to the rapid increase in the population size and the number of households, the population structure has experienced a dramatic change (*27*). From 1982 to 1996, the labor force (people 20 to 59 years of age) of local residents in the reserve jumped by 60% (*27*).

Local people in the reserve were the direct driving force behind the destruction of the forest and of panda habitat (*27*). Most of the labor force are farmers, and there are a variety of economic activities in the reserve, including agriculture, fuelwood collection, timber harvesting, road construction and maintenance, Chinese herbal medicine collection, and tourism. The reserve attracts thousands of tourists each year, and the booming tourism has helped to transform the reserve from a closed economy to an open economy. For example, the tourism has significantly stimulated the extraction of natural resources such as fuelwood to produce marketable goods. These human activities in the reserve have had very negative impacts on the forest and on panda habitat (*12*). After the forests with easy access or close proximity to people were exhausted, forests in more remote areas at higher elevations (often high-quality panda habitat) became targets of destruction through activities such as fuelwood collection. In comparison, households outside the reserve have tighter restrictions on birth rate and have become less dependent on fuelwood as they have switched to coal, electricity, and other types of energy. These socioeconomic differences are among the causes of the discrepancy between the rates of habitat loss and fragmentation inside and outside the reserve.

Biodiversity conservation is faced with a much greater challenge than previously thought because even a flagship protected area such as Wolong was not better protected after its establishment. Quantitative analyses of pre- and post-establishment conditions inside and outside protected areas produce insightful results and provide much-needed information to develop strategies for truly effective biodiversity conservation. Because

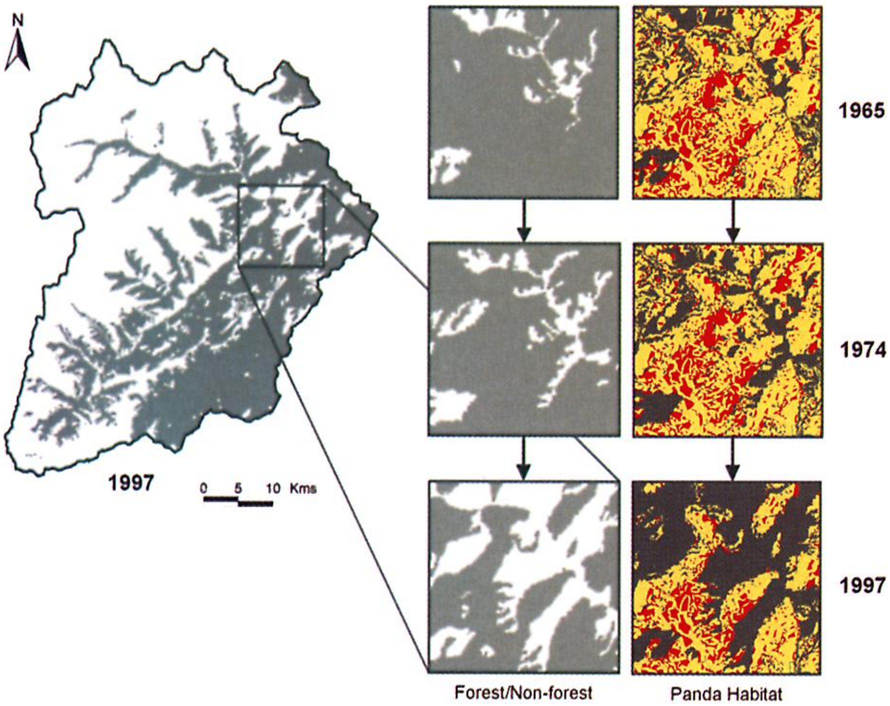

Fig. 2. Forest distribution pattern across Wolong Nature Reserve in 1997 (left), with illustration of loss and fragmentation of forest (center) and panda habitats (right) within a representative area before and after the reserve was established. Gray areas are forested; those shown in white are nonforested. Highly suitable, suitable, marginally suitable, and unsuitable habitats are indicated in red, yellow, green, and black, respectively.

Table 2. Ratios of mean annual rates of change (the amount and mean patch size of panda habitats) inside the reserve to those outside the reserve, before and after the reserve was established. A ratio of <1 indicates that the absolute rate of change inside the reserve was lower than the rate outside the reserve; a ratio of >1 indicates that the absolute rate of change was higher. The signs within parentheses represent the directions of change ("+" indicates an increase and "–" indicates a decrease between two time points), inside and outside the reserve, respectively.

Habitat type	Amount of habitat		Mean patch size	
	Before establishment	After establishment	Before establishment	After establishment
Highly suitable	0.29 (–,–)	1.15 (–,–)	0.05 (–,–)	4.38 (–,–)
Suitable	0.71 (–,–)	0.98 (–,–)	4.37 (–,–)	4.79 (–,–)
Marginally suitable	0.61 (–,–)	0.96 (–,+)	1.01 (–,–)	0.88 (+,+)
Unsuitable	0.64 (+,+)	1.17 (+,+)	1.28 (+,+)	1.16 (+,+)

most of the world's protected areas have been established since the early 1970s (*1*), satellite imagery has been obtained at periodic intervals since 1972, and aerial photographs of many regions date back years or even decades earlier (*16*), it is also feasible to assess the effectiveness of many protected areas on the basis of their pre- and post-establishment conditions, using the approach presented here. To better understand the effectiveness of protected areas and develop more feasible policies, it is essential to integrate ecology with human demography, human behavior, and socioeconomics (*12*, *28*).

References and Notes

1. International Union for Conservation of Nature and Natural Resources (IUCN), *United Nations List of Protected Areas* (World Conservation Monitoring Centre and IUCN Commission on National Parks and Protected Areas, IUCN, Gland, Switzerland, 1998).
2. R. F. Noss, in *National Parks and Protected Areas: Their Role in Environmental Protection*, R. G. Wright, Ed. (Blackwell Science, Cambridge, MA, 1996), pp. 91–120.
3. S. L. Pimm, J. H. Lawton, *Science* **279**, 2068 (1998).
4. A. G. Bruner, R. E. Gullison, R. E. Rice, G. A. B. da Fonseca, *Science* **291**, 125 (2001).
5. M. E. Soulé, M. A. Sanjayan, *Science* **279**, 2060 (1998).
6. J J. Armesto, R. Rozzi, C. Smith-Ramirez, M. T. K. Arroyo, *Science* **282**, 1271 (1998).
7. V. Dompka, Ed., *Human Population, Biodiversity and Protected Areas: Science and Policy Issues* (American Association for the Advancement of Science, Washington, DC, 1996).
8. C. P. van Schaik, R. A. Kramer, in *Last Stand: Protected Areas and The Defense of Tropical Biodiversity*, R. Kramer, C. van Schaik, J. Johnson, Eds. (Oxford Univ. Press, New York, 1997), pp. 212–230.
9. G. B. Schaller, *The Last Panda* (Univ. of Chicago Press, Chicago, IL, 1994).
10. C. P. van Schaik, J. Terborgh, B. Dugelby, in *Last Stand: Protected Areas and The Defense of Tropical Biodiversity*, R. Kramer, C. van Schaik, J. Johnson, Eds. (Oxford Univ. Press, New York, 1997), pp. 64–89.
11. G. B. Schaller, J. Hu, W. Pan, J. Zhu, *The Giant Pandas of Wolong* (Univ. of Chicago Press, Chicago, IL, 1985).
12. J. Liu *et al.*, *Conserv. Biol.* **13**, 1360 (1999).
13. N. H. Sulliavan, W. B. Bowden, W. H. McDowell, *Biotropica* **31**, 382 (1999).
14. K. Basnet, G. E. Likens, F. N. Scatena, A. E. Lugo, *J. Trop. Ecol.* **8**, 47 (1992).
15. The remotely sensed data used were Corona photographs from 1965, Landsat MSS data from 1974 (the year right before the reserve was established), and Landsat TM data from 1997. The Corona data are stereopair photographs acquired 20 January 1965 as part of the Corona photoreconnaissance satellite project (U.S. Geological Survey Eros Data Center, Sioux Falls, SD). Both Landsat MSS (3 January 1974) and Landsat TM data (27 September 1997) were obtained from China's Satellite Ground Station (Beijing, China).
16. T. M. Lillesand, R. W. Kiefer, *Remote Sensing and Image Interpretation* (Wiley, New York, ed. 3, 1994).
17. D. A. Stow, D. Collins, D. McKinsey, *Geocarto International* **3**, 3 (1990).
18. J. R. Jensen, *Introductory Digital Image Processing: A Remote Sensing Perspective* (Prentice Hall, Upper Saddle River, NJ, ed. 2, 1996).
19. All images were georeferenced to ground control points collected throughout the reserve, using Global Positioning System (GPS) receivers (Pathfinder Pro XRS) with submeter accuracy. Because the Corona data are black-and-white photos, we did a forest/nonforest classification using photo interpretation (or visual classification) to provide a consistent methodology for each of the three time points (1965, 1974, and 1997). The area of interest within each Corona photo was scanned into a digital image at 1200 dots per inch, giving a ground resolution of approximately 10 m. The individual Corona images were then combined into a single coverage and were classified on the basis of photo interpretation. To enhance the classification accuracies, we used general vegetation delineations on topographic maps, field observation information, interviews with local residents, and observations of areas that were undisturbed over time. The Landsat MSS and TM data were classified with the same procedure used for the Corona photos. To provide consistency, the visual interpretations of the Landsat data were done using false-color infrared images with similar band combinations (MSS bands 4, 5, and 6 and TM bands 2, 3, and 4), and the TM images (30 m by 30 m) were degraded and resampled to a resolution of 80 m by 80 m. To validate the visual interpretations, we surveyed 250 ground-truth plots (the size of each plot was equal to 60 m by 60 m, or 2 × 2 TM image pixels) in the summers of 1998 and 1999 in the reserve, using GPS units (with 1- to 3-m accuracy after differential corrections), and we used digital methods [supervised and unsupervised classifications (*16*, *18*)] based on all four MSS bands and on comparable TM bands to classify the Landsat MSS and TM imagery. The overall correspondences between the digital and visual classifications ranged from 82 to 87%. Based on standard accuracy assessment methods (*16*), the accuracy for forest classifications of the 1997 TM data using visual and digital methods was between 80 and 88% when the results were compared with the independent data from the ground-truth plots. The visual and digital methods resulted in consistent total forest areas (the forest areas resulting from the digital methods were only 0.61 to 5.76% different from those resulting from the visual method). These testing results indicate that the visual classifications in our study were of high quality and comparability.
20. R. T. T. Forman, *Land Mosaics: The Ecology of Landscapes and Regions* (Cambridge Univ. Press, Cambridge, 1995).
21. K. McGarigal, B. J. Marks, *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure* (*Version 2.0*) (Oregon State Univ., Corvallis, OR, 1994).
22. G. A. Sanchez-Azofeifa, C. Quesada-Mateo, P. Gonzalez-Quesada, S. Dayanandan, K. S. Bawa, *Conserv. Biol.* **13**, 407 (1999).
23. T. M. Caro *et al.*, *Afr. J. Ecol.* **36**, 303 (1998).
24. Giant Panda Expedition, *Acta Zool. Sin.* **20**, 162 (1974) (in Chinese).
25. China's Ministry of Forestry and WWF, *Conservation and Management Plan for Giant Pandas and Their Habitat* (Beijing, China, 1989) (in Chinese).
26. M. L. Morrison, B. G. Marcot, R. W. Mannan, *Wildlife-Habitat Relationships: Concepts and Applications* (Univ. of Wisconsin Press, Madison, WI, 1992).
27. J. Liu, Z. Ouyang, Y. Tan, J. Yang, H. Zhang, *Popul. Environ.* **21**, 45 (1999).
28. J. Liu, Ed., Integration of Ecology with Human Demography, Behavior, and Socioeconomics, *Ecol. Model.* (special issue), in press.

29. We thank S. Pimm, C. Lepczyk, J. Qi, and two anonymous reviewers for helpful suggestions and comments on earlier drafts of this paper; D. Rutledge, A. Thomas, and J. Xie for technical assistance; Q. Wang, S. Song, W. Taylor, and the Wolong Nature Reserve for logistic support (especially the assistance of J. Huang, Y. Tan, and S. Zhou); and NSF, NASA, NIH, the American Association for the Advancement of Science/The John D. and Catherine T. MacArthur Foundation, Michigan State University, the National Natural Science Foundation of China, the Ministry of Science and Technology of China (grant number G2000046807), and China Bridges International for financial support.

8 December 2000; accepted 20 February 2001

Delayed Compensation for Missing Keystone Species by Colonization

S. K. Morgan Ernest* and James H. Brown

Because individual species can play key roles, the loss of species through extinction or their gain through colonization can cause major changes in ecosystems. For almost 20 years after kangaroo rats were experimentally removed from a Chihuahuan desert ecosystem in the United States, other rodent species were unable to compensate and use the available resources. This changed abruptly in 1995, when an alien species of pocket mouse colonized the ecosystem, used most of the available resources, and compensated almost completely for the missing kangaroo rats. These results demonstrate the importance of individual species and of colonization and extinction events in the structure and dynamics of ecosystems.

Single species or functional groups of closely related, ecologically similar species can affect the structure and dynamics of ecosystems in several ways: (i) as "mechanical engineers," they can alter physical structure and flows of energy and materials (*1*); (ii) as predators, parasites, and pathogens, they can affect the dynamics of prey or host populations (*2*); (iii) as mutualists, they can supply essential resources or services (*3*); and (iv) as producers and consumers, they can influence the levels and flows of energetic and material resources (*4*). Species that have large ramifying effects on ecosystems through direct and indirect pathways are often called "keystones" (*2*, *5*, *6*). Studies that combine experimental manipulations with long-term moni-

Department of Biology, University of New Mexico, Albuquerque, NM 87131 USA.

*To whom correspondence should be addressed at Program in Ecology, Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA. E-mail: morgan.ernest@ttu.edu