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TEMPORAL CHANGES IN GIANT PANDA HABITAT CONNECTIVITY ACROSS BOUNDARIES OF WOLONG NATURE RESERVE, CHINA

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Abstract. Global biodiversity loss is largely driven by human activities such as the conversion of natural to human-dominated landscapes. A popular approach to mitigating land cover change is the designation of protected areas (e.g., nature reserves). Nature reserves are traditionally perceived as strongholds of biodiversity conservation. However, many reserves are affected by land cover changes not only within their boundaries, but also in their surrounding areas. This study analyzed the changes in habitat for the giant panda (*Ailuropoda melanoleuca*) inside Wolong Nature Reserve, Sichuan, China, and in a 3-km buffer area outside its boundaries, through a time series of classified satellite imagery and field observations. Habitat connectivity between the inside and the outside of the reserve diminished between 1965 and 2001 because panda habitat was steadily lost both inside and outside the reserve. However, habitat connectivity slightly increased between 1997 and 2001 due to the stabilization of some panda habitat inside and outside the reserve. This stabilization most likely occurred as a response to changes in socioeconomic activities (e.g., shifts from agricultural to nonagricultural economies). Recently implemented government policies could further mitigate the impacts of land cover change on panda habitat. The results suggest that Wolong Nature Reserve, and perhaps other nature reserves in other parts of the world, cannot be managed as an isolated entity because habitat connectivity declines with land cover changes outside the reserve even if the area inside the reserve is well protected. The findings and approaches presented in this paper may also have important implications for the management of other nature reserves across the world.

Key words: Ailuropoda melanoleuca; *buffer area; China; cross-boundary; giant panda; habitat connectivity; land cover change; protected areas; reserve boundary; Wolong Nature Reserve.*

INTRODUCTION

Agricultural areas currently cover approximately one-quarter of Earth's terrestrial surface, with worldwide increases occurring at the expense of natural ecosystems. Future scenarios project that 10–20% of the remaining natural grasslands and forests will be converted primarily to agriculture by 2050 (Millennium Ecosystem Assessment 2005). This conversion of natural to human-dominated landscapes constitutes one of the main drivers of global biodiversity loss (Vitousek et al. 1997, Sala et al. 2000, Pereira et al. 2004, Waltert et al. 2004). Although the specific impacts of this conversion differ widely among taxonomic groups, all species in general are affected by habitat loss and modification (Schulze et al. 2004).

The establishment of protected areas (e.g., nature reserves) has been a popular approach to conserving biodiversity. Worldwide, more than 100 000 protected areas have been established to minimize human impacts on biodiversity (IUCN 2003). Although the designation of nature reserves is the cornerstone of biodiversity conservation policies, in many instances biodiversity inside reserves is not necessarily better protected than that outside (Liu et al. 2001, Caro 2002, Parks and Harcourt 2002, Meir et al. 2004). This reduced protection occurs because nature reserves might not meet the requirements established during their initial designation. For example, conservation investments are constrained by budgets and opportunities to implement conservation actions tend to be unpredictable, both in space and through time (Meir et al. 2004). Therefore, human land cover changes may not be reduced inside reserves (Liu et al. 2001, Meir et al. 2004). Bruner et al. (2001) analyzed 93 protected areas in 22 tropical countries and found that most of them are successful at stopping land clearing and mitigating human

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FIG. 1. Location and topography of the Wolong Nature Reserve in Sichuan Province, China.

activities such as logging and hunting, but effectiveness is correlated with management activities.

In China, a country that has very high biodiversity (Li et al. 2003, Liu et al. 2003), the first nature reserve was established in 1956. By the end of 2003 there were ~2000 nature reserves, comprising an area of ~13.4% of the total land area of China (Liu and Diamond 2005). Because local people live inside many nature reserves, changes in land cover occur both inside reserves and adjacent to their borders. For example, Wolong Nature Reserve (Fig. 1), which was mainly designed for the protection of the endangered giant panda (*Ailuropoda melanoleuca*; see Plate 1), is home to more than 6000 animal and plant species as well as close to 5000 local residents. Local residents in Wolong Nature Reserve carry out diverse socioeconomic activities such as farming, fuelwood collection, livestock breeding, Chinese herbal medicine collection, road construction, and ecotourism. These human activities are the main reasons for the rapid degradation of panda habitat, with fuelwood collection being one of the key factors (Schaller et al. 1985, Schaller 1993, Liu et al. 1999, 2001, An et al. 2001, 2002). Fuelwood collection constitutes the primary source of energy for farmers, both inside and outside the reserve. It constitutes the entire source of energy used for cooking pig fodder and about one-half and one-third of the energy used for heating during winter and cooking human food, respectively. Cooking pig fodder accounts for more than 80% of the total fuelwood consumption per household (X. Chen et al., *unpublished data*).

More than 90% of the people living inside the reserve are farmers. This high percentage is presumably the result of a lack of alternative economic developments. In contrast, rapid industrial development has occurred outside the reserve in the adjacent townships of Yingxiu, Baihua, and Shuimo (Fig. 2). During the last decade these townships exhibited an increase in industrial production (e.g., aluminum and manganese in Yingxiu, plastics and steel in Baihua, and silicon, aluminum and steel in Shuimo), providing employment with higher incomes to local communities. This is the primary reason why only ~60% of the local residents in these three townships outside the reserve are farmers (Fig. 3), because the increase in industrial production has shifted about 30% of the local residents from agriculture to nonagricultural activities (Yingxiu, Baihua, and Shuimo officials, *personal communication*).

Land cover changes occurring adjacent to nature reserves may pose additional challenges to biodiversity conservation inside the reserves (Hansen et al. 2002). One of the challenges is the likely reduction in habitat connectivity between areas inside and outside nature reserves. Habitat connectivity between Wolong Nature Reserve and its surrounding areas should constitute an important consideration for panda conservation, partic-

FIG. 2. Map of the townships inside and outside Wolong Nature Reserve and the location and boundaries of the nature reserves (NR) adjacent to Wolong Nature Reserve. The eastern boundary of the reserve, used for calculating habitat connectivity between the inside of Wolong Nature Reserve and the outside, is also shown.

ularly in the establishment of corridors that enhance the movement of pandas among different nature reserves (Xu et al. 2006). Such is the case of three nature reserves adjacent to Wolong (Fig. 2): Caopo in the northern part of the reserve, and Anzihe and Heishuihe in the southern part. A higher degree of panda habitat connectivity among these nature reserves will reduce the possible detrimental effects of stochastic processes such as fire, disease, localized extreme weather events (Tilman et al. 1994), and, most importantly, bamboo flowering (Taylor and Qin 1988, Reid and Hu 1991) on panda populations. On the contrary, if population isolation continues or increases, the long-term viability of the species in the wild will be heavily threatened, because small populations of giant pandas have a greater probability of extinction by inbreeding depression (Schaller et al. 1985, MacKinnon and De Wulf 1994, Yan et al. 2000). Therefore, the evaluation of the degree of habitat connectivity between the interior and the surrounding areas of Wolong Nature Reserve is necessary in order to assess its degree of isolation. Even if areas inside the reserve are well protected, pandas may eventually become restricted to only those habitats within the reserve because humans continue to use areas outside its boundaries. This increases the likelihood of panda population isolation and subjects the panda to higher demographic extinction pressures.

Although much work has been done in Wolong Nature Reserve with regard to giant panda habitat assessments (e.g., Schaller et al. 1985, De Wulf et al. 1988, MacKinnon and De Wulf 1994, Ouyang et al. 1995), these early studies have been performed with up to two dates of imagery and cover only the first years from the establishment of the reserve. Therefore, to address the challenge of giant panda habitat isolation across space and through time, we conducted a land cover change study inside Wolong Nature Reserve as well as its adjacent areas. This case study builds upon the time series analysis of satellite imagery (1965, 1974, and 1997) performed by Liu et al. (2001), with additional imagery acquired in 2001, in order to: (1) evaluate the changes in giant panda habitat along the time series of imagery acquisitions, both inside and outside Wolong Nature Reserve; (2) evaluate the temporal changes in panda habitat connectivity across the boundaries of the reserve; and (3) analyze the habitat suitability scheme used in terms of actual giant panda use, as defined by the presence of feces in the different habitat suitability classes.

METHODS

Study area

Wolong Nature Reserve is located in Sichuan Province, southwest China (Fig. 1). It was initially established during the early 1960s with 200 km^2 and then expanded to 2000 km^2 in 1975 (Li et al. 2003). It is one

FIG. 3. Percentage of farmers in the total population of Wolong Nature Reserve (NR) and its east-bordering townships in 2004. Numbers above bars correspond to total population sizes. Data were obtained from interviews with officials in each of the townships (X. Chen et al., *unpublished data*). Gray bars represent values of townships that occur outside Wolong Nature Reserve; the black bar represents the combined value of Gengda and Wolong townships, both completely within the reserve.

of the largest nature reserves in China designed to protect the endangered giant panda. Situated between the Sichuan Basin and the Qinghai-Tibet Plateau, it is characterized by high mountains and deep valleys, with elevation ranging from 1200 m to 6250 m above sea level, encompassing several climatic zones (Schaller et al. 1985). Together with this strong altitudinal and climatic gradient there is an enormous variation in topography, soils, and hydrology that leads to a diverse flora and fauna. The forests in the reserve grow in a characteristic vertical zonation, from evergreen and deciduous broad-leaf forests at lower elevations (~1500 m above sea level) to subalpine coniferous forests at higher elevations (~2700 m above sea level) (Schaller et al. 1985). Wolong Nature Reserve is part of the international Man and Biosphere Reserve Network (He et al. 1996), protects the habitat of ~10% of the wild panda population (Zhang et al. 1997), and has drawn unmatched domestic and international attention (Liu et al. 1999).

The surrounding areas located in the western side of the reserve are characterized by extremely high mountains (Fig. 1), which constitute barriers to panda movement and have very few small and isolated patches of panda habitat. In contrast, the surrounding areas located on the eastern side of the reserve contain a significant amount of panda habitat. Wolong Nature Reserve consists of two townships completely within its boundaries (Gengda and Wolong), while four townships (Yingxiu, Baihua, Shuimo, and Sanjiang) lie adjacent on its eastern boundary (Fig. 2). Although Yingxiu, Baihua, and Shuimo are completely outside the reserve, Sanjiang has more than half of its area inside the reserve (Fig. 2).

Giant panda habitat suitability mapping

The spatial distribution of suitable habitat for the panda has been normally established based on four of its main biological requirements (Schaller et al. 1985, Johnson et al. 1988, Reid et al. 1989, Ouyang et al. 1995): (1) areas under forest cover; (2) presence of bamboo; (3) altitudinal range between 1500 and 3500 m, with an optimal range between 2500 and 3000 m; and (4) slopes of less than 45°, with optimal slopes of less than 15°. A combination of these four characteristics is required to obtain an accurate habitat assessment for the pandas (see Liu et al. 1999: Table 1).

To determine changes in forest cover over time, land cover maps of 1965, 1974, and 1997 were obtained from a previous study (Liu et al. 2001) that used satellite imagery acquired in 1965 (Corona), 1974 (Landsat MSS), and 1997 (Landsat TM), with a visual classification that separated forest from non-forest cover (Liu et al. 2001). A map for 2001 was obtained by means of a digital classification algorithm applied to a Landsat TM acquired on 13 June 2001. Corona photographs were scanned into a digital image at 1200 dots per inch, providing a ground resolution of about 10 × 10 m. Landsat MSS and TM have spatial resolutions of 80 × 80 m and 30 × 30 m, respectively. Therefore, the factor of spatial resolution (i.e., the area of ground covered by each pixel) constitutes an important issue for depicting changes in the panda habitat through time. One way to overcome the differences in spatial resolution of different sensor systems is to degrade and resample the finer resolution images into coarser ones. This is normally performed by means of integrating (i.e., averaging) a group of finer resolution pixels into a single coarser resolution one. Although this assumes an idealized square wave response on the part of the sensor (Woodcock and Strahler 1987, Cao and Lam 1997), it provides a way of making different data sets more comparable. In the present study, the scanned Corona and Landsat TM data sets were degraded into 80 × 80 m pixels to match the spatial resolution of the Landsat MSS.

Table 1. Accuracy assessment of the visual and digital forest/non-forest classifications of the 1997 Landsat TM data set, using ground control points acquired during the summer of 1998.

Accuracy	Visual classification	Digital classification
Overall accuracy	75.1	74.6
Omission error	19.5	28.0
Commission error	31.9	22.0

Notes: Values are expressed as percentages. Errors of omission correspond to pixels classified as non-forest when in reality they were forest. Errors of commission correspond to pixels classified as forest when in reality they were non-forest.

The digital classification of the 2001 data set consisted of an unsupervised algorithm using the ISODATA technique, which is an iterative process for nonhierarchical pixel classification (Jensen 1996). The classification used a maximum of 100 iterations with a convergence (the maximum percentage of the pixels in the image whose class values are allowed to be unchanged between iterations) of 0.99, and produced an output of 24 spectral classes. We then applied a post-classification sorting method in which the 24 spectral classes were combined into three information classes: forest, non-forest, and shadows. These information classes were attributed through a combination of visual interpretation and information on land cover, collected in the field during the summers of 2000 and 2001. In order to further separate forest from non-forest pixels under shadowed areas, all of the pixels classified as shadow were isolated from the original Landsat image, and a second unsupervised classification was applied only to these pixels. This classification used a maximum of 50 iterations with a final convergence of 0.99 and produced an output of six spectral classes that were sorted into forest and non-forest. The outputs of both unsupervised classifications were merged into a final forest/non-forest map. Accuracy assessment of this map was calculated by using a total of 119 ground truth points (not used in the attribution of the information classes) obtained in the field during the summers of 2000

(80 points) and 2001 (39 points). These points were collected using a real-time, differentially corrected GPS unit, which provided accuracy below 1 m. Overall accuracy, omission, and commission errors were calculated (Jensen 1996). In order to assess the consistency of the visual and digital classifications, the same approach of nested, unsupervised classification was applied to the 1997 Landsat TM data set, the output was compared to the visual classification obtained by Liu et al. (2001), and the accuracy of both classifications (i.e., visual vs. digital) was determined by using a total of 200 ground truth points obtained in the field during the summer of 1998 (Liu et al. 2001).

Overall accuracy of the maps from 1965 to 1997 ranged from 80% to 88% (Liu et al. 2001). Accuracy of the 1965 and 1974 maps was assessed using areas in the ground known to have not changed since at least the 1960s, based on information obtained from the local people during the field data acquisitions in 1998 (M. Linderman, *personal observation*). The agreement between visual and digital classification into forest and non-forest classes performed in the 1997 data set was 83.2%. When these classifications were compared with the ground truth data, both provided an overall accuracy of ~75%, with the visual classification exhibiting higher errors of commission and the digital classification showing higher errors of omission (Table 1). Thus, visual and digital algorithms provide comparable results, and both classification algorithms depict most of the forest cover areas. However, there are still areas of uncertainty, particularly in the attribution of secondary forests, which range from young to mature forests. They provide the biggest source of classification error because they constitute intermediate steps between abandoned agricultural areas and mature forests. Our accuracy analysis shows that the visual classification algorithm attributes more young secondary forest into the forest class than the digital classification algorithm does. For this reason, we used a more conservative approach in the classification of the 2001 Landsat TM data set, in which areas spectrally associated with young secondary forests in the field surveys were placed under the forest cover category. Using the ground truth points acquired during the summers of 2000 and 2001, the overall accuracy of the forest cover map obtained from the 2001 Landsat TM data set was 78.2%, with errors of omission and commission of 22.2% and 21.3%, respectively. Some of these classification errors could be attributed to changes in land cover between field data collection (i.e., summer of 2000) and remotely sensed data collection (i.e., June 2001).

Linderman et al. (2004) developed a method to map the bamboo distribution using remotely sensed data from 1997 in an artificial, nonlinear neural network, and an assessment of the effects of having this information layer for panda habitat mapping was performed (Linderman et al. 2005). However, no accurate ground truth data on bamboo distribution are available for the earlier time steps (1965 and 1974). Therefore, bamboo information was not included in this study and panda habitat suitability was classified using only a combination of forest cover, elevation, and slope, following the four-category scheme suggested by Liu et al. (2001): highly suitable, moderately suitable, marginally suitable, and unsuitable. Information on elevation and slope was derived from a digital elevation model developed for the study area (Liu et al. 2001).

Spatiotemporal changes of panda habitat

Analyses of the spatiotemporal changes of panda habitat were performed inside the boundary of the nature reserve and within a 3-km buffer area outside this boundary. Although some studies have used a distance of $\geq$10 km as buffers around natural reserves (e.g., Curran et al. 2004, DeFries et al. 2005), our selection of 3 km as a buffer distance was dictated by data limitations, because no remotely sensed data were available for the entire study period beyond 3 km outside the reserve.

Because the study area is truncated by an artificial boundary (the boundary of the nature reserve), there are biases in the comparison of panda habitat between the inside and the outside of the reserve, particularly in the degree of habitat fragmentation. Thus, it is better to express the changes in relative terms (i.e., as a percentage of the potential habitat) as opposed to the actual values, in order to make fair comparisons. Therefore, we established a potential habitat baseline condition from which the changes can be compared on relative terms. For this, a map of the potential habitat (maximum area in each of the suitability categories) was modeled by using the digital elevation model (Liu et al. 2001) to derive a map of maximum forest cover, because this land cover class is expected to occur at elevations below 3600 m, and in slopes less than 60° (Schaller et al. 1985).

Average rates of suitable panda habitat change (in each of the three categories of habitat suitability), both inside and outside the reserve, for the periods 1965–1974, 1974–1997, 1997–2001, and 1965–2001 (entire study period) were determined by

$$r = \left[\left(\frac{A_e - A_b}{A_b}\right)/t\right] \times 100 \quad (1)$$

where r is the habitat change rate (percentage) per year, A_b is habitat area at the beginning of the period, A_e is habitat area at the end of the period, and t is the number of years for a given period (Liu et al. 2001). If the changes are due to losses (increases) of habitat, r takes negative (positive) values.

Habitat connectivity at the eastern boundary of Wolong Nature Reserve

In order to meet daily needs, pandas must move across heterogeneous landscapes comprising suitable and unsuitable areas. Such movements are influenced by

PLATE 1. Adult female giant panda (*Ailuropoda melanoleuca*) in the Panda Valley (altitude 2500 m) of Wolong Nature Reserve (China), 31 December 2006. Photo credit Wei Liu.

the distance between habitat patches and the pandas' mobility. Daily distances traveled by radio-collared pandas among patches of habitat without feeding varied, on average, between 100 m and 600 m (Schaller et al. 1985). These authors also reported that several uncollared and undisturbed pandas moved with no feeding for 1 km or more, with 4.2 km being the longest distance recorded. Therefore, to quantify habitat connectivity between the Wolong Nature Reserve and its surrounding 3-km buffer area, we assessed the portion of habitat present within linear distances of 100, 200, 400, 1000, 1600, and 2000 m across the eastern boundary of the reserve (see Fig. 2). We only focused on the eastern boundary of the reserve because the western boundary has no panda habitat due to high elevations (Fig. 1). In addition, in order to evaluate the effects of land cover change on habitat connectivity across this eastern boundary, we compared the potential (i.e., with no changes in land cover) amount of habitat connected vs. the amount of habitat connected if: (1) both the inside and the outside of the nature reserve experienced changes in land cover (the actual output at each time step); (2) only the outside of the reserve experienced changes in land cover; and (3) only the inside of the reserve experienced changes in land cover.

Assessment of giant panda occurrence

The classification of habitat suitability described earlier is based on the potential of the pandas to occupy a particular area, without considering whether the pandas are actually using the areas. Thus, it is important to assess the frequency of panda presence in each of the suitability classes in order to evaluate their significance in terms of actual panda occurrences. Panda occurrence was assessed using the distribution patterns of fecal droppings. Fecal droppings are an accurate and straightforward indicator for the presence of pandas because they are deposited frequently (an average of 97 droppings/day or 4 droppings/hour) and remain visible for several months (Schaller et al. 1985). Field sampling of panda fecal droppings was carried out in May–August 2001, May–November 2002, and June–August 2003 (Bearer 2005). In total, 436 plots (30 $\times$ 30 m) were located throughout Wolong Nature Reserve, in places with contrasting land cover types (e.g., forest, shrubland, cropland, and grassland). The location of these plots was as random as the topography of the nature reserve allowed (i.e., some areas chosen through the randomization process could not be visited due to access difficulties). The presence of panda feces was determined in each plot, combined with a visual assessment of

FIG. 4. Time series of forest cover in Wolong Nature Reserve and in a 3-km buffer outside of the reserve boundary. (A) Potential forest cover map modeled from a digital elevation model based on a hypothetical distribution of forest below 3600 m and in slopes less than 60 degrees. (B–E) Forest cover in 1965, 1974, 1997, and 2001, respectively. Areas under cloud cover in the 1965 and 1974 imagery were masked-out from all other maps.

bamboo cover. The center of each plot was georeferenced with a real-time differentially corrected GPS unit. These plots were sorted into areas with bamboo (≥10% cover) and without bamboo (<10% cover). This 10% threshold was established because values less than 10% bamboo cover do not provide useable biomass for the pandas (Linderman et al. 2004). Using digital overlaying techniques (in a Geographic Information System), this data set was linked with the land cover and habitat suitability data sets just described. This was done in order to determine how pandas used different land cover types, as well as the areas classified under the different habitat suitability categories. In order to evaluate if secondary forests can be converted into giant panda habitat, we assessed the frequency of plots with giant panda feces in secondary forests that were cleared between 1960–1965, 1970–1975, 1995–1997, and 1999–2001. These dates were chosen to correspond with the

TABLE 2. Temporal change of giant panda habitat suitability expressed as a percentage of the potential habitat modeled for each class.

	Suitability inside			Suitability outside		
Year	Marginal	Moderate	High	Marginal	Moderate	High
1965	70.7	88.2	90.7	77.0	96.0	100.0
1974	51.8	81.6	90.5	40.4	83.7	93.0
1997	50.5	70.1	76.4	56.1	69.6	81.3
2001	45.7	70.1	75.1	44.1	72.3	78.7

TABLE 3. Annual rates of giant panda habitat change (r) between 1965 and 2001, both inside the Wolong Nature Reserve boundary and within a 3-km buffer outside the boundary.

Year	Inside				Outside			
	MS	S	HS	Total habitat	MS	S	HS	Total habitat
1965–1974	−2.96	−0.84	−0.02	−1.02	−5.28	−1.43	−0.81	−1.86
1974–1997	−0.12	−0.61	−0.68	−0.56	1.69	−0.73	−0.55	−0.50
1997–2001	−2.35	−0.01	−0.42	−0.38	−5.36	0.97	−0.80	−0.14
1965–2001	−0.98	−0.57	−0.48	−0.62	−1.19	−0.69	−0.60	−0.74

Notes: The rate of panda habitat change, r, is expressed as the percentage of remaining habitat that changed per year (Eq. 1). Negative values represent a decrease in suitable habitat, whereas positive values represent an increase. Abbreviations: MS, marginally suitable; S, moderately suitable; HS, highly suitable.

dates of remote sensing imagery. Five-year time spans were used in older forests because it was more difficult to estimate the exact years when the forests were cleared.

RESULTS

Dynamics of forest cover

Between 1965 and 2001, the forests inside and outside of Wolong Nature Reserve had been significantly transformed to other land cover types (Fig. 4). Even though forest cover has the potential to be the dominant feature in Wolong Nature Reserve (ideally occupying ~55.6% of the reserve; Fig. 4A), much of it has been converted into other land cover types. At the time of the establishment of the reserve in 1975 (Liu et al. 2001), forests occupied ~42.7% of the entire nature reserve (i.e., the area during 1974; Fig. 4C). By 2001, forests occupied only ~36.3% of the reserve (Fig. 4E).

Changes in giant panda habitat

Between 1965 and 2001, the overall trend was toward a loss of panda habitat over time. The temporal progression of the amount of habitat present and its annual rates of change both inside and outside the reserve are shown in Tables 2 and 3, respectively. With the exception of the highly suitable habitat class inside the reserve, the 1965–1974 period showed higher annual rates of habitat loss than the 1974–1997 period (Table 2), both inside and outside of the Wolong Nature Reserve, but the absolute amount of panda habitat loss was larger in the latter than in the former due to a longer time period. Rates of habitat loss along the entire study period (i.e., between 1965 and 2001) were, on average, ~17% lower inside the Wolong Nature Reserve than in the 3-km buffer outside the reserve (Table 3).

The 3-km buffer area outside the reserve exhibited an increase in moderately suitable habitat during the 1997–2001 period (Tables 2 and 3), although the total panda habitat exhibited an overall decrease (Table 3). Wolong Nature Reserve did not exhibit any increases in panda habitat during the entire study period, but the loss of moderately suitable habitat was stopped or stabilized during the 1997–2001 period (Tables 2 and 3).

FIG. 5. Percentage of 30 × 30 m sampling plots found to have giant panda feces within old-growth forests and secondary forests that were cleared during the approximate time periods of the classified imagery (i.e., 1965, 1974, 1997, and 2001). Numbers above bars are the sample sizes.

Giant panda occurrence

Giant panda use/presence tended to be higher in areas with older forests (i.e., old-growth, 40-year-old stands) than in areas more recently cleared, as there was a monotonic increase in the frequency of panda feces with an increase in the age of the forest (Fig. 5). With respect to land cover type, the highest frequencies of feces were found in forested areas with ≥10% bamboo cover, whereas no feces were found in forested areas with bamboo cover of <10% (Table 4). Moreover, feces were found with a frequency of 17% in shrubland areas with bamboo ≥10% (Table 4). In addition, frequency of plots with feces varied from 25% to 42.9% in the marginally suitable, moderately suitable, and highly suitable habitat classes in which ≥10% bamboo cover was present, whereas no feces were found in areas classified as panda habitat (all three categories) but with <10% bamboo cover (Table 4).

Habitat connectivity at the eastern boundary of Wolong Nature Reserve

Giant panda habitat connectivity (i.e., the percentage of habitat connected) increases with the distance that giant pandas are able to travel between patches of suitable habitat (Fig. 6). However, habitat connectivity

TABLE 4. Giant panda habitat selection based on feces frequency inside Wolong Nature Reserve.

	Plots with feces (%), <10% bamboo cover			Plots with feces (%), ≥10% bamboo cover		
Parameter	Mean	95% CI	n	Mean	95% CI	n
Land cover type						
Forest	0		79	31.2	0.5	202
Shrub	0		71	17.9	2.7	28
Grazing/grass	0		15	66.7	31.4	3
Cropland/barren	2.8	0.9	36	0		2
Habitat suitability						
Unsuitable	0.85	0.2	117	25.7	2.5	35
Marginal	0		20	25.0	1.1	48
Moderately suitable	0		59	31.2	0.7	138
Highly suitable	0		5	42.9	7.1	14

Notes: Land cover types and giant panda habitat suitability for each plot were obtained from the digital classification of the 2001 Landsat TM data. Values are expressed as percentages of 30 × 30 m field plots with giant panda feces, with 95% confidence intervals based on a binomial probability distribution; n is total sample size.

between the Wolong Nature Reserve and its 3-km buffer surrounding area diminished between 1965 and 2001. When the distance was set at 1000 m, the connectivity dropped from a potential value of ~65% to ~46% in 2001 (Fig. 6). A slight increase in connectivity was observed in the 1997–2001 period (Fig. 6).

Habitat connectivity was lowest when land cover changes affected panda habitat both inside and outside the reserve (Fig. 7). In addition, land cover changes outside the reserve were more drastic in reducing the habitat connectivity between Wolong Nature Reserve and its surrounding areas than were land cover changes inside the reserve (Fig. 7). Therefore, even if the reserve had been fully protected (i.e., without changes in land cover that affected panda habitat), its degree of isolation drastically increased with the land cover changes occurring outside its boundaries.

DISCUSSION

Although the habitat suitability scheme used in this study provided a baseline to assess the amount of potential panda habitat present at a given moment, it constitutes a crude representation of the true suitable habitat present. Thus, the rates of habitat change reported here should be viewed more as general trends and not as rigid and exact values of habitat transformation. This is because approximately one-quarter of the plots with bamboo cover of >10% had panda feces, even though they were classified as unsuitable by the habitat suitability scheme used in this study. No feces were found in plots with ≤10% bamboo cover, even if they were classified as moderately or highly suitable habitats, based on the suitability scheme used. Thus, bamboo cover constitutes the single most important characteristic of the giant pandas' habitat selection

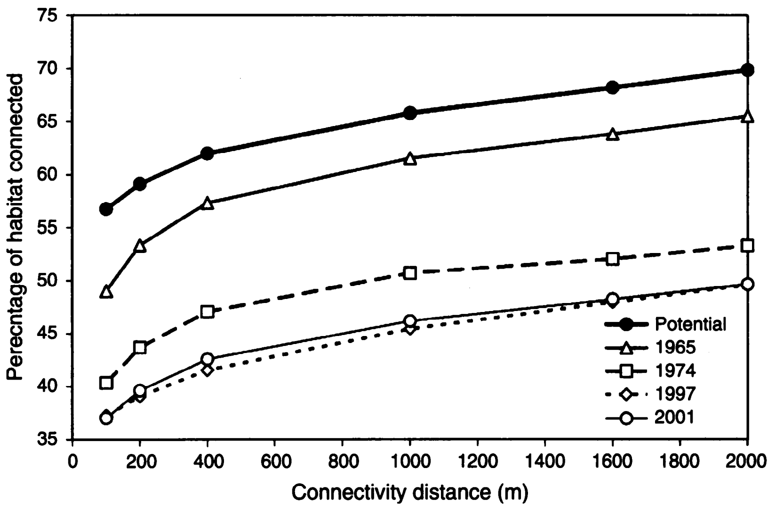

FIG. 6. Percentage of the total habitat (including marginally, moderately, and highly suitable) connected within the eastern boundary area vs. distance between patches (connectivity) of panda habitat for each of the dates of imagery analyzed and for the potential habitat modeled.

FIG. 7. Temporal changes (1965–2001) in the percentage of the total habitat (including marginally, moderately, and highly suitable) connected within 1 km distance, at the eastern boundary area of Wolong Nature Reserve. Bars represent the effect of habitat change occurring on both sides of the boundary, only outside of the reserve, and only inside of the reserve. The dashed line represents the potential connectivity without any changes in habitat.

(Schaller et al. 1985, Reid and Hu 1991). In addition, giant pandas seem to prefer old-growth and late-successional forest conditions to young secondary forests (Ran et al. 2004, Bearer 2005). Nevertheless, further analyses should be conducted to fully understand the forest age preferences by the pandas, in order to synoptically assess the age requirements or structural conditions needed for secondary forests to become adequate habitats for the pandas, particularly because life histories of tree species, gap characteristics, and bamboo growth cycles interact in complex ways to modify the structural characteristics of the forest (Taylor and Qin 1988, 1992).

Between 1965 and 2001 a significant amount of forest was converted into cropland, grassland, and shrubland, particularly along the rivers and the main roads, which are used as access routes. Although highly diminished, forests are still a common land cover type present in the study area after more than 35 years of human-induced land cover transformations. Nevertheless, the areas under this land cover type are a spatially heterogeneous patchwork of different successional stages, ranging from young, secondary growth to mature, undisturbed forests. The transformation of forest into other land cover types has negative effects on panda habitat. However, the 3-km buffer experienced a slight increase in the forest cover during the 1997–2001 period, which induced an increase in the moderately suitable habitat class. The temporal analysis also showed that habitat connectivity between the Wolong Nature Reserve and its 3-km buffer surrounding area has drastically diminished between 1965 and 2001, enhancing the damaging effects of population isolation. Nevertheless, a slight increase in connectivity was observed in 2001, which reached slightly higher values than those seen during 1997. This increase, however, is within the errors of habitat classification, and therefore constitutes more a process of stabilization of the habitat connectivity across the boundaries of Wolong Nature Reserve. This stabilization in connectivity is consistent with the observed reductions in the rates of total habitat loss, particularly outside the reserve during the 1997–2001 period.

The reductions in the rates of habitat loss observed, particularly outside the reserve, could be a response to afforestation and shifts from agriculture to nonagriculture activities. In addition to reducing agricultural activities, this socioeconomic shift provided local residents with higher incomes, allowing them to afford energy sources other than fuelwood, such as coal and electricity. This was not the case inside Wolong Nature Reserve, which did not experience a similar rapid change in the socioeconomic structure, due to its protected status. Nevertheless, some seasonal shifts to nonagricultural activities have been seen during recent years, particularly due to the increase in the tourism industry inside the reserve (the number of visitors increased fourfold, from 20 000 in 1995 to 80 000 in 1998; Lew [2003]), although its effects need to be further studied. In addition, as in many rural areas across China, some local residents of Wolong are working temporarily in cities and industrial areas outside the reserve. Preliminary results (X. Chen, *unpublished data*) suggest that these temporary labor out-migrants help local people to further switch the energy consumption from fuelwood to electricity through direct and indirect economic contributions. Therefore, we speculate that the reduction in the direct dependence on local natural resources has a positive effect on panda habitat by providing alternatives to agro-pastoral activities, as well as to fuelwood collection. Nevertheless, other environmental consequences might result from a rapid economic development (e.g., road construction), which could affect the giant panda habitat in the long term.

To protect panda habitat from further degradation and to restore previously degraded habitat, Wolong Nature Reserve has been implementing three conservation programs: Grain To Green Program, GTGP (since 2000); Natural Forest Conservation Program, NFCP (since 2001); and Eco-hydropower Plant Program, EPP (since 2002). The NFCP bans the harvesting of natural forests and provides economic incentives to local households for policy enforcement (accounting for an average of 16–20% of household income by 2003; X. Chen et al., *unpublished data*). The GTGP was developed to control soil erosion and return croplands on steep slopes to forests. The EPP provides electricity to local residents in order to limit their needs for fuelwood. Because NFCP and GTGP are national programs, these two policies also have been implemented in the surrounding areas of Wolong, although the methods of implementation and the effectiveness differ from those inside Wolong Nature Reserve. These conservation policies have modified the energy consumption strategy in recent years (after 2001) by switching ~40% of fuelwood consumption to electricity (Wolong Nature Reserve 2005). Therefore, the implementation of these policies is probably benefiting panda habitat, as has been observed in the field (J. Liu et al., *unpublished manuscript*).

Because the implementation of these conservation policies could potentially restore panda habitat both inside and outside the reserves and increase habitat connectivity among nature reserves (Xu et al. 2006), we urge the continuation of these conservation programs in order to enhance the conservation of panda habitat across reserve boundaries in the decades to come (Liu et al. 2004). In addition, the effects of these policies should be studied further in the future, particularly to assess how their implementation has affected land cover changes both inside and outside nature reserves.

As shown in this study, land cover changes inside and outside nature reserves are dynamic in time and directly respond to changes in socioeconomic drivers (Liu et al. 2001, DeFries et al. 2005). Therefore, nature reserves should not be seen as isolated entities without also considering impacts of changes in land cover in their adjacent areas. These changes have different ecological effects (Curran et al. 2004, DeFries et al. 2005), particularly the formation of migration corridors for wildlife (Gude et al. 2007, Hansen and DeFries 2007), enhancement of edge effects from hunting (Vester et al. 2007), changes in the effective size of forest types (Vester et al. 2007), and loss of critical dispersal areas outside nature reserves (Hansen and DeFries 2007). In this study, in addition to understanding the changes in the amount and location of habitat for the pandas, we illustrated the changes in the degree of panda habitat connectivity between Wolong Nature Reserve and its surrounding areas (which include three nature reserves: Caopo, Anzihe, and Heishuihe). All of these findings offer insights for biodiversity conservation and reserve management, in terms of enhancing the movement of pandas among nature reserves, as well as the establishment of buffer areas to mitigate the influence of human activities. Policies that enhance the connectivity among patches of suitable habitat for native species, both within and between nature reserves, as well as establish appropriate buffer areas surrounding nature reserves, are critical for an effective management of nature reserves, not only in China but also in many other parts of the world.

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