BIODIVERSITY RESEARCH

Gauging the impact of management expertise on the distribution of large mammals across protected areas

Sheng Li[1,2,*], William J. McShea[1], Dajun Wang[2], Zhi Lu[2,3] and Xiaodong Gu[4]

[1]*Smithsonian Conservation Biology Institute, Front Royal, VA, 22630, USA,* [2]*Center for Nature and Society, School of Life Sciences, Peking University, Beijing, 100871, China,* [3]*Shanshui Conservation Center, Beijing, 100871, China,* [4]*Sichuan Forestry Department, Chengdu, 610081, China*

ABSTRACT

Aim The world's network of protected areas (PAs) plays a critical role in biodiversity conservation. The management expertise within PAs is a function of the training, support and depth of the staff tasked with protecting the resources and should be a significant factor determining the distribution of wildlife species. However, there are few measurable linkages between wildlife populations and management effectiveness. Here, we addressed whether the management expertise within a PA is an important covariate explaining the occupancy of large terrestrial mammals, and identify the attributes of mammal species that would be effective for comparative monitoring of management effectiveness within PAs of developing countries.

Location Six PAs within giant panda region, south-west China.

Methods We used systematic camera-trapping as the primary field methodology to detect the presence of large mammals and used expert scoring to assess the management level of these PAs. Occupancy modelling and logistic regression were used to determine those mammal species with adequate detections to control for ecological covariates and to compare differences in management level between the sampled PAs.

Results Thirty-eight mammal species were recorded with a total sampling effort of 16,521 camera-days at 722 sample sites. Among the 14 examined mammals, Takin (*Budorcas taxicolor*) was the most detected mammal (333 detections at 153 locations), whereas Asiatic black bear (*Ursus thibetanus*) was estimated with the highest occupancy rate ($\psi = 0.49$) and leopard cat (*Prionailurus bengalensis*) was estimated with the highest detection probability ($P = 0.55$). The independently assessed estimate of management expertise was a significant positive predictor for the occupancy of 11 of the 14 mammal species.

Main conclusions Our results suggest that there are measurable consequences for increasing PA patrolling and that standardized monitoring of large mammals is an adequate comparative measure of management effectiveness across diverse PAs that experience extensive poaching pressure.

Keywords

Camera-trapping, large mammals, management effectiveness, occupancy modelling, protected area network.

*Correspondence: Sheng Li, Smithsonian Conservation Biology Institute, 1500 Remount Rd., Front Royal, VA 22630, USA. E-mail: shengli@pku.edu.cn

INTRODUCTION

Establishing protected areas (PAs) is an effective approach to the conservation of biodiversity and critical ecosystems confronted with threats posed by rapidly increasing human population and urbanization (Bruner *et al.*, 2001; Andam *et al.*, 2008). Immense financial and public resources are devoted to the maintenance and development of the present

world-wide network of PAs, which includes 12% of the world's land area and 18.7% of the coral reefs (Chape *et al.*, 2005; Mora *et al.*, 2006). To varying degrees, current PAs face shortfalls in sustainable funding, training of staff and enforcement of laws and regulations (Ervin, 2003; Rodrigues *et al.*, 2004; Joppa *et al.*, 2008; Radeloff *et al.*, 2010). These limitations frequently cause researchers and conservationists to doubt the overall performance of PAs in carrying out their mission (Liu *et al.*, 2001; Chape *et al.*, 2005; Mora *et al.*, 2006). Poor management of established PAs has been linked to poor conservation outcomes (Liu *et al.*, 2001), and improving management effectiveness should support the goals of maintaining biodiversity and preventing habitat degradation.

Measuring management effectiveness of PAs is challenging, and there is no globally accepted metric (Hockings, 2003; Chape *et al.*, 2005; Hockings *et al.*, 2006). Multiple indicators and criteria have been used by researchers to measure management effectiveness and coverage (Ervin, 2003), including deforestation rate (Bruner *et al.*, 2001; Andam *et al.*, 2008), overlap of PAs with the distribution of endangered species and critical ecosystems (Brooks *et al.*, 2004; Rodrigues *et al.*, 2004; Mora *et al.*, 2006; Ma *et al.*, 2007), the intensity of human activity (Radeloff *et al.*, 2010) and the α-diversity of animals or plants (Ma *et al.*, 2007; Vieira *et al.*, 2011). The measure chosen must be an adequate surrogate for broader biodiversity, be sensitive to human activity and be easily measured.

Large mammals are commonly used for measuring management effectiveness across PAs because of their relative ease of detection and identification, as well as their essential role in terrestrial ecosystems (McNaughton *et al.*, 1988; Bowen, 1997; Brashares *et al.*, 2004; Morrison *et al.*, 2007). The life history traits of these species normally include long generation times, slow reproductive rates, low population density and large home ranges; all these characteristics making them sensitive to disruption of demographics because of direct (e.g. poaching) or indirect (e.g. habitat alteration) human activities (Wikramanayake *et al.*, 1998; Carrillo *et al.*, 2000; Kinnaird *et al.*, 2003). Therefore, both the diversity and distribution of large mammals have potential as surrogate measures of effectiveness of PAs management.

Like many large developing countries, China is rich in biodiversity, contains several global biodiversity hotspots and vast areas with global conservation priority (Myers *et al.*, 2000; Olson & Dinerstein, 2002; Mittermeier *et al.*, 2005). A PA network (i.e. nature reserve system) has been established in China to conserve numerous endangered species and critical ecosystems (Xie, 2004). Although the current network covers 14% of China's land, the management of these PAs varies broadly (Deng & Li, 2004; Xie, 2004). Most PAs were not established until the early 1990s and many are not fully functional, because of insufficient and poorly trained staff, limited financial support and/or complex conflicts with local communities over natural resources (Deng & Li, 2004). Although improving PA management has been advocated by

scientists and conservation managers as a major requirement to advance wildlife conservation in China (Zhang *et al.*, 1998; Lu *et al.*, 2003; Liu *et al.*, 2008; Quan *et al.*, 2009), no field studies have quantitatively measured the effect of management level on the large fauna within China's PAs.

From 2004 to 2008, we conducted an extensive field survey on large terrestrial mammals in six PAs in south-west and central China. We used systematic camera-trapping as the primary field method to detect the presence of large terrestrial mammals (Cutler & Swann, 1999) and used expert scoring to assess the management level of these PAs (Hockings *et al.*, 2006). To account for the habitat variability and compare between PAs, we conducted an occupancy modelling exercise for those large mammals that were distributed across the range of the reserves to determine whether management activities contribute significant additional information to the occurrence of these species. Using occupancy modelling, we were able to account for variability because of both reserve differences in habitat distribution, elevation and climate, and differences in sampling (MacKenzie *et al.*, 2002; O'Connell *et al.*, 2006). By examining the relationship between animal occupancy and ecological and sampling variables, we addressed three major questions in this study: (1) The occupancy and distribution of large mammal species across each reserve; (2) Whether management expertise within a reserve is an important covariate explaining the occupancy of these mammals; and (3) The potential of large mammals as an appropriate surrogate group for comparative monitoring of management effectiveness for PAs experiencing extensive poaching pressure.

METHODS

Study area

Our study area is located in central to south-western China and includes three mountain ranges: Qinling Mountains, Minshan Mountains and Qionglai Mountains (Fig. 1), comprised of rugged terrain with elevation ranging from 1200 to 6000 m. The major vegetation types are alpine meadow (>3200 m), conifer forest (2800–3200 m), conifer–deciduous mixed forest (2400–2800 m), broadleaf forest (<2400 m) and early successional fields or agriculture along river valleys. We selected five nature reserves (Changqing, Wanglang, Tangjiahe, Xuebaoding, Wolong) and one area previously used for timber collection (Laohegou) within this region as our survey sites (Fig. 1, Table 1), covering a vast land area of 330 km from north to south and 550 km from east to west. The large mammal fauna within this region was heavily exploited prior to reserve establishment, and poaching is still currently considered one of the most important threats to the large mammals throughout the region (Hu, 2002). These six sampled sites possessed similar mountainous landscape and vegetation along an elevational gradient, but varied in conservation histories and management levels (Table 1). All five nature reserves were established primarily for protecting

giant panda (*Ailuropoda melanoleuca*) and their habitat (SFA, 2006). Laohegou was previously managed for commercial logging and converted to forest restoration after the China national logging ban in 1998. Laohegou contains potential giant panda habitat and wildlife monitoring, and patrolling was initiated in 2004 with support from World Wildlife Fund (WWF) and Sichuan Forestry Department (SFD). Prior to our study, there were no comparable occupancy estimates for the large mammals in these PAs, primarily owing to the lack of systematic monitoring using similar methods other than sign transects along patrolling routes.

Camera-trapping

We used camera-trapping to detect the presence of large terrestrial mammals and birds at each study site (Cutler & Swann, 1999; Wang *et al.*, 2006; Li *et al.*, 2010b). The reserves were divided into 1 km × 1 km blocks within a Geographic Information System (GIS), and all forested blocks were considered potential sampling blocks as our original intent. We set one passive infrared-triggered camera in each sampled block for 1 month. Our camera types included two film models (DeerCamTM, Non Typical, WI, USA and CamTrakker^TM, CamTrakker, GA, USA. Trigger speed 1.0–2.5 s) and one digital model (CamTrakker^TM, Digital Ranger. Trigger speed 2.0–3.0 s). Cameras were attached to trees along animal trails approximately at knee height (0.4–0.6 m) and >300 m apart from other sample locations. All cameras were set to work 24 h per day with a 2.5- to 3.0-min delay between consecutive exposures. Cameras were checked in the middle of the 1-month sampling period to replace batteries, film and memory card as needed and relocated to another block at the end of the sampling period. All camera locations

were baited with commercial small carnivore scent lure (Carman's Magna-Glan Lure, PA, USA). The sampling effort at each location (number of camera-days) was the time between camera deployment and collection. If the camera did not trigger when the sensor was activated by field staff at the time of collection, we used the date of the last animal photograph as the last known day of operation.

At each location, we recorded the latitude and longitude using GPS units and vegetation and habitat measurements within a 50 m radius, including forest type, tree Diameter at Breast Height (DBH), percentage shrub cover, slope and aspect. Elevation and distance to closest road for each location were calculated on the basis of fine-scale Digital Elevation Model (DEM) and road vector layer (National Geomatics Center of China 2005) through spatial analysis using ArcGIS 9 (ESRI, CA, USA). All camera-trapping data were managed within a Microsoft Access database developed by the authors.

Management level assessment

Expert scoring was used to assess the management level of our six sampled PAs (Hockings *et al.*, 2006). We invited six experts who have been working on ecological research and/or conservation projects for 10+ years in our study area and were familiar with the history and management status of all the six sampled sites. These experts included two from SFD, one from Peking University, one from Sichuan University, one from WWF, China, and one from Conservation International, China. Without knowledge of the intended use of the information, the experts were asked to score the six PAs on the basis of the following criteria: (1) Length of protection history; (2) Number of field staff; (3) Intensity and frequency
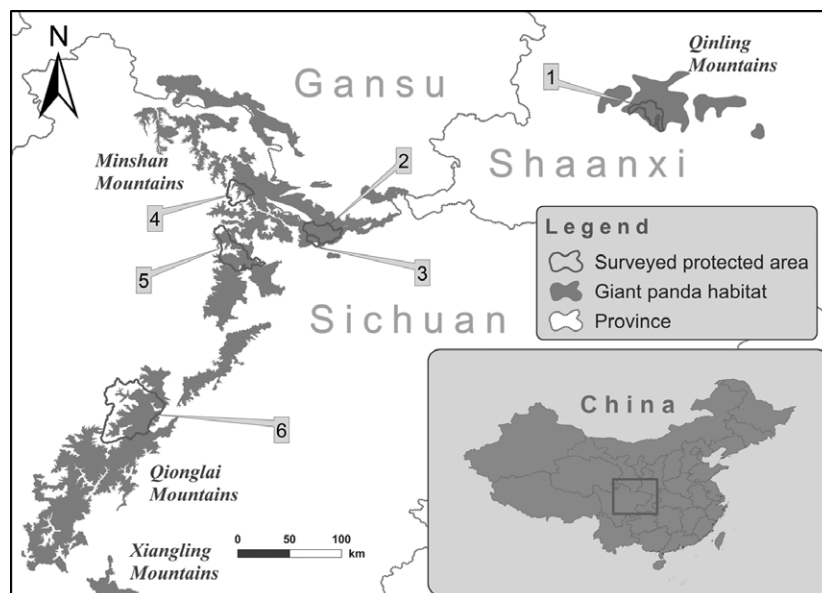
Figure 1 Location of the six surveyed protected areas in south-west and central China. 1. Changqing Nature Reserve. 2. Tangjiahe Nature Reserve. 3. Laohegou Timber Area. 4. Wanglang Nature Reserve. 5. Xuebaoding Nature Reserve. 6. Wolong Nature Reserve.

Table 1 Summary of management level assessment of the six surveyed protected areas in China

	Changqing	Wanglang	Wolong	Tangjiahe	Xuebaoding	Laohegou
Area(km^2)	299	323	2000	300	636	73
Forest area(km^2)	270	110	799	270	356	68
Establishment history*,†	15	44	34	31	16	11
Law enforcement authorization†	Yes	Yes	Yes	Yes	Yes	No
No. of Field staff†	24	17	39	16	42	7
No. of Field monitoring routes†	34	31	30	16	14	7
Monitoring route length/km†	107.7	98.8	192.0	42.1	45.9	44.3
Annual monitoring/patrolling effort (No. of staff-day)†	2568	519	891	550	835	75
Mean expert score	4.42	4.33	4.08	3.75	3.42	2.17

*As of 2009.
†Criteria used for management assessment.

of monitoring activities; (4) Strength of patrolling and anti-poaching activities; and (5) Staff capability in wildlife management (Table 1). The scores ranged from 0 to 5, with the higher score indicating better management. Each factor was equally weighted, and the averaged score of each PA was used as a measurement of its management effectiveness (Table 1).

Occupancy modelling and analysis

To account for imperfect detection of species, we used occupancy modelling (MacKenzie *et al.*, 2002, 2006) to estimate the site occupancy rate (ψ) of large terrestrial mammals with sufficient detections (D) during our survey. All the examined species occur throughout the range of our study sites on the basis of established distribution maps (Zhang, 1999). We divided the sampling history of each location into nine 5-day sampling segments and defined $D_{i,j} = 1$, if a species was detected during sampling period i ($i = 1, 9$; data beyond the ninth period were excluded from analysis) at location j (defined as one detection for this species); if the species remained undetected, then $D_{i,j} = 0$. By examining the sampling history across all locations, we developed the detection matrix of $D_{i,j}$ for each species for occupancy modelling. The occupancy analysis was conducted by using program PRESENCE (Hines, 2006) and involved eight habitat variables and four detection variables, which were all rescaled to appropriate extent prior to analysis (Table 2). Prior to model construction, we examined the performance of each variable by comparing the model Akaike Information Criterion value (AIC, Akaike, 1973) and model weight of each single-variable model to that of the null model. We excluded all variables whose model AIC value and model weight were not better than the null models for >3 species.

Occupancy models of each species were ranked according to their AIC values and model weights. We considered all models whose ΔAIC ≤ 2 equivalent models for each species (Burnham & Anderson, 2002; McShea *et al.*, 2009; Li *et al.*, 2010a). We estimated the average site occupancy rates and detection probabilities of each examined species on the basis

of these top occupancy models (Table 3). We then examined all habitat variables included in top models for significance using logistic regression (method: Enter) in SPSS 17 (SPSS, IL, USA). The management level score of each PA was included as an independent variable in the regression analyses. We examined all selected habitat variables for significant collinearity prior to analysis and found no significant correlation between these variables.

RESULTS

From 2002 to 2008, we completed an extensive camera-trapping effort of 16,521 camera-days at the six PAs, resulting in 5322 mammal photographs from 722 sampled locations (Table 4). Despite the original design of 1-month sampling at each location, the actual sampling duration varied from 2 to 8 weeks because of various reasons (e.g. logistic, weather, camera failure). Thirty-eight mammal species (including three primates, two Lagomorpha, nine rodents, nine ungulates and 15 carnivore species) were detected during the survey (Table 5).

We had sufficient detections for 14 terrestrial mammal species (number of detections per selected species = 24–333; number of detected locations per selected species = 24–153) to support further occupancy modelling, including one rodent, six ungulates and seven carnivores (Table 3). Among these species, *Mustela* was considered a combined species group because of the difficulty of species identification on the basis of photographs. Prior to occupancy modelling, three habitat variables (tree DBH, aspect and slope) were excluded from further analysis because of their poor performance compared to the null model for the majority of species (Table 2). Five occupancy variables (latitude, elevation, forest type, percentage shrub cover and distance to nearest road) and four detection variables (camera model, rain/dry season, warm/cold season and scent lure durability) were included in the modelling process (Table 2, also see Appendix S1). One to eight models were selected as best equivalent models for each species on the basis of their ΔAIC values (see Appendix S1). Takin (*Budorcas taxicolor*) was the most detected mammal (333 detections at 153 locations), followed

Table 2 Habitat and detection variables included in occupancy modelling analysis (Program PRESENCE). All variables were rescaled to appropriate extent prior to analysis

Abbreviations	Name	Description
Habitat variables		
LAT	Latitude	Numeric (N 30.81785–33.72053)
ELE	Elevation	Numeric (Range 1192–4220 m)
VEG	Forest type	Categorical (Broadleaf, Broadleaf–conifer mixed, Coniferous)
DBH (Diameter at Breast Height)*	Tree size	Categorical (<30 cm, 30–50 cm, >50 cm)
SHR	Percentage shrub cover	Categorical (<25%, 25–50%, >50%)
DTT	Distance to nearest road	Numeric (Range 0–7401 m)
ASP*	Aspect	Categorical (Warm - NE, E, SE, S; Cold - N, NW, W, SW)
SLP*	Slope	Categorical (Flat: <25°, Steep: >25°)
Detection variables		
CAM	Camera model	Film model or digital model
SEA1	Season 1	Rain (Jun.-Aug.) or Dry (September–May)
SEA2	Season 2	Warm (Apr.-Oct.) or Cold (November–March)
LUR	Scent lure durability	Numeric (Days since application)

*Variables that are excluded prior to occupancy modelling.

Table 3 The model summaries for the 14 terrestrial mammal species examined by using occupancy modelling and logistic regression (Sample size: $N = 722$ sampled locations)

Common name	Scientific name	No. of detected locations	No. of detections[†]	Occupancy modelling[‡] $\hat{\psi}$	ψ	P	Logistic regression Significant variables[§]
Rodentia							
Short-tailed porcupine	*Hystrix brachyura*	50	68	0.07	0.15	0.14	+MAN**, −ELE**, −LAT***
Carnivora							
Giant panda	*Ailuropoda melanoleuca*	39	68	0.06	0.13	0.15	+MAN*, +LAT*
Asiatic black bear	*Ursus thibetanus*	24	24	0.03	0.49	0.01	+MAN**, +LAT**, +DTT**
Hog badger	*Arctonyx collaris*	68	125	0.09	0.13	0.28	+MAN*, −LAT***, +DTT**
Yellow-throated marten	*Martes flavigula*	35	48	0.05	0.17	0.09	+MAN***
Weasel[¶]	*Mustela spp.*	43	54	0.06	0.42	0.04	+MAN*, +ELE***
Himalayan palm civet	*Paguma larvata*	36	53	0.05	0.08	0.19	+MAN**, −ELE**, −LAT***, +DTT**
Leopard cat	*Prionailurus bengalensis*	41	54	0.06	0.12	0.55	-SHR**
Artiodactyla							
Wild boar	*Sus scrofa*	83	147	0.12	0.21	0.20	+MAN***, −ELE***, +LAT*, +DTT*
Tufted deer	*Elaphodus cephalophus*	84	122	0.12	0.23	0.16	−LAT***
Reeves' muntjac	*Muntiacus reevesi*	42	72	0.06	0.11	0.50	−ELE***
Takin	*Budorcas taxicolor*	153	333	0.21	0.31	0.32	+MAN***, −ELE***, +LAT***, +DTT***
Serow	*Capricornis milneedwardsii*	50	58	0.07	0.31	0.06	+MAN**, +DTT**
Goral	*Naemorhedus goral*	75	118	0.11	0.25	0.14	+MAN***, +LAT*, +DTT**

[†]If one species was detected at one camera location during a 5-day sampling period, it is defined as one detection for this species.
[‡]$\hat{\psi}$: naive estimate of occupancy rate; ψ: average estimate of site occupancy rates on the basis of top equivalent models; P: detection probability of single sampling period.
[§]+: positive effect, −: negative effect; *$0.01 < P < 0.05$, **$0.001 < P < 0.01$, ***$P < 0.001$.
[¶]Combined group because of difficulty with species identification on the basis of camera-trapping photographs.

by wild boar (*Sus scrofa*, 147 detections at 83 locations) and tufted deer (*Elaphodus cephalophus*, 122 detections at 82 locations; Table 3). Asiatic black bear (*Ursus thibetanus*) was

estimated to have the highest occupancy rate ($\psi = 0.49$), and Himalayan palm civet (*Paguma larvata*) the lowest ($\psi = 0.08$). Leopard cat (*Prionailurus bengalensis*) was

Table 4 Sampling effort and summary result of camera-trapping in the six surveyed protected areas

Nature reserve	Changqing	Wanglang	Wolong	Tangjiahe	Xuebaoding	Laohegou	Total
Mount. range	Qinling	Minshan	Qionglai	Minshan	Minshan	Minshan	
Area (km^2)	299	323	2000	300	636	73	3631
Start	March 2008	September 2004	August 2005	March 2002	August 2004	July 2005	
End	December 2008	October 2005	August 2009	October 2004	May 2007	April 2007	
No. of Cameras	30	30	35	22	20	15	152
No. of Sampled locations	119	131	90	326	23	33	722
No. of Camera-days	4307	3767	2209	4734	526	978	16,521
No. of Mammal photographs	2150	312	1828	754	110	168	5322
No. of Mammal species detected*	21	20	27	17	14	14	38

*Excludes mammals that could not be identified by photographs (e.g. shrews, small rodents, arboreal mammals and bats).

estimated to have the highest detection probability ($P = 0.55$), and Asiatic black bear the lowest ($P = 0.01$) (Table 3).

Among the six surveyed PAs, Changqing Nature Reserve received the highest management score; whereas Laohegou Timber Area received the lowest (Table 1). The management level score of each PA was assessed as a significant positive factor for 11 of the 14 mammal species, including one large rodent (i.e. short-tailed porcupine), six carnivores (i.e. giant panda, Asiatic black bear, hog badger, yellow-throated marten, weasels and Himalayan palm civet) and four large ungulates (i.e. wild boar, takin, serow and goral) (Table 3). The three species where management level was not a significant predictor of occupancy included one small carnivore (leopard cat) and two smaller ungulates (Reeves' muntjac *Muntiacus reevesi* and tufted deer). Other important factors for predicting the occupancy of these terrestrial animals included elevation, latitude and distance to road (which we considered a surrogate measure of human disturbance). No species showed a preference for living closer to roads, while seven exhibited significant avoidance for roads, including three carnivores (i.e. Asiatic black bear, hog badger and Himalayan palm civet) and four ungulates (i.e. wild boar, takin, serow and goral). We found no significant correlation between the number of mammal species detected in our survey and the reserve establishment history (number of years since establishment) (Pearson test, $r = 0.53$, $P = 0.27$, $n = 6$), nor did with the size of the PA (Pearson test, $r = 0.76$, $P = 0.07$, $n = 6$) or sampling effort (i.e. the number of camera-days; Pearson test, $r = 0.36$, $P = 0.48$, $n = 6$).

DISCUSSION

Large- and medium-sized mammals are vulnerable to human activities, both directly through hunting and indirectly through habitat loss and degradation (Carrillo *et al.*, 2000; Morrison *et al.*, 2007). Some mammal species within our study area, such as forest musk deer (*Moschus berezovskii*) (Hu, 2002; Yang *et al.*, 2003), golden snub-nosed monkey

(*Rhinopithecus roxellana*) (Li *et al.*, 2002), Asiatic black bear (Ma *et al.*, 2001; Liu *et al.*, 2009) and giant panda (Loucks *et al.*, 2001, 2003), have experienced dramatic decreases in suitable habitat and population during the last half-century, while at least one species, the tiger (*Panthera tigris*), has become regionally extinct (Hu & Wang, 1984; Luo, 2010).

Although all six surveyed PAs were established for protecting one flagship species, the giant panda (Caro & O'Doherty, 1999; SFA, 2006; Li *et al.*, 2010b), our survey revealed diverse large terrestrial fauna living within reserve boundaries. This is in contrast with studies conducted outside PA boundaries in the same region, which indicate large mammal populations have suffered a dramatic decrease in recent decades (Hu, 2002; Liu *et al.*, 2009). Our results suggest that vulnerable mammals benefit from government efforts to improve and strengthen the management of PAs, even when efforts are largely focused on a single species (Lu *et al.*, 2000; Loucks *et al.*, 2001; Li *et al.*, 2010b). In our study, the distribution of this species was positively correlated with management scores, but so were those of several other species with entirely different habitat and food requirements.

There is probably a limited benefit of the smaller reserves in this study, because large carnivores require large areas of suitable habitat (Norton & Lawson, 1985; Long *et al.*, 2007; Li *et al.*, 2010c). On the basis of our data, the Asiatic black bear would benefit from more protected space than currently available. The 24 detections of Asiatic black bears occurred at 24 different sampled locations across all six PAs, resulting in the highest occupancy rate ($\psi = 0.49$) but the lowest detection probability ($P = 0.01$). Besides the possible biases in occupancy modelling owing to extremely low detection probability, we believe this result is partly owing to their large home range requirements (16–202 km^2; Reid *et al.*, 1991; Hwang, 2003) relative to other species in this survey, and a trap shyness that may result from the heavy poaching pressure. The detection rates of other large carnivores (snow leopard *Uncia uncia* and leopard *Panthera pardus*) were too low for modelling within this project. Therefore, there is still a critical need for developing management plans for

Table 5 Mammal species detected in the six PAs during our survey in China, 2002–2008

Common name	Scientific name	Status		Protected areas					
		National*	IUCN†	CQ‡	WL	WWL	TJH	XBD	LHG
Primates									
Golden snub-nosed monkey	*Rhinopithecus roxellana*	I	EN	+§	−	+	+	−	+
Tibetan macaque	*Macaca thibetana*	II	NT	−	−	+	+	−	−
Rhesus monkey	*Macaca mulatta*	II	LC	−	−	−	+	−	−
Lagomorpha									
Wooly hare	*Lepus oiostolus*	-	LC	−	+	−	−	−	−
Moupin pika	*Ochotona thibetana*	-	LC	−	+	+	−	−	−
Rodentia									
Chinese white-bellied rat	*Niviventer confucianus*	-	LC	+	+	+	+	+	+
Perny's long-nose squirrel	*Dremomys pernyi*	-	LC	+	−	−	−	−	−
Pere David's rock squirrel	*Sciurotamias davidianus*	-	LC	+	+	+	+	+	+
Complex-toothed flying squirrel	*Trogopterus xanthipes*	-	NT	−	+	−	−	−	−
Spotted giant flying squirrel	*Petaurista elegans*	-	LC	+	−	−	−	−	−
Siberian chipmunk	*Tamiops macclellandi*	-	LC	−	+	+	−	−	−
Swinhoe's striped squirrel	*Tamiops swinhoei*	-	LC	−	+	+	−	+	+
Himalayan marmot	*Marmota himalayana*	-	LC	−	−	+	−	−	−
Short-tailed porcupine	*Hystrix brachyura*	-	LC	+	+	+	+	+	+
Carnivora									
Giant panda	*Ailuropoda melanoleuca*	I	EN	+	+	+	−	+	−
Asiatic black bear	*Ursus thibetanus*	II	VU	+	+	+	+	+	+
Red panda	*Ailurus fulgens*	II	EN	−	−	+	−	−	−
Hog badger	*Arctonyx collaris*	-	LC	+	+	+	+	+	+
Chinese ferret-badger	*Melogale moschata*	-	LC	+	−	+	−	−	−
Himalayan palm civet	*Paguma larvata*	-	LC	+	+	+	+	+	+
Yellow-throated marten	*Martes flavigula*	II	LC	+	+	+	+	+	+
Himalayan weasel	*Mustela sibirica*	-	LC	+	+	+	+	+	+
Mountain weasel	*Mustela altaica*	-	LC	−	+	+	−	−	−
Stone marten	*Martes foina*	II	LC	−	−	+	−	−	−
Leopard	*Panthera pardus*	I	NT	+	−	−	−	−	−
Snow leopard	*Uncia uncia*	I	EN	−	−	+	−	−	−
Asiatic golden cat	*Catopuma temminckii*	II	NT	+	−	−	+	−	−
Leopard cat	*Prionailurus bengalensis*	-	LC	+	+	+	+	+	+
Red fox	*Vulpes vulpes*	-	LC	−	−	+	−	−	−
Artiodactyla									
Wild boar	*Sus scrofa*	-	LC	+	+	+	+	+	+
Sambar	*Cervus unicolor*	II	VU	−	−	+	−	−	−
Tufted deer	*Elaphodus cephalophus*	-	NT	+	+	+	+	+	+
Reeves' muntjac	*Muntiacus reevesi*	-	LC	+	−	−	+	−	−
Forest musk deer	*Moschus berezovskii*	I	EN	+	+	+	+	−	−
Takin	*Budorcas taxicolor*	I	VU	+	+	+	+	+	+
Blue sheep	*Pseudois nayaur*	II	LC	−	+	+	−	−	−
Serow	*Capricornis milneedwardsii*	II	NT	+	+	+	+	+	−
Goral	*Naemorhedus goral*	II	NT	+	+	+	+	+	+

*Class I as the highest protection priority, Class II as the secondary priority.

†The IUCN Red List of Threatened Species, 2010.

‡PA code: CQ, Changqing; WL, Wanglang; WWL, Wolong; TJH, Tangjiahe; XBD, Xuebaoding; LHG, Laohegou.

§+: detected during our survey; −: not detected during our survey.

wide-ranging species, which may require space beyond the current extent of PAs.

In our study, the PAs that received higher management scores devoted relatively more effort to monitoring and anti-poaching patrolling, which we consider the major contributions to the higher occupancy rates of large mammals; activities shown to reduce poaching pressure (Hilborn *et al.*, 2006; Jachmann, 2008). Our results showed that better management was a positive factor for the seven species who demonstrated a significant avoidance to human disturbance (as measured by distance to road). Within our study area, poached mammals are consumed by local villagers and

restaurants or exported from the region as illegal bushmeat (examples include takin, bear and Himalayan palm civet; Zhang *et al.*, 2008). Local poaching also focuses on species desired for traditional medicine (e.g. forest musk deer *Moschus berezovskii*, Yang *et al.*, 2003; and Asiatic black bear, Liu *et al.*, 2010) or trophies (leopard and blue sheep *Pseudois nayaur*, Hu, 2002; Zhang *et al.*, 2008). Management activities in these PAs are normally restricted to surveys for giant panda, fire prevention and enforcing regulations against human disturbance (e.g. poaching, illegal logging, firewood and herb collecting, Gu *et al.*, 2004; SFA, 2006). Current law permits PA staff to deny entry of people engaged in illegal activities and remand them to local police for arrest or payment of fines. For the three species that did not demonstrate a significant relationship with our management score (leopard cat, Reeves' muntjac and tufted deer), management activities either do not adequately protect these species or are inconsequential to their persistence.

The large mammal fauna is a fundamental element in most ecosystems world-wide, and their preservation is among the original goals of many PAs (McNaughton *et al.*, 1988; Morrison *et al.*, 2007). Our study has demonstrated the potential of using the large mammal occurrence as a surrogate measure of management effectiveness across PAs. We are not the first to recommend using large mammals as a monitoring metric (Carrillo *et al.*, 2000; Tognelli, 2005), but their utility has been compromised by uneven staff expertise, imperfect detection and identification and lack of a standard protocol (Plumptre, 2000; O'Connell *et al.*, 2006; Li *et al.*, 2010b). Camera-trapping is an effective and reliable field tool to detect large mammals in dense and remote habitat (Cutler & Swann, 1999; Carbone *et al.*, 2001), and recent advances in statistical analysis during the last two decades, such as mark–recapture (Karanth & Nichols, 1998), occupancy modelling (MacKenzie *et al.*, 2003, 2006) and hierarchical model for density estimation (Royle *et al.*, 2009), provide the basis for monitoring temporal and spatial changes in large mammal distribution. Use of a wildlife picture index as a biodiversity indicator has been proposed by O'Brien *et al.* (2010) to monitor medium- and large-sized terrestrial birds and mammals and desires consideration as a standardized measure that countries can adopt. There are caveats to this recommendation, as the monitored species should be a known focus of poaching activity, be a conservation goal of the PA, persist at population levels below carrying capacity and be readily measured by standard techniques such as camera-trapping. Increases for some mammals do not always reflect successful PA management. High densities of large mammals because of predator removal or feeding on agriculture will bring complex consequences, usually negative, to the ecosystem and increased human–wildlife conflicts (Lombard *et al.*, 2001; Cote *et al.*, 2004; Sitati *et al.*, 2005). In addition, although we did not detect significance in the correlation between the number of mammal species detected in our survey and the size of PAs, there was a considerable correlation (Pearson test, $r = 0.76$, $P = 0.07$) given the small sample size

($n = 6$). Therefore, we would not recommend comparing species richness across reserves that differ widely in size, as species richness–area relationships may significantly alter expected occurrences (Ruggiero, 1999; Lomolino & Weiser, 2001; Cook *et al.*, 2002). Governments strive to provide credible metrics to evaluate among their management teams and to demonstrate to the international community their commitment to conservation (Danielsen *et al.*, 2000; Hockings, 2003; Chape *et al.*, 2005). A standardized protocol that involves camera-based detections of large mammals may provide the needed metric.

REFERENCES

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *Proceeding of 2nd International Symposium on Information Theory*, Budapest: 267–281.

Andam, K.S., Ferraro, P.J., Pfaff, A., Sanchez-Azofeifa, G.A. & Robalino, J.A. (2008) Measuring the effectiveness of protected area networks in reducing deforestation. *Proceedings of the National Academy of Sciences USA*, **105**, 16089–16094.

Bowen, W.D. (1997) Role of marine mammals in aquatic ecosystems. *Marine Ecology Process Series*, **158**, 267–274.

Brashares, J.S., Arcese, P., Sam, M.K., Coppolillo, P.B., Sinclair, A.R.E. & Balmford, A. (2004) Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science*, **306**, 1180–1183.

Brooks, T.M., Bakarr, M.I., Boucher, T., da Fonseca, G.A.B., Hiltontaylor, C., Hoekstra, J.M., Moritz, T., Olivieri, S., Parrish, J., Pressey, R.L., Rodrigues, A.S.L., Sechrest, W., Stattersfield, A., Strahm, W. & Stuart, S.N. (2004) Coverage provided by the global protected-area system: is it enough? *BioScience*, **54**, 1081–1091.

Bruner, A.G., Gullison, R.E., Rice, R.E. & da Fonseca, G.A.B. (2001) Effectiveness of parks in protecting tropical biodiversity. *Science*, **291**, 125–128.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York, USA.

Carbone, C., Christie, S., Conforti, K. *et al.* (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, **4**, 75–79.

Caro, T.M. & O'Doherty, G. (1999) On the use of surrogate species in conservation biology. *Conservation Biology*, **13**, 805–814.

Carrillo, E., Wong, G. & Cuaron, A.D. (2000) Monitoring mammal populations in Costa Rican protected areas under different hunting restrictions. *Conservation Biology*, **14**, 1580–1591.

Chape, S., Harrison, J., Spalding, M. & Lysenko, I. (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B*, **360**, 443–455.

Cook, W.M., Lane, K.T., Foster, B.L. & Holt, R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619–623.

Cote, S.D., Rooney, T.P., Tremblay, J., Dussault, C. & Waller, D.M. (2004) Ecological impact of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 113–147.

Cutler, T.L. & Swann, D.E. (1999) Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin*, **27**, 571–581.

Danielsen, F., Balete, D.S., Poulsen, M.K., Enghoff, M., Nozawa, C.M. & Jensen, A.E. (2000) A simple system for monitoring biodiversity in protected areas of a developing country. *Biodiversity and Conservation*, **9**, 1671–1705.

Deng, W. & Li, S. (2004) Report on capability building of nature reserves in China. *China's protected areas*. (ed. by Y. Xie, S. Wang and P. Schei), pp. 553–584. Tsinghua University Press, Beijing, China.

Ervin, J. (2003) Protected area assessment in perspective. *BioScience*, **53**, 819–822.

Gu, X.D., Yang, Z.S. & Wang, G. (2004) Status analysis of eco-monitoring in giant panda nature reserves, Sichuan. *Sichuan Journal of Zoology*, **23**, 146–148 (In Chinese).

Hilborn, R., Arcese, P., Borner, M., Hando, J., Hopcraft, G., Loibooki, M., Mduma, S. & Sinclair, A.R.E. (2006) Effective enforcement in a conservation area. *Science*, **314**, 1266.

Hines, J.E. (2006) PRESENCE v2.2 – Software to estimate patch occupancy and related parameters. USGS-PWRC. http://www.mbr-pwrc.usgs.gov/software/PRESENCE.html. (accessed November 2008)

Hockings, M. (2003) Systems for assessing the effectiveness of management in protected areas. *BioScience*, **53**, 823–832.

Hockings, M., Stolton, S., Leverington, F., Dudley, N. & Courrau, J. (2006) *Evaluating effectiveness: a framework for assessing management effectiveness of protected areas*, 2nd edn. IUCN and Cambridge, Switzerland and UK.

Hu, J. (2002) Diversity of terrestrial vertebrates in Minshan Mountains. *Zoological Research*, **23**, 521–526 (In Chinese).

Hu, J. & Wang, Y. (1984) *The resource animals in Sichuan (Volume 2: Mammals)*. Sichuan Science and Technical Press, Chengdu, China. (In Chinese)

Hwang, M.H. (2003) *Ecology of Asiatic black bears and people-bear interactions in Yushan National Park, Taiwan*. PhD thesis, University of Minnesota, Minneapolis, MN.

Jachmann, H. (2008) Illegal wildlife use and protected area management in Ghana. *Biological Conservation*, **141**, 1906–1918.

Joppa, L.N., Loarie, S.R. & Pimm, S.L. (2008) On the protection of "protected areas". *Proceedings of the National Academy of Sciences USA*, **105**, 6673–6678.

Karanth, K.U. & Nichols, J.D. (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, **79**, 2852–2862.

Kinnaird, M.F., Sanderson, E.W., O'Brien, T.G., Wibisono, H.T. & Woolmer, G. (2003) Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology*, **17**, 245–257.

Li, B., Pan, R. & Oxnard, C.E. (2002) Extinction of snub-nosed monkeys in China during the past 400 years. *International Journal of Primatology*, **23**, 1227–1244.

Li, S., McShea, W.J., Wang, D., Shao, L. & Shi, X. (2010a) The use of infrared-triggered cameras for surveying phasianids in Sichuan Province, China. *Ibis*, **152**, 299–309.

Li, S., Wang, D.J., Gu, X.D. & McShea, W.J. (2010b) Beyond pandas, the need for a standardized monitoring protocol for large mammals in Chinese nature reserves. *Biodiversity Conservation*, **19**, 3195–3206.

Li, S., Wang, D., Lu, Z. & McShea, W.J. (2010c) Cats living with pandas: the status of wild felids within giant panda range. *Cat News*, **52**, 20–23.

Liu, J., Linderman, M., Ouyang, Z., An, L., Yang, J. & Zhang, H. (2001) Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science*, **292**, 98–101.

Liu, J., Miao, H., Ouyang, Z., Xu, W. & Zheng, H. (2008) Analyzing the effectiveness of community management in Chinese nature reserves. *Biodiversity Science*, **16**, 289–398 (In Chinese).

Liu, F., McShea, W.J., Garshelis, D.L., Zhu, X., Wang, D., Gong, J. & Chen, Y. (2009) Spatial distribution as a measure of conservation needs: an example with Asiatic black bears in south-western China. *Diversity and Distributions*, **15**, 649–659.

Liu, F., McShea, W.J., Garshelis, D.L., Zhu, X., Wang, D. & Shao, L. (2010) Human-wildlife conflicts influence attitudes but not necessarily behaviors: factors driving the poaching of bears in China. *Biological Conservation*, **144**, 538–547.

Lombard, A.T., Johnson, C.F., Cowling, R.M. & Pressey, R.L. (2001) Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation*, **102**, 191–203.

Lomolino, M.V. & Weiser, M.D. (2001) Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, **28**, 431–445.

Long, R.A., Donovan, T.M., Mackay, P., Zielinski, W.J. & Buzas, J.S. (2007) Comparing scat detection dogs, cameras,

and hair snares for surveying carnivores. *Journal of Wildlife Management*, **71**, 2018–2025.

Loucks, C.J., Lu, Z., Dinerstein, E., Wang, H., Olson, D.M., Zhu, C. & Wang, D.J. (2001) Giant Pandas in a changing landscape. *Science*, **294**, 1465.

Loucks, C.J., Lu, Z., Dinerstein, E., Wang, D., Fu, D. & Wang, H. (2003) The giant pandas of the Qinling Mountains, China: a case study in designing conservation landscapes for elevational migrants. *Conservation Biology*, **17**, 558–565.

Lu, Z., Pan, W.S., Zhu, X.J., Wang, D.J., Wang, H. (2000) What has the panda taught us? *Priorities for the conservation of mammalian diversity-Has the panda had its day?* (ed. by A. Entwistl and N. Dunstone), pp. 325–334. Cambridge University Press, Cambridge, UK.

Lu, Y., Chen, L., Fu, B. & Liu, S. (2003) A framework for evaluating the effectiveness of protected areas: the case of Wolong Biosphere Reserve. *Landscape and Urban Planning*, **63**, 213–223.

Luo, S.J. (2010) The status of the tiger in China. *Cat New's Special Issue*, **5**, 10–13.

Ma, Y., Xu, L. & Hu, J. (2001) On the resources and conservation of bears in China. *Proceedings of the third international symposium on the trade in bear parts*. (ed. by D.F. Williamson and M.J. Phipps), pp. 38–43. TRAFFIC East Asia, Hong Kong, China.

Ma, C., Moseley, R.K., Chen, W.Y. & Zhou, Z.K. (2007) Plant diversity and priority conservation areas of Northwestern Yunnan, China. *Biodiversity and Conservation*, **16**, 757–774.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200–2207.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) *Occupancy estimation and modeling*. Academic Press, New York.

McNaughton, S.J., Ruess, R.W. & Seagle, S.W. (1988) Large mammals and process dynamics in African ecosystems. *BioScience*, **38**, 794–800.

McShea, W.J., Stewart, C., Peterson, L., Erb, P., Stuebing, R. & Giman, B. (2009) The importance of secondary forest blocks for terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. *Biological Conservation*, **142**, 3108–3119.

Mittermeier, R., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., da Fonseca, G.A.B., Ford, H. & Seligmann, P.A. (2005) *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. Conservation International, Washington, DC.

Mora, C., Andrefouet, S., Costello, M.J., Kranenburg, C., Rollo, A., Veron, J., Gaston, K.J. & Myers, R.A. (2006) Coral reefs and the global network of marine protected areas. *Science*, **312**, 1750–1751.

Morrison, J.C., Sechrest, W., Dinerstein, E., Wilcove, D.S. & Lamoreux, J.F. (2007) Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy*, **88**, 1363–1380.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Norton, P.M. & Lawson, A.B. (1985) Radio tracking of leopards and caracals in the Stellenbosch area, Cape Province. *South African Journal of Wildlife Research*, **15**, 17–24.

O'Brien, T.G., Baillie, J.E.M., Krueger, L. & Cuke, M. (2010) The Wildlife Picture Index: monitoring top trophic levels. *Animal Conservation*, **13**, 335–343.

O'Connell, A.F. Jr, Talancy, N.W., Bailey, L.L., Sauer, J.R., Cook, R. & Gilbert, A.T. (2006) Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. *Journal of Wildlife Management*, **70**, 1625–1633.

Olson, D.M. & Dinerstein, E. (2002) The Global 200: priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden*, **89**, 199–224.

Plumptre, A.J. (2000) Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology*, **37**, 356–368.

Quan, J., Ouyang, Z., Xu, W. & Miao, H. (2009) Management effectiveness of China nature reserves: status quo assessment and countermeasures. *Chinese Journal of Applied Ecology*, **20**, 1739–1746 (In Chinese).

Radeloff, V.C., Stewart, S.I., Hawbaker, T.J., Gimmi, U., Pidgeon, A.M., Flather, C.H. & Hammer, R.B. (2010) Housing growth in and near United States protected areas limits their conservation value. *Proceedings of the National Academy of Sciences USA*, **107**, 940–945.

Reid, D., Jiang, M., Teng, Q., Qin, Z. & Hu, J. (1991) Ecology of the Asiatic black bear (*Ursus thibetanus*) in Sichuan, China. *Mammalia*, **55**, 221–238.

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I. *et al.* (2004) Effectiveness of the global protected area network in representing species diversity. *Nature*, **428**, 640–643.

Royle, J.A., Nichols, J.D., Karanth, K.U. & Gopalaswamy, A. M. (2009) A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, **46**, 118–127.

Ruggiero, A. (1999) Spatial patterns in the diversity of mammal species: a test of the geographic area hypothesis in South America. *Ecoscience*, **6**, 338–354.

SFA (State Forestry Administration), (2006) *The 3rd national survey report on giant panda in China*. Science Press, Beijing. (In Chinese)

Sitati, N.W., Walpole, M.J. & Leader-Williams, N. (2005) Factors affecting susceptibility to crop raiding by African elephants: using a predictive model to mitigate conflict. *Journal of Applied Ecology*, **42**, 1175–1182.

Tognelli, M.F. (2005) Assessing the utility of indicator groups for the conservation of South American terrestrial mammals. *Biological Conservation*, **121**, 409–417.

Vieira, L.C., Oliveira, N.G. & Gayubo, S.F. (2011) On the use of Apiformes and Spheciformes (Insecta: Hymenoptera) populations as a management tool. *Biodiversity and Conservation*, **20**, 519–530.

Wang, D.J., Li, S., McShea, W.J. & Li, M.F. (2006) Use of remote-trip cameras for wildlife surveys and evaluating the effectiveness of conservation activities at a nature reserve in Sichuan Province, China. *Environment Management*, **38**, 942–951.

Wikramanayake, E.D., Dinerstein, E., Robinson, J.G., Karanth, U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Conner, M., Hemley, G. & Bolze, D. (1998) An ecology-based method for defining priorities for large mammal conservation: the tiger as case study. *Conservation Biology*, **12**, 865–878.

Xie, Y. (2004). Review on the management system of China's nature reserves. *China's protected areas*. (ed. by Y. Xie, S. Wang and P. Schei), pp. 315–338. Tsinghua University Press, Beijing.

Yang, Q., Meng, X., Xia, L. & Feng, Z. (2003) Conservation status and causes of decline of musk deer (*Moschus spp.*) in China. *Biological Conservation*, **109**, 333–342.

Zhang, R.Z. (1999) *Zoogeography of China*. Science Press, Beijing, China (In Chinese).

Zhang, J.L., Li, H.F., Zhang, M.X. & Hou, L.Y. (1998) Some of the main problems of the Qinling nature reserves and managing strategies. *Chinese Biodiversity*, **6**, 312–315 (In Chinese).

Zhang, L., Hua, N. & Sun, S. (2008) Wildlife trade, consumption and conservation awareness in southwest China. *Biological Conservation*, **17**, 1493–1516.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Top equivalent models of the 14 mammal species examined by occupancy modelling.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Sheng Li is an ecology researcher at Peking University and Smithsonian Conservation Biology Institute. He is interested in wildlife ecology and conservation. His current focus is on the distribution pattern, population estimation and adaptive management of terrestrial large mammals.

Author contributions: S.L., W.J.M., D.W. and Z.L. conceived the original ideas and sampling design of this study. D.W., S.L. and X.G. organized the field work and collected the data, and X.G. provided administration support. S.L. led the data management and analysis with help from W.J.M., D.W. and Z.L.. All authors contributed to the writing of the manuscript, led by L.S.

Editor: Graeme Cumming