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Effects of fuelwood collection and timber harvesting on giant panda habitat use

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ABSTRACT

Timber harvesting and fuelwood collection have dramatically reduced the total amount of forestland around the world, including in China. To understand how timber harvesting and fuelwood collection activities affect use by wildlife, we examined giant panda (*Ailuropoda melanoleuca*) use within Wolong Nature Reserve, Sichuan Province, southwest China. We evaluated giant panda use of habitat by observing the presence/absence of panda feces in 913 field plots. Newly harvested areas (0–10 years) had the lowest frequency of feces presence (3%), while unharvested forests had the highest (36%). Feces presence is influenced by bamboo cover, overstory and midstory composition, slope, aspect and distance to human activity. Results suggest that timber harvesting and fuelwood collection have important impacts on the use of forested habitats and panda use is reduced for several decades after harvests. However, as the forest regenerates, panda habitat may begin to recover after a period of at least 37 years. This has potential implications for the long-term conservation of panda habitats and suggests that if forestland is maintained via the Natural Forest Conservation Program (China's logging ban), habitats that were previously harvested may eventually regenerate and increase the potential for the species long-term survival.

1. Introduction

Global forestland declined by 0.22% each year during the 1990s (Food and Agriculture Organization, 2003). Loss of forest has been particularly significant in developing countries, which experienced a total loss of forest area equal to 13.7 million ha/year in 1990–1995 (Food and Agriculture Organization, 2001). In some developing countries that have increasing amounts of forestland, such as China, which increased the size of its forest between 1980 and 1995, the per capita amount of forestland continues to decline due to rapid population growth (Population Action International, 1999). Declines in the amount of forested landcover, especially from various types of harvesting, can have a significant effect on biodiversity (Caldecott et al., 1996; Jenkins, 2003).

While there are various types of timber harvests, one of the most significant ones in the world today is fuelwood collection. Fuelwood acts as the primary energy source for approximately 3 billion people worldwide (Population Action International, 1999). Over half of the wood harvested each year is used for fuel (Population Action International, 1999), accounting for over 7 million ha of forest area harvested annually. Developing countries are the primary users of fuelwood, and 75% of forest harvesting in these countries is for fuelwood use (Food and Agriculture Organization, 2000). Yet, despite the widespread use and the potential impacts

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harvesting can have on forested landscapes and wildlife habitats, we are unaware of any study that investigates the effects of fuelwood collection on wildlife habitat use.

Recent investigations are beginning to uncover the processes involved in how wildlife may respond to certain harvesting regimes, thereby allowing better management policies to be developed and implemented. More specifically, timber harvesting activities have been found to affect various species, including invertebrates (Hill, 1999; Ghazoul, 2002; Hamer et al., 2003; Hill et al., 2003; Gibb et al., 2006), reptiles (Prior and Weatherhead, 1994), amphibians (Petranka, 1994; Harper and Guynn, 1999; Harpole and Haas, 1999; Duguay et al., 2001; Duguay and Wood, 2002; Knapp et al., 2003), birds (Ward et al., 1994; Sallabanks et al., 2000; Duguay et al., 2001; Sekercioglu, 2002; King and DeGraaf, 2004), small mammals (Cole et al., 1998; Malcolm and Ray, 2000; Sullivan et al., 2000; Simard and Fryxell, 2003; Lloyd et al., 2006) and large mammals such as bear (McLellan and Shackleton, 1989; Wielgus and Vernier, 2003). While there is evidence to suggest some bear species, such as the grizzly (*Ursus arctos* Ord) are not deterred by harvesting activities (McLellan and Shackleton, 1989) and may actually prefer early succession forests (Mattson, 1997; Waller and Mace, 1997), the giant panda (*Ailuropoda melanoleuca* David) appears to spend little time in heavily logged areas (Schaller et al., 1985) and prefers interior, old-growth forests.

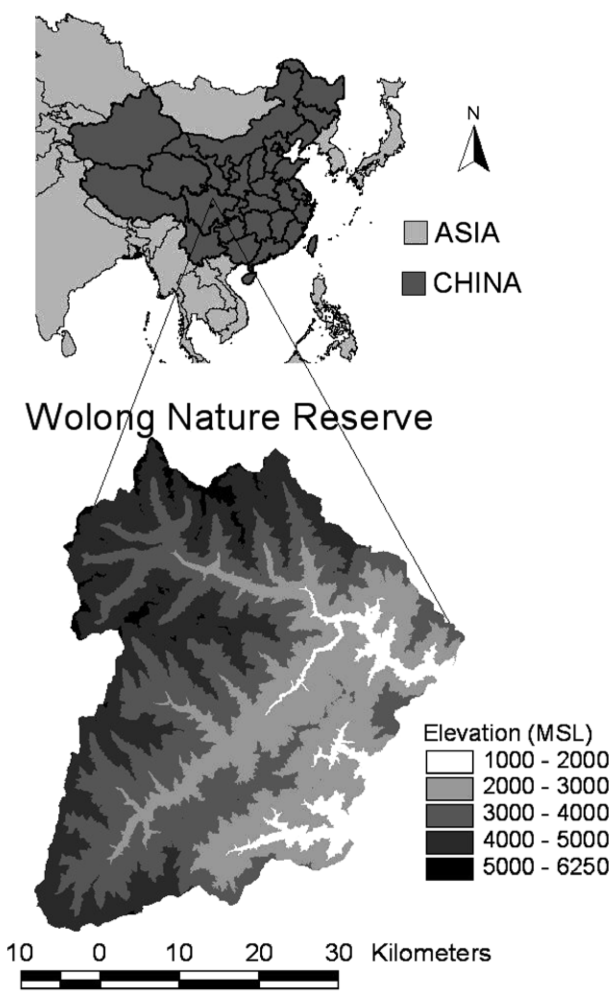

Fig. 1 – Location of the People's Republic of China and Wolong Nature Reserve, in Sichuan Province, southwest China. Shaded relief of Wolong demonstrates the elevation gradient within the Reserve.

To better understand how a species that prefers old-growth forests is affected by forest harvesting (i.e., timber harvesting and fuelwood collection), we investigated the effects of harvesting on giant panda habitat use in Wolong Nature Reserve, Sichuan, China (Fig. 1). Despite extensive research and insights into how forests regenerate and interact with bamboo in Wolong (see Section 2), there has been no investigation to date that monitors the age or size of harvested area and how associated forest characteristics directly relate to giant panda use. In addition, the timing of this study is crucial because no direct studies of panda habitat have been conducted after the bamboo recovery from a mass-flowering episode during the early 1980s in which 80–90% of the bamboo in Wolong died off (Taylor and Qin, 1993a). This investigation reports on the effect of timber harvesting and fuelwood collecting on the use of habitats by the giant panda approximately seventeen years after the most recent bamboo mass-flowering event. Our primary objectives were to: (1) evaluate forest structure composition changes in various sizes and ages after harvesting, (2) assess if a size of harvest effect on panda use was present (i.e., did use in fuelwood collection sites (<10 ha) differ from use in timber harvested areas 10–100 ha), (3) determine if time since harvest affected panda use, and (4) quantify the environmental factors important to giant panda use over periods of time after harvesting.

It is our hope that by providing a better understanding of how giant pandas use previously harvested areas, we cannot only ensure the sustainability of panda habitats, but also provide a baseline for understanding how fuelwood harvest and utilization of other forest resources may better coexist with wildlife conservation.

2. Study area

The Wolong Nature Reserve (102°52′–103°24′E, 30°45′–31°25′N) (Fig. 1) is a nature reserve specifically established for the conservation of panda habitat. However, extensive timber harvesting, along with other human activities (An et al., 2001, 2002; Liu et al., 2004a; Linderman et al., 2005a), were performed in Wolong throughout much of the 1960s to the mid 1970s. Typical practices included removal of >50% of the overstory canopy cover in areas usually approximating 10 ha but occasionally exceeding 100 ha. The Sichuan Department of Forestry officially banned timber harvesting within Wolong in 1975, however, some amount of timber harvesting and fuelwood collection (fluctuating around 7000–9400 m^3/year) has continued to occur in the Reserve until recently (Liu et al., 1999a,b, 2001).

Several investigations have given some insights into the way natural vegetation in Wolong has been influenced by historical timber harvesting and fuelwood collection and how the habitat matrix of the giant panda would be affected by later forest development (Schaller et al., 1985; Taylor and Qin, 1988a,b, 1989, 1993b, 1997; Reid et al., 1989, 1991; Liu et al., 2004b; Linderman et al., 2005b; Vinã et al., 2007). When large openings in the canopy are formed, such as those created by large-scale clear-cut harvesting, the density of arrow bamboo (a thin-stemmed, high density bamboo species occurring above 2500 m) increases to such a degree that tree establishment is severely hindered (Taylor and Qin, 1987, 1988c, 1993a,b; Reid et al., 1991). Because of this encumbrance, regenerating forest is slow in areas with this type of harvest regime. Harvesting methods of this kind occurred in several areas within Wolong during the 1930s which led primarily to a hardwood stand that is now composed mainly of *Betula* spp. with few conifers remaining (Taylor and Qin, 1988a, b, 1989). Large clear-cuts also occurred during the 1970s which have left many areas in a low basal area shrub layer consisting mainly of *Rubus* spp., *Sorbus* spp., and *Rosa* spp. (Reid et al., 1991), with few tree species able to compete.

Selective timber logging and fuelwood collection throughout Wolong impact the forest differently than all-tree removal methods. Typically, fuelwood collection activities occur over a much smaller area, as usually only several trees are removed at one time. Yet, the cumulative effect of continual fuelwood collection over several years does increase the size of the area impacted. Because of this collective effect, harvest areas vary in size from several square meters (single tree removal) to several hectares or larger, depending on the temporal extent and the number of local people who collected fuelwood.

For our study, complex and undocumented site histories made it difficult to characterize any harvesting as a clear-cut, selectively cut or fuelwood collection operation. We therefore used size of harvest to quantify type of cut, where smaller sized harvests are typically associated with fuelwood collection, or selective cutting, and clear-cuts were larger in size. This proxy was justifiable based on conversations with local people regarding harvesting histories in Wolong and our personal observations. While there is the potential that smaller-scale timber harvests (<10 ha) could have occurred in Wolong, and therefore have similar effects as a larger fuelwood collection site, we believe these instances were rare because of the criminal risks in large-scale fuelwood collection and the economic and logistic inefficiencies of small scale timber harvesting.

3. Methods

3.1. Field sampling method

To determine whether harvesting a forest for timber or fuelwood affects the use of habitats by the giant panda, we examined use patterns in previously harvested forests and compared them to those in uncut forests. Data collection took place during May–August 2001, May–November 2002, and June–August 2003. Use was determined by the presence of fecal droppings, which was considered a useful indicator of panda use because although actual sightings of animals are extremely rare, feces are deposited frequently (97 droppings/day) (Schaller et al., 1985) and remain for several months (personal observation). In an earlier study of panda habitat use, Reid and Hu (1991) used the sample unit of feces groups to determine use mainly associated with feeding behaviors. Our study used general presence/absence of feces to indicate use because it also incorporated habitat use not associated with feeding, such as traveling routes. This was significant because panda use in harvested areas may be more closely associated with daily or seasonal movement, escape or thermal cover, or mate location and may not be as important as foraging habitat (Schaller et al., 1985). Although frequency of defecation is high, the small number of panda individuals, extent of the forest and ability of the animal to travel large distances make detection of feces infrequent.

Due to the infrequency of observing giant panda feces in bamboo forests, we used adaptive cluster sampling to concentrate our sampling effort on areas where feces was more likely to occur. This allowed us to avoid a situation where most sample plots had no feces present. Adaptive cluster sampling is valuable because it is designed to sample rare events (e.g., feces in our study) and allows for focused research in areas where the rare events occur while maintaining proper statistical hypothesis testing protocol (Thompson, 1991; Thompson et al., 1992). Whenever feces were found (i.e., presence = 1) in a 30 × 30 m sample plot, all units in its neighborhood (those 30 × 30 m plots to the forward, rear, left, and right) were added to the sample. If in turn any of these subsequently added plots had feces that were detected by the observer, the plots of its neighborhood were also added to the sample, so that finally the sampling neighborhood contained 1, 5 (1 primary, 4 secondary), or 8 (1 primary, 7 secondary) sample plots. Adaptive cluster sampling allowed us to increase our sampling efforts around areas that had a higher potential of giant panda activity.

Thirty × thirty-meter sampling plots were located while the team was in the field and were identified by local residents knowledgeable of historical, recent past and present land-use in the area. Age of forest was defined by the last time the forest within the sample plot had been harvested, which was known by the locals. Size of harvest was defined as a relatively homogenous area that differed from its surroundings (Forman, 1995). The center position of each 30 × 30 m plot was geo-referenced with a Pathfinder® Pro XRS GPS unit (Trimble Navigation Limited) for subsequent analysis and modeling of the data. Due to logistical and time constraints which prohibit revisitation and reexamination of sample plots for passed droppings, equal probability of feces detection in all habitats was assumed. This assumption was supported by Reid and Hu (1991), who found a low ratio of missed droppings (1.3%) throughout their study sites in Wolong.

Forest characteristics measured within each plot include: basal area (m^2/ha, 10-factor prism), total overstory canopy cover (all canopy covers measured with spherical densiometer), conifer overstory cover, deciduous overstory cover, average overstory height, total midstory canopy cover, average midstory height, total shrub cover, average shrub height, total bamboo cover, total understory cover, and average understory height. Topographic factors include: ecological aspect (aspect converted into ecologically significant units (Parker, 1982)), elevation (MSL), and slope (degrees).

3.2. Statistical analysis

Sites were grouped into four harvest age categories to reflect stages of forest succession and were based on our ability to identify forest ages in the field as well as sample size issues:

0–10 years, 11–30 years, 31–100 years and old-growth forest. Sites were also grouped into two patch/harvest size categories: small < 10.0 ha and large harvest 10–100 ha. Sample sizes varied because only sites that could definitively be categorized were included in this analysis.

We used analysis of variance (ANOVA) to test for the differences of forest and topographic characteristics across forest age groups (size classes combined) using the Horvitz–Thompson estimator calculated from the adaptive cluster sampling method (Thompson and Seber, 1996; Turk and Borkowski, 2005). We used two-way contingency tables along with the binomial proportion test (Ott, 1993) to test for differences in the proportion of feces in forests of various ages and sizes. Proportion of feces in harvested areas was compared to that in unharvested sites. We then used the binomial proportion test (Ott, 1993) to determine significant differences between proportions of feces present at sites.

To enhance the interpretation of contingency table results, we used autologistic regression incorporating an autocovariate term to patch age and harvest size variables as well as forest and geographic characteristics to determine which were important in predicting panda feces presence. We constructed one independent autologistic regression model for each age class, each of which used feces as the response variable. Prior to running each autologistic regression analysis, we conducted univariate logistic regression analysis (PROC LOGISTIC, SAS Institute) and removed all variables that had *p* values less than 0.25 associated with the likelihood ratio test scores (*G*-tests). This somewhat liberal *p* value was chosen based on the distribution of *p* values of the variables. We then ran a correlation analysis (PROC CORR, SAS Institute) on remaining variables to detect collinearity. Pairs of variables that had $r < 0.6$ were considered for variable elimination. We eliminated the variable with the less significant univariate *G*-test score. If scores were similar, we eliminated the variable that led to the most parsimonious multivariate logistic regression model. We tested a variety of logit models by deliberately adding certain topographic and forest variables and determining which made a significant contribution to the prediction of feces presence. Akaike information criteria (AIC) were used to determine which model had the best fit (Quinn and Keough, 2002).

While autologistic regression provided information as to which forest characteristics were significant in predicting feces presence, classification trees (Venables and Ripley, 1999; De'ath and Fabricius, 2000) were used to provide more specific information on variable thresholds and their relationship to panda use. Four separate trees were performed on: (1) all independent variables, (2) the age of forest and size of forest patch, (3) geographic variables including distance to road, elevation, slope, ecological aspect, and basal area, and (4) forest characteristics, including components of the overstory, midstory, shrub, bamboo, and understory layers. All classification trees used a minimum node size of 5 with deviance = 0.05 and incorporated a cost complexity pruning using deviance pruning methods to return a minimal node tree as implemented in S-Plus (Venables and Ripley, 1999; De'ath and Fabricius, 2000). Tree sizes were selected after running a series of 10-fold cross-validations using the 1-SE rule (De'ath and Fabricius, 2000).

4. Results

We surveyed a total of 913 30 × 30 m sample plots (443 primary and 470 secondary) during the 2001–2003 sampling period. Age of harvests in Wolong ranged from several months to approximately 100 years. Older harvests were typically associated with large-scale timber harvesting operations and newer harvests associated with multiple tree removal for fuelwood. Pandas did not use larger, newly harvested areas (10–100 ha) (Age = 3.0 ± 0.6 years) (mean ± SE) (Fig. 2). Use generally increased as the forest aged $\left(\chi^2_{(3,N=99)} = 24.9,\ p < 0.001\right)$. There was some use in large, mid-successional forests (22.1 ± 2.1 years), but it was not significantly higher than new harvests. Use was 5.0 and 4.7 times higher, however, in late successional (50.0 ± 2.3 years) and old-growth forests (203.6 ± 3.6 years), respectively, than in mid-successional harvests (Fig. 2).

In fuelwood collection areas (<10 ha), use in old-growth forest (180.7 ± 4.3 years) and late successional forest (44.6 ± 1.7 years) was 8.0 and 5.3 times higher than in newly harvested forests (3.7 ± 0.4 years), respectively $\left(\chi^2_{(3,N=295)} = 35.2,\ p < 0.001\right)$, suggesting even small-scale tree removal may reduce use by pandas for decades (Fig. 2). Overall, we found giant panda feces more frequently in older forests than in newly harvested areas $\left(\chi^2_{(3,N=393)} = 56.3,\ p < 0.001\right)$.

Comparisons of patch sizes $(\chi^2_1 = 0.37,\ p = 0.6)$ and harvest sizes $(\chi^2_1 = 0.41,\ p = 0.5)$ indicated no difference between the proportions of feces found in small and large patches and between fuelwood collection and timber harvest sites. Patch sizes were significantly related to distances from roads, with smaller patches occurring close to the roads (0.06 ha, 0–500 m from roads), and larger patches farther from the roads (0.29 ha, 3–3.5 km from roads) ($F_{8,862} = 6.159$, $p < 0.001$). In harvested areas that were 0–10 years old, use

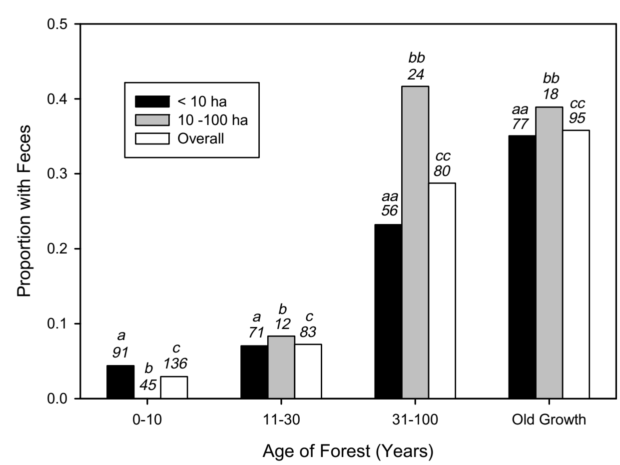

Fig. 2 – Proportion of primary plot sites with giant panda feces in areas with varying forest ages and sizes. Italicized numbers above bars represent plot sample size. Symbols (*a*, *aa*, *b*, *bb*, *c*, *cc*) above bars represent significance groupings in the proportion of survey plots with panda feces by age class for each size using binomial proportion test. The same number (and type) of letter-symbols above bars indicates no significant difference.

was not detected in the larger harvest sizes (10–100 ha) (Fig. 2).

We found significant changes in all forest and topographic characteristics with age of regrowth except average understory and shrub height, which did not vary over time (Table 1). As the forests increased in age, the values of three forest and bamboo characteristics (basal area, overstory forest and bamboo covers) increased ($F_{3,390} = 72.8$, $p < 0.001$; $F_{3,375} = 60.9$, $p < 0.001$; and $F_{3,385} = 43.0$, $p < 0.001$, respectively). The increasing forest cover and bamboo cover created a more suitable environment for the giant panda (Table 1). Later successional (31–100 years) and old-growth sites occurred significantly farther away from the road, farther into the interior forest, than newly harvested (0–10 years) and mid-successional (11–30 years) forests (Table 1). Later successional and old-growth forests also had significantly higher basal areas than younger forests. Conifer, deciduous and total overstory percent cover all increased as the forests aged (Table 1). The conifer component of the overstory was greatest in the large, unharvested areas but was significantly lower in areas that were cut 0–30 years ago (Table 1), while the deciduous overstory was lower in new harvests and highest in large, later successional forests (Table 1). The lowest mean bamboo percent cover was in large, new harvests while higher bamboo cover was found in old-growth areas. Larger, unharvested patches had the highest amounts of bamboo (Table 1).

The autologistic models indicated that for recently harvested forests (0–10 years), presence of bamboo was the most significant indicator of giant panda feces presence, as well as shallow slopes and distances from roads (Table 2). In mid-successional forests (11–30 years), the deciduous component of the overstory and midstory and distance from roads were also important (Table 2). In late successional forests, high bamboo cover continued to predict the presence of giant panda feces

Table 1 – Summary of mean (±SE) forest and topographic attribute data in various age and size classes along with univariate ANOVA results on age-class for data measured in neighborhoods (primary + secondary plots)

Size of harvest:		Years after harvesting								Univariate ANOVA on neighborhood means		
		0–10 years		11–30 years		31–100 years		Old-growth				
		<10 ha	10–100 ha	<10 ha	10–100 ha	<10 ha	10–100 ha	<10 ha	10–100 ha			
N (primary plots only)		94	42	74	9	44	23	93	14			
Proportion with feces		0.04	0	0.08	0	0.18	0.53	0.35	0.43	F	d.f.	P
Age (years)	Mean	3.68	3	22.43	22.11	44.55	50	180.65	203.57			
	SE	0.36	0.6	0.74	2.08	1.7	2.31	4.26	3.57			
Patch size (ha)	Mean	2.64	59.79	3.24	21.83	1.49	52.59	2.15	56.64			
	SE	0.31	6.64	0.37	2.77	0.28	5.78	0.28	11.25			
Distance to roadway (m)	Mean	754.43	833.52	1381.6	1005.16	1567.6	2166.97	2066.3	2934.09	97.9	3,437	<0.001
	SE	40.87	74.01	92.57	95.47	67.88	50.09	57.44	70.71			
Elevation (MSL)	Mean	2127.9	2457.53	2288	2127.61	2376.5	2666.12	2686.7	2782.25	54.65	3,437	<0.001
	SE	45.28	49.17	28.47	69.73	45.1	53.22	31.82	31.03			
Slope (degrees)	Mean	19.51	20.05	23.25	39.33	16.8	18.76	21.37	13.86	9.01	3,436	<0.001
	SE	1.48	1.83	1.22	19.1	1.52	2.11	1.35	1.59			
Ecological aspect	Mean	12.07	10.14	8.95	5.56	10.45	7.87	12.17	12.86	8.83	3,436	<0.001
	SE	0.46	0.79	0.67	2.31	0.82	1.32	0.58	0.98			
Basal area (sq m/ha)	Mean	1.32	1.7	6.12	3.32	8.36	8.6	12.51	19.38	69.76	3,435	<0.001
	SE	0.34	0.66	0.8	2.03	1.19	1.52	0.9	1.83			
Total overstory cover (%)	Mean	7.27	8.29	29.3	16.67	40.01	37.71	42.28	54.43	85.52	3,422	<0.001
	SE	1.62	3.17	2.91	6.72	3.73	5.71	2.51	6.21			
Conifer overstory cover (%)	Mean	5.45	6.03	17.98	15	25.21	26.36	29.28	49.43	31.72	3,395	<0.001
	SE	1.52	3.13	3.3	6.97	4.23	7.51	3.09	6.38			
Deciduous overstory cover (%)	Mean	1.58	0.77	10.83	1.67	13.24	16.71	13.6	5.38	23.47	3,394	<0.001
	SE	0.63	0.49	2.02	1.67	3.07	6.22	2.08	4.02			
Average overstory height (m)	Mean	6.46	4.41	12.17	7.44	20.82	21.35	22.89	28.57	111.02	3,396	<0.001
	SE	1.11	1.44	1.01	2.08	1.2	2.16	1	1.49			
Total midstory cover (%)	Mean	5.86	8.2	20.26	14.11	23.19	22.41	22.92	20.57	36.39	3,435	<0.001
	SE	1.13	3.31	2.44	4.69	2.94	4.18	1.58	4.68			
Conifer midstory cover (%)	Mean	0.95	2.74	3.45	11.33	3.17	4.35	5.45	4.93	4.41	3,396	<0.005
	SE	0.33	2.27	1.18	4.56	1.27	2.06	0.95	1.87			
Deciduous midstory cover (%)	Mean	4.2	1.56	15.28	2.78	20.62	12.26	16.68	15.43	34.02	3,396	<0.001
	SE	1.03	0.59	2.46	1.88	2.99	3.07	1.77	4.99			
Average midstory height (m)	Mean	4.37	3	6.92	3.89	12	10.03	14.15	15.54	75.66	3,419	<0.001
	SE	0.73	0.82	0.84	1.37	1	1.61	0.69	1.7			
Average shrub height (m)	Mean	2.52	1.99	3.15	3.39	4.01	3.68	4.93	4.04	41.96	3,396	0.013
	SE	0.24	0.46	0.22	0.34	0.31	0.54	0.26	0.24			
Total shrub cover (%)	Mean	21.77	15.15	21.79	39.89	21.36	29.51	23.79	15.93	3.62	3,420	<0.001
	SE	2.78	3.91	2.39	9.1	2.67	6.3	1.81	3.96			
Bamboo cover (%)	Mean	25.98	18.59	25.45	20.11	34.48	53.05	67.08	83.36	57.76	3,431	<0.001
	SE	3.38	4.98	3.68	13.3	5.42	7.47	3.59	6.12			
Total understory cover (%)	Mean	55.33	67.95	43	46	49.35	33.05	22.49	9.93	27.84	3,418	<0.001
	SE	4.28	6.34	4	10.49	5.4	7.67	3.17	3.74			
Average under height (cm)	Mean	37.56	29.93	32.48	37.22	41.66	20.45	28.78	16.77	1.76	3,413	0.15
	SE	3.33	4.45	2.83	5.94	5.52	4.33	3.16	7.06			

Neighborhood calculations were based on Horvitz–Thompson means of all plots in that neighborhood.

Table 2 – Significant forest and geographic characteristics in autologistic models developed from Horvitz–Thompson means (primary and secondary plots)

	AIC	Variable	Estimate	P value
0–10 years	60.48	Intercept	−6.56	<0.01
		Slope	−0.08	0.03
		Bamboo cover	0.05	0.01
		Distance to road	0.00	0.02
11–30 years	56.47	Intercept	−14.40	<0.01
		Deciduous overstory cover	0.08	0.01
		Deciduous midstory cover	0.07	<0.01
		Distance to road	0.01	<0.01
31–100 years	159.87	Intercept	−2.86	<0.0001
		Aspect	−0.06	0.05
		Bamboo cover	0.04	<0.0001
Old-growth	337.28	Intercept	−3.57	<0.01
		Slope	−0.05	<0.01
		Aspect	−0.08	<0.01
		Average overstory height	0.11	<0.0001
		Deciduous overstory cover	−0.01	0.08
		Bamboo cover	0.01	0.04
		Average understory height	0.02	<0.0001
		Patch size	−2.15	<0.0001

in addition to southwest aspects. In old-growth forests, higher bamboo cover, low slope, low ecological aspect (south–southwest facing slopes), tall overstory trees with a low deciduous component, and a smaller patch size were the best predictors of giant panda feces (Table 2).

Classification trees were used to provide further understanding as to which forest and geographic characteristics are used by the giant panda (Fig. 3). The first classification tree using all independent variables found bamboo percent cover to be the primary distinguishing factor, with cover percent over 17.5% having more use (Fig. 3). Other useful factors included having a tall overstory (>26 m) and a high basal area (>0.13 m^2/ha). When considering age of forest and size of forest patch only, a forest that has had 38 years to regenerate from a harvesting event is more likely to have giant panda feces (Fig. 3). For the geographic and topographic characteristics of plots, a greater distance from roads (>1100 m) was the most important factor in determining panda feces presence (Fig. 3). Additionally, an interior forest with a low basal area (<0.125 m^2/ha) was not used, either. Classification trees on forest characteristics not only reiterated the importance of bamboo cover (>17%) and overstory height (>26 m), but also indicated the conifer overstory component need not be too dense (< 59%) (Fig. 3).

5. Discussion

Our study found use of forested habitats was lowest in newly harvested areas (0–10 years) and highest in unharvested, old-growth areas and later successional forests that had been cut between 31 and 100 years ago. The high amount of feces in later successional forests was notable because previous studies have found use to be lower (Schaller et al., 1985) and habitat to be less suitable (Schaller et al., 1985; Reid and Hu, 1991; Taylor and Qin, 1997) in harvested areas. Our results indicate that forests need approximately 37 years to regenerate from a harvesting event before pandas begin to use these areas again.

Parsimonious autologistic regression models demonstrate that bamboo percent cover continues to be the best predictor of giant panda habitat. Classification tree models support this, but additionally indicate that the bamboo percent cover does not need to be extremely high (>17%) in order to be panda habitat. In newly harvested forests, the traditional characteristics of panda habitat (i.e., high bamboo cover, low slope, and far from roads (interior forest)) were found to be the best predictors of giant panda feces in areas where fuelwood collection occurred. Larger, newly harvested forests were not

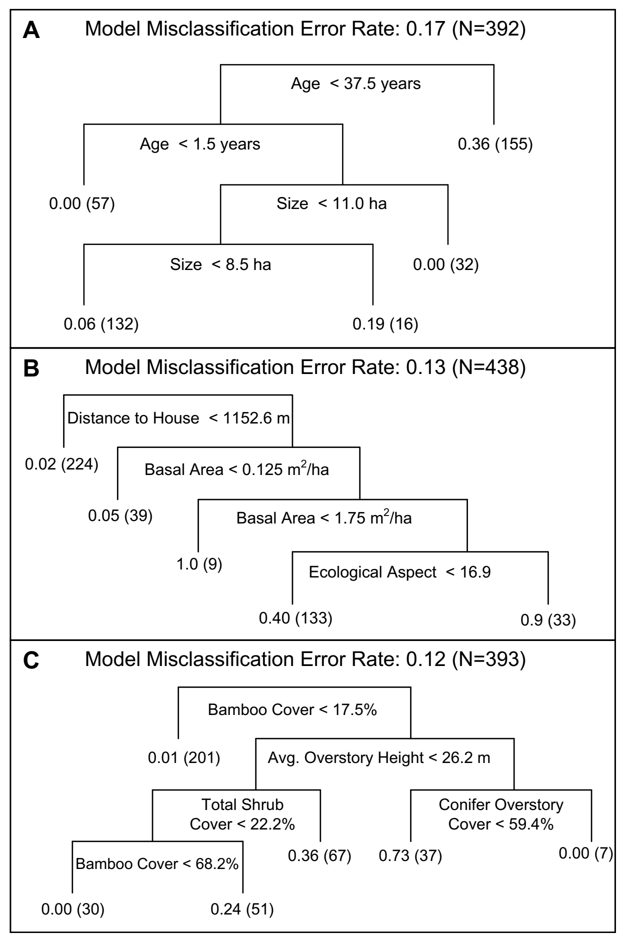

Fig. 3 – Regression trees for Horvitz–Thompson neighborhood means (estimated from primary + secondary plots) of (A) age and size of harvested and unharvested patches, (B) geographic characteristics, slope, ecological aspect, and basal area (m^2/ha), and (C) all forest characteristics. Trees show classification based on the presence of giant panda feces. Residual mean deviance= (A) 0.183, (B) 0.186, and (C) 0.159. Values at tree leaves represent proportion of plots with feces and sample size (within parentheses).

used. As the forest aged (11–30 years), the deciduous component of the midstory and overstory became important indicating the significance of regenerating forests (regardless of whether conifer or deciduous). The forest structure provided by deciduous trees may be a useful component of the forest as pandas seasonally move through the lower elevation forests that have been harvested more recently. Panda use in later successional forests was found to be primarily dependent on bamboo cover and also a south–southwest aspect (low ecological aspect). For unharvested and old-growth forest, smaller forest patches with more bamboo, taller understories, less deciduous overstory cover, and low slope with south–southwest aspect (low ecological aspect) indicated the greatest likelihood of encountering panda feces. The reoccurrence of deciduous cover and southern aspects as being a significant predictor for suitable habitat was a curious result that has been documented in a few other studies (Yong et al., 2004) and provides an interesting recharacterization of habitats for a species believed to rely primarily on coniferous forests.

There are two likely explanations why the proportion of feces in later successional areas is as high as unharvested, old-growth forests, which has traditionally been considered the primary habitat for the giant panda. First, early harvesting occurred in highly suitable habitats and forests in less suitable habitats (e.g., steep slopes) were not harvested because of difficulty extracting the wood. Second, several decades of forest regeneration has created a forest cover that provides more suitable habitat characteristics for the giant panda.

Historic harvesting focused on cutting the large conifers (*Abies*, *Picea*, and *Tsuga*) that grew within the subalpine coniferous forests of Wolong. Trees were selected based on their overall sizes and the ability to access the trees and transport them out to the nearest road. Because site quality was highest on the shallow slopes, and because these areas were easier to access, harvesting was most frequently done on the interior ridge tops and nearby areas with low slope. However, the giant panda also prefers sites with low slopes (Reid and Hu, 1991) because there is a large increase in the metabolic requirements to move up steep inclines (Taylor et al., 1972). On the other hand, steep areas were often left uncut by early loggers since it was difficult to access precipitous forests and the ability to move the timber was difficult and often dangerous. To the giant panda, steep, uncut forests are not ideal for the same metabolic reasons and tend to be underutilized, helping to explain why use in unharvested areas was less than that of later successional forests.

Another explanation why the proportion of feces is high in later successional forests is because early timber harvesting took place within the higher elevation (above 2700 m, Table 1) subalpine coniferous forest. Elevations here include the primary vertical range of the giant panda as well as its primary food, arrow bamboo (Schaller et al., 1985). In addition, access to these regions by humans is more difficult, allowing areas to remain somewhat undisturbed since the harvesting events occurred. We should note that humans still use these areas intermittently for wildlife research, herb collecting, bamboo gathering, and occasionally for snaring musk deer (currently illegal; personal observation). In contrast, newer harvested areas typically occur in lower elevations near the Pitiao River valley (below 2600 m, Table 1), where human disturbance is more common and the less preferred umbrella bamboo grows (Schaller et al., 1985). Lower elevation forests have a complex site history that stems from intense human use over the centuries. This is especially true in areas where illegal fuelwood collection, poaching and medicinal herb collections are still active. These activities have created a landscape in the lower elevations that is heterogeneous and frequently visited and disturbed by humans, which may help to explain why use is low at these sites.

The high amount of use in the later successional forests may also be explained by the relationship between overstory canopy density and bamboo cover percent that coincides with the findings of Taylor and Qin (1997), with the frequency of feces increasing as forest cover and bamboo cover percent increase. Use decreased after timber harvesting due to decreased overstory canopy cover, decreased conifer component, increased hardwoods component, and increased bamboo densities. We found some use in fuelwood collection sites that were recently harvested, suggesting that pandas are able to use these areas shortly after harvesting. While we were not able to determine type of use, we believe pandas most likely were not foraging in these areas, but were instead able to use these newly disturbed areas for some other purposes, such as a traveling route. As the forest recovered from the harvesting activity, and as the midstory and later the overstory cover percent increased, feces was found more often in the harvested area, as demonstrated by the increased proportion of use in later successional forests. Later successional forests ranged in age by 40 years, making a detailed recovery timetable unavailable. However, it can be seen that as the forest progresses through succession following a harvesting event, suitable habitat can be restored.

Timber harvesting and fuelwood collection have created a patchy mosaic of forests in various stages of succession throughout Wolong Nature Reserve. This has several implications for the use of these habitats by the giant panda and also for the conservation of this endangered species. Previous studies on panda use of harvested areas and the surrounding forests show that these activities decrease use because of lower canopy cover, increased bamboo densities, decreased bamboo seedling densities and changed bamboo growth form (Schaller et al., 1985; Reid and Hu, 1991; Reid et al., 1991; Taylor and Qin, 1993a,b). However, the majority of those studies were conducted during or shortly after the arrow bamboo flowering and subsequent die-off in 1983. During the die-off period, giant panda activity was altered because of resource limitations, especially those associated with food availability. Our study was performed at a time when bamboo populations would have recovered from the flowering event (i.e., approximately 18 years after flowering) and returned to normal, pre-flowering densities (Taylor et al., 1991). Information from this study shows patterns of use during a period when the bamboo populations are healthy and therefore may not be a limiting factor to pandas. While we do not advocate any harvesting within the habitats of the giant panda, our findings are significant because they suggest that forests which were previously harvested, for either fuelwood or for timber, may eventually regenerate and become suitable panda habitat. The Natural Forest Conservation Program (China's logging ban), implemented in 2001, was established to reduce illegal harvesting within China (Liu and Diamond, 2005). We find this program has been effective towards this goal, and is therefore helping to improve and accelerate the recovery of giant panda habitats. Recovery of habitats for species that prefer old-growth forests has important implications for the long-term conservation of giant pandas and other species worldwide.

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