Animal Conservation. Print ISSN 1367-9430

Effects of human–carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR

A. Johnson, C. Vongkhamheng, M. Hedemark & T. Saithongdam

Wildlife Conservation Society-Lao PDR Program, Vientiane, Lao People's Democratic Republic

Keywords
Laos; carnivores; human–wildlife conflict; mark–recapture; protected areas.

Correspondence
Arlyne Johnson, Wildlife Conservation Society-Lao PDR Program, Box 6712, Vientiane, Lao People's Democratic Republic. Fax: 856 21 215400
Email: ajohnson@wcs.org

Received 2 January 2006; accepted 24 May 2006

doi:10.1111/j.1469-1795.2006.00049.x

Abstract

Unique to South-east Asia, Lao People's Democratic Republic contains extensive habitat for tigers and their prey within a multiple-use protected area system covering 13% of the country. Although human population density is the lowest in the region, the impact of human occurrence in protected areas on tiger *Panthera tigris* and prey populations was unknown. We examined the effects of human–carnivore conflict on tiger and prey abundance and distribution in the Nam Et-Phou Louey National Protected Area on the Lao–Vietnam border. We conducted intensive camera-trap sampling of large carnivores and prey at varying levels of human population and monitored carnivore depredation of livestock across the protected area. The relative abundance of large ungulates was low throughout whereas that of small prey was significantly higher where human density was lower. The estimated tiger density for the sample area ranged from 0.2 to 0.7 per 100 km^2. Tiger abundance was significantly lower where human population and disturbance were greater. Three factors, commercial poaching associated with livestock grazing followed by prey depletion and competition between large carnivores, are likely responsible for tiger abundance and distribution. Maintaining tigers in the country's protected areas will be dependent on the spatial separation of large carnivores and humans by modifying livestock husbandry practices and enforcing zoning.

Introduction

Once widely distributed across Asia, today breeding populations of tigers *Panthera tigris* remain only in scattered sites across the continent (Wikramanayake *et al*., 1998; Sunquist & Sunquist, 2002). Studies show that tiger persistence is largely dependent on prey abundance (Karanth & Stith, 1999; Karanth *et al*., 2004) and protection from poaching (Karanth & Nichols, 1998). Unique to South-east Asia, the Lao People's Democratic Republic (hereafter Laos) has over 40% forest cover and only 22 people km^{-2} (ICEM, 2003*a*). The country has several tiger conservation landscapes of global and regional significance (WCS/WWF/SI, 2006) containing national protected areas (NPAs) that may harbor viable tiger populations (Duckworth, Salter & Khounboline, 1999). The NPAs are classified as Category VI Managed Resource Areas (IUCN, 1994; Robichaud *et al*., 2001) with villages remaining inside NPA boundaries in designated management zones (Berkmuller *et al*., 1995) in contrast to Category II parks prohibiting human residence in most other parts of Asia where tigers persist. Little is known about the status of tigers and factors affecting tiger survival in Laos under this multiple-use arrangement (Duckworth & Hedges, 1998; Rabinowitz, 1999).

Where humans and large carnivores interface, conflicts of three types are common: livestock depredation, prey depletion from overhunting and direct human-caused mortality of carnivores (Treves & Karanth, 2003; Frank, Woodroffe & Ogada, 2005; Miquelle *et al*., 2005; Rabinowitz, 2005). Across Indochina, tiger attacks on humans are infrequent but livestock loss on agricultural frontiers is common (Duckworth & Hedges, 1998). Half of Laos' 5.2 million residents are subsistence farmers (UNDP, 2002) whose principal source of income is livestock (Roder, 2001). Livestock graze freely in remote mountain grasslands (Phensavanh *et al*., 1999), providing conditions where conflict is likely. The influence of these husbandry practices on human–tiger conflict in Laos' protected areas has never been systematically evaluated.

Where people live inside protected areas, controlling resource extraction is typically a management challenge (Terborgh & Peres, 2002). Studies have linked human density to declining ungulate densities as a result of hunting (Woodroffe, 2000), which consequently leads to declines in tiger abundance (Karanth & Stith, 1999; Madhusudan & Karanth, 2002; Karanth *et al*., 2004). Although Laos' human density remains low, its growth rate is high (3.4%; EIU, 2003) and the rural population is thinly but widely dispersed on the landscape (Sandewall, Ohlsson & Sawathvong, 2001). Overhunting for subsistence and trade is recognized as a major threat to wildlife populations (Duckworth *et al.*, 1999; Nooren & Claridge, 2001; Johnson, Singh & Duongdala, 2005).

To evaluate factors affecting tiger persistence under a multiple-use protected area system, we initiated the country's first systematic surveys of tiger, prey and human–tiger conflict in the Nam Et-Phou Louey (NEPL) NPA on the Lao–Vietnam border. Designated as a Class 1 Tiger Conservation Landscape, the area is a global priority for conservation (WCS/WWF/SI, 2006) and reported a relatively high incidence of tiger attacks on livestock (Davidson, 1998, 1999; Duckworth & Hedges, 1998). In this paper, we examine the impact of human density, disturbance and livestock husbandry practices on tigers and their prey.

Methods

Study area

The 3446-km^2 NEPL NPA, with proposed extensions (854 km^2), is the second largest protected area in Laos (Fig. 1). Elevation ranges from 400 to 2257 m, with 91% of the area along slopes greater than 12%. Annual rainfall fluctuates from 1400 to 1800 mm; climate is monsoonal and temperatures range seasonally from 5 to 30 °C. The landscape is dominated by mixed evergreen and deciduous forest interspersed with agricultural lands, secondary forest and anthropogenic grasslands (Davidson, 1998). Ninety-eight villages live a subsistence lifestyle in and around the NPA (Schlemmer, 2002). The sale of buffalos and cows (hereafter called livestock) is the principal source of cash income and most villages graze livestock inside the NPA (ICEM, 2003*b*).

Tiger and prey abundance and distribution

We surveyed tiger and prey using 50 CamTrakker passive infrared camera traps (CamTrak South Inc., GA, USA) set in five 100 km^2 sampling blocks in areas where tiger sign was previously reported (Davidson, 1998; Vongkhamheng, 2002; Fig. 1). Each block was divided into 25 4-km^2 subunits and a random UTM coordinate was chosen within each. We placed a camera pair, to photograph both sides of individual tigers, in an optimal location near active animal trails within 500 m of the random coordinate. A Garmin 12XL global positioning system (GPS) was used to record camera locations. Cameras were mounted on trees at 45 cm and set to operate 24 h day with a 20-s delay between sequential photographs. Cameras were left in the forest for a minimum of 37 days. The number of trap days per camera (CTD) was calculated from the time the camera was mounted until the date of the final photo or the date the camera was retrieved.

We entered photo results into an Access database, recording the frame number, date, time and object/s for each film. Each photo was identified to species and rated as a dependent or independent event, with an 'independent capture event' defined as (1) consecutive photographs of different individuals of the same or different species, (2) consecutive photographs of individuals of the same species taken more than 0.5 h apart and (3) nonconsecutive photos of individuals of the same species (O'Brien, Kinnaird & Wibisono, 2003). For each species, we calculated the number of independent photographs (IP) per 100 CTD as an index of relative abundance (RAI), using CTD from only one camera of each camera pair. If CTD varied within the pair, the largest number was used. As tigers tend to select large prey (mean weight 92 kg) if available (Karanth & Sunquist, 1995; also see Sunquist & Sunquist, 2002), we separated prey into large (100 kg +) and small species (< 100 kg) to determine

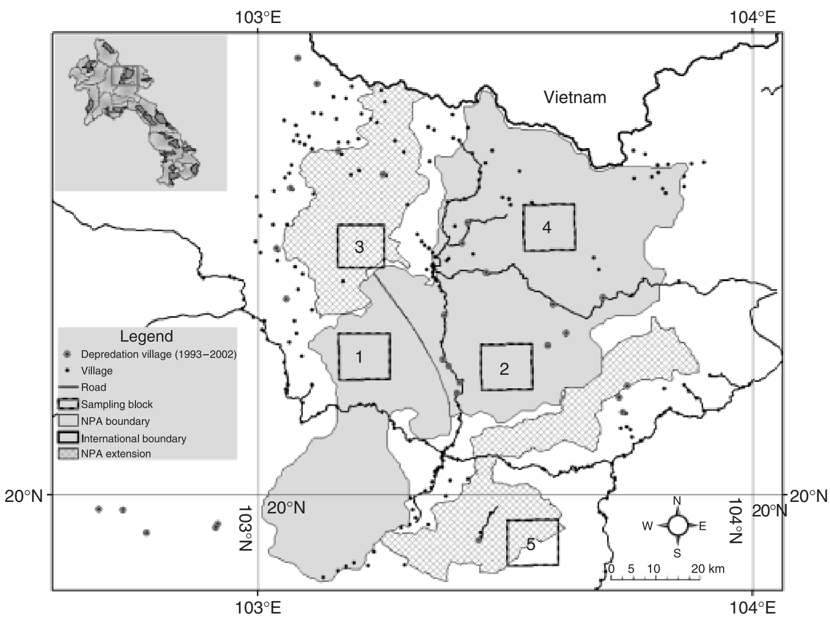

Figure 1 Location of five camera-trap sampling blocks relative to villages reporting tiger *Panthera tigris* depredation of livestock from 1993 to 2002 in the Nam Et-Phou Louey National Protected Area and proposed extensions, Laos.

the relative abundance and distribution of each group in the study area.

We used an index of prey abundance rather than more preferable mark–recapture-based estimates of abundance that incorporate capture probability (Jennelle, Runge & MacKenzie, 2002; Karanth *et al.*, 2004) because photographs of prey species could not be reliably identified to individuals by their markings. Under these conditions, a camera-trap index is proposed as a useful indicator of animal abundance (Carbone *et al.*, 2001, 2002). Ideally the index is calibrated against an independent measure of density such as line transects (see O'Brien *et al.*, 2003), although conditions at hill evergreen forest sites in Indochina (rarity of animal sightings and limited visibility) frequently violate assumptions of distance sampling methods (Buckland *et al.*, 1993). At other evergreen forest sites in the region, relative abundance indices based on camera-trapping data have been used in estimates of prey densities where independent density estimates were lacking (Kawanishi & Sunquist, 2004). As our surveys were conducted within a single study area, we assumed that capture probabilities for prey were comparable between sampling blocks as habitat was similar, all surveys were carried out within the monsoonal dry season, and methods were standardized to ensure that size of area sampled, camera-trapping equipment, criteria for selecting trap sites and individuals setting cameras did not differ between blocks.

We identified tiger individuals by stripe patterns to establish capture histories for each tiger (Karanth, 1995). Applying closed population assumptions (Nichols & Karanth, 2002), we estimated capture probabilities (*P*-hat) and population size using the computer program CAPTURE (Otis *et al.*, 1978; White *et al.*, 1982). We derived estimates of tiger density (tigers per 100 km^2) for an effective sampling area that included the area of the sampling blocks plus a buffer strip on all sides of the blocks (Nichols & Karanth, 2002). Taking into account that the distance moved by large far-ranging carnivores between cameras may be a poor representation of true ranging behavior (Soisaloa & Cavalcanti, 2006), we estimated a series of effective sampling areas with buffers ranging from half of the mean maximum distance (HMMD) to mean maximum distance (MMD) and the maximum distance (MD) moved between recapture photographs for the entire study area.

Human effects on tigers and prey

We calculated the distance from each camera location to the nearest village and the total human population within a 10-km radius, classifying camera locations into three groups: low (<550 people), medium (550–1100 people) and high (>1100 people). We compared the mean RAI of prey between groups. We used standardized forms to record the presence/absence of nine indicators of human disturbance (walking tracks, old roads, livestock grazing, forest fires, hunting camps, snares, blinds, vegetation cutting or non-timber forest product collection) within 10 m of each location. Survey teams also recorded hunting evidence (hunting camps, trip-wire explosive traps and the remains of wildlife killed by humans) encountered in blocks.

We trained district officers to use standardized forms and GPS to systematically collect historical information from villages that had reported tiger attacks on livestock to district offices from 1993 to 2002 and from farmers reporting attacks during our study (April 2003–June 2004). Officers recorded the number and age of livestock attacked, kill date, location, distance from village and evidence used to determine predator identity. For each new attack, officers also recorded the farmer's husbandry methods, number of livestock owned and weight of livestock killed. At the kill site, officers recorded the distance from water bodies and grasslands and, if visible, measured drag distance, carcass puncture marks, carnivore tracks and scats. Officers also interviewed every village to gauge interest in a possible livestock insurance program, where farmers could pay an annual premium ($<$US$ 1/animal) ensuring full value payment for an insured livestock if evidence collected by officers could conclusively show that the animal was killed by a tiger. The stated prerequisites for farmer participation in the program (following Nyhus *et al.*, 2003) were to keep livestock less than 1 km from the village and immediately report attacks, facilitating the collection of fresh evidence for predator identification.

Results

Tiger and prey abundance and distribution

We deployed cameras at 247 points (Table 1), of which 94.3% had unexposed film remaining at the end of the sampling period. Of cameras with no unexposed film remaining, only 2.4% misfired and finished the film in the first week of the sampling period, 1.2% within 15–21 days of pickup, 1.2% within 8–14 days of pickup and 0.8% within the final week of the sampling period. Given that all cameras were paired, the relatively low average misfire rate of only 2.8 cameras per sampling block was unlikely to affect analyses of survey results.

We conducted camera-trap surveys in five sampling blocks over 14 months for 3588 total trap days (Table 1). Cameras recorded 1322 photos of 32 mammal and 13 bird species including 382 independent photos of 10 prey species (Fig. 2). Although several other prey species, small

Table 1 Sampling effort for estimating tiger abundance in 2003–2004 in Nam Et-Phou Louey National Protected Area, Laos

(Sampling block) Site name	Month/year	Duration (days)	Tigers (recaptures)	Camera points (cameras)	Trap days
(1) Phou Louey	3–4/2003	55	2 (2)	25 (49)	828
(2) Nam Pa	10–11/2003	39	1 (2)	24 (48)	667
(3) Nam Ngao	12/2003–1/2004	37	2 (1)	25 (50)	704
(4) Phou Jae	2–3/2004	37	0	25 (50)	659
(5) Thamla	4–5/2004	37	0	25 (50)	730

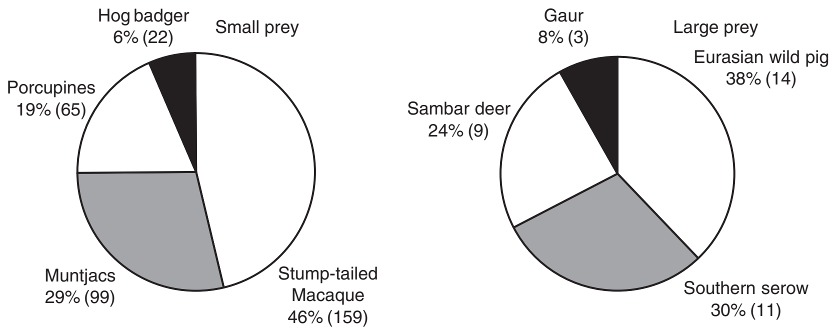

Figure 2 Relative number of independent photos of small ($n=345$) and large ($n=37$) prey recorded from five sampling blocks in the Nam Et-Phou Louey National Protected Area, Laos. Muntjacs include *Muntiacus muntjak* and *Muntiacus rooseveltorum/truongsonensis*; porcupines include *Hystrix brachyra* and *Atherurus macrourus*.

Table 2 Large mammals and birds recorded from camera-trap surveys in five sampling blocks, Nam Et-Phou Louey National Protected Area, Laos

			Sampling block				
Family	Scientific name	Common name	1	2	3	4	5
Phasianidae	*Arborophila brunneopectus*	Bar-backed partridge		x		x	x
	Bambusicola fytchii	Mountain bamboo partridge				x	
	Gallus gallus	Red junglefowl	x	x	x		x
	Lophura nycthemera	Silver pheasant	x	x	x	x	x
	Polyplectronbicalcaratum	Grey-peacock pheasant	x	x	x	x	x
Cercopithecidae	*Macaca arctoides**	Stump-tailed macaque*	x	x	x	x	x
	Macaca assamensis	Assamese macaque		x			
Canidae	*Cuon alpinus*	Dhole		x	x	x	x
Ursidae	*Ursus thibetanus*	Asiatic black bear	x	x			
	Ursus malayanus	Sun bear	x	x	x	x	
Mustelidae	*Mustela strigidorsa*	Back-striped weasel	x				
	Martes flavigula	Yellow-throated marten	x	x	x	x	x
	*Arctonyx collaris**	Hog badger*	x	x			
	Aonyx cinera	Oriental small-clawed otter		x			
Viverridae	*Viverra zibetha*	Large Indian civet	x	x	x	x	x
	Viverricula indica	Small Indian civet				x	
	Prionodon pardicolor	Spotted linsang	x		x	x	
	Paradoxurus hermaphroditus	Common palm civet	x	x	x	x	x
	Paguma larvata	Masked palm civet	x	x	x	x	x
	Chrotogale owstoni	Owston's civet	x				
Herpestidae	*Herpestes urva*	Crab-eating mongoose			x	x	x
Felidae	*Prionailurus bengalensis*	Leopard cat	x	x	x	x	x
	Catopuma temminckii	Asian golden cat	x	x	x	x	
	Pardofelis marmorata	Marbled cat	x		x	x	x
	Pardofelis nebulosa	Clouded leopard	x	x	x	x	x
	Panthera pardus	Leopard	x				
	Panthera tigris	Tiger	x	x	x		
Suidae	*Sus scrofa**	Eurasian wild pig*	x	x	x	x	x
Cervidae	*Cervus unicolor**	Sambar deer*	x	x		x	x
	*Muntiacus muntjak**	Red muntjac*	x	x	x	x	x
	*Muntiacus rooseveltorum /truongsonensis**	Small dark muntjac*	x		x		x
Bovidae	*Bos frontalis**	Gaur*					x
	*Naemorhedus sumatraensis**	Southern serow*	x		x		x
Hystricidae	*Hystrix brachyura**	East Asian porcupine*	x	x	x	x	x
	*Atherurus macrourus**	Asiatic brush-tailed porcupine*	x	x	x		x

Prey species considered in the analyses are indicated with an asterisk.

carnivores (weighing <10 kg; Mustelidae, Viverridae, Herpestidae and Felidae) and gallinaceous birds (weighing <1 kg; Phasianidae), were identified (Table 2), our analyses included only those most frequently recorded as prey items in tiger diets (Sunquist & Sunquist, 2002). Large prey (weighing 100+ kg; gaur, sambar deer, southern serow and wild pig) made up only 10% of independent photos of prey (Fig. 2). The remaining independent photos were of small prey (weighing <100 kg; stump-tailed macaque, muntjac, porcupine and hog badger).

We recorded large prey from all sampling blocks (Table 2), ranging in abundance from wild pig (mean 0.4 IP per 100 CTD) to gaur (mean 0.08 IP per 100 CTD; Table 3). Large prey abundance was not significantly different between blocks (Kruskal–Wallis $\chi = 7.96$, d.f. = 4, $P = 0.093$), although the mean RAI in blocks 4 and 5 (1.7 IP per 100 CTD) was higher than in other blocks (0.57 IP per 100 CTD). Small prey was widely distributed (Table 2), with mean RAI ranging from 4.26 IP per 100 CTD (stump-tailed macaque) to 0.54 IP per 100 CTD (hog badger). Abundance did not vary significantly between sampling blocks (Kruskal–Wallis $\chi = 6.46$, d.f. = 4, $P = 0.17$). Across blocks, the relative abundance of large prey was significantly less than that of small prey (Mann–Whitney U, $Z = -8.08$, $n = 124$, $P < 0.001$).

We recorded 13 photos of five individual tigers from three sampling blocks at an abundance of 276 CTD per photo (Table 1). Across blocks, the mean RAI of tigers ranged from zero to 0.48 IP per 100 CTD (Table 3). The mean relative abundance of tigers was significantly less in blocks 4 and 5 than in other blocks (Mann–Whitney U, $Z = -2.392$, $n = 124$, $P = 0.017$).

Applying closed population assumptions, we calculated two estimates of tiger density: one for block 1 (sampled from March to April 2003) and another for blocks 2–5 (sampled over a consecutive 7-month period from October 2003 to May 2004). CAPTURE Model M_o provided the best fit estimating capture probabilities (P-hat) of 0.0364 for block 1 and 0.0421 for blocks 2–5, with an estimated population size of 2 ± 0.66 [95% confidence interval (CI) of two individuals] for block 1 and 3 ± 1.18 (95% CI of three to 11 individuals) for blocks 2–5. Following Karanth & Nichols (1998), we used CAPTURE Model M_h, with a jackknife estimator permitting each individual to have a different capture probability, which estimated capture probabilities (P-hat) of 0.0242 for block 1 and 0.0338 for blocks 2–5. The estimated population size was 3 ± 1.75 for block 1, with a 95% CI of three to 12 individuals, and 4 ± 1.54 for blocks 2–5, with a 95% CI of four to 11 individuals.

The MD traveled by individual tigers ($n = 3$) between recaptures ranged from 1.2 to 8.3 km. We calculated a range of effective sample areas by applying a buffer to all sides of the blocks using MD (8.3 km), MMD (3.8 km) and HMMD (1.9 km) moved between recapture photographs (Table 4). The effective sample area for block 1 ranged from 190 to 710 km^2, with densities ranging from 0.5 tiger per 100 km^2 (95% CI = 0.5–1.5 tigers per 100 km^2) to 1.6 tigers per 100 km^2 (95% CI = 1.6–6.3 tigers per 100 km^2). The effective sample area for blocks 2–5 ranged from 762 to 2839 km^2, with densities ranging from 0.1 tiger per 100 km^2 (95% CI = 0.1–0.4 tiger per 100 km^2) to 0.5 tiger per 100 km^2 (95% CI = 0.5–1.4 tigers per 100 km^2). Averaging across all blocks, we estimated densities ranging from 0.2 tiger per 100 km^2 (95% CI = 0.2–0.7 tiger per 100 km^2) to 0.7 tiger per 100 km^2 (95% CI = 0.7–2.4 tigers per 100 km^2) (Table 4), with a minimum of seven and possibly as many as 23 tigers present in the total effective sampled area (range 952–3548 km^2).

Table 3 Mean and range of relative abundance index (RAI) values (independent photos per 100 camera trap days) for tiger and prey from five sampling blocks in NEPL NPA (March 2003–May 2004)

Common name	Mean (RAI)	Range (RAI)
Tiger		
Panthera tigris	0.24	0–0.48
Stump-tailed macaque		
Macaca arctoides	4.26	1.50–7.85
Muntjacs		
Muntiacus spp.	2.77	1.85–3.95
Porcupines		
Hystrix brachyura and *Atherurus macrourus*	1.79	0.43–2.60
Hog badger		
Arctonyx collaris	0.54	0–2.54
Eurasian wild pig		
Sus scrofa	0.40	0.14–1.06
Southern serow		
Naemorhedus sumatraensis	0.29	0–0.69
Sambar deer		
Cervus univcolor	0.25	0–0.55
Gaur		
Bos frontalis	0.08	0–0.41

NEPL NPA, Nam Et–Phou Louey National Protected Area.

Table 4 Range of tiger *Panthera tigris* density estimates using a buffer of maximum distance (MD), mean maximum distance (MMD) and half the mean maximum distance (HMMD) traveled between recapture photographs to determine effective sampling area

Distance used to estimate buffer	km	Total effective sampling area (km^2)	Tiger density [individuals per 100 km^2 (95% CI)]
MD	8.3	3548	0.2 (0.2–0.7)
MMD	3.8	1548	0.5 (0.5–1.5)
HMMD	1.9	952	0.7 (0.7–2.4)

CI, confidence interval.

Human effects on tigers and prey

Camera locations ($n = 124$) differed in elevation, proximity to human population and RAI of humans recorded by camera traps (Table 5). The distance to the nearest village ranged from 2.2 to 13.6 km and human population within 10 km of cameras ranged from 0 to 1641 individuals. A strong, negative relationship existed between human population within 10 km of cameras and distance to the nearest village (Pearson correlation $r = -0.6$, $n = 124$, $P < 0.0001$). The relative abundance of small prey was significantly higher at camera locations where human population was lower (<550 people within 10 km; Kruskal–Wallis $\chi = 7.4$, d.f. = 2, $n = 124$, $P = 0.03$). There was a strong negative relationship between mean distance of cameras to villages and proportion of cameras located near hunting camps

Table 5 Characteristics of camera locations and sampling blocks in the Nam Et-Phou Louey National Protected Area, including number of camera locations (*n*), elevation (*m*), human population within 10 km of each camera location, distance to nearest village [mean ± SD (range)] and relative abundance of humans (RAI = independent photos per 100 CTD) recorded by camera traps

(Block) Site	*n*	Elevation (m)	Human population (within 10 km)	Distance from village (km)	Human abundance (RAI)
(1) Phou Louey	25	1575 ± 252 (1137–2288)	241 ± 288 (0–1139)	9.7 ± 2.3 (5.6–13.4)	0.12
(2) Nam Pa	24	1075 ± 154 (826–1521)	415 ± 494 (0–1560)	8.7 ± 1.2 (5.9–11)	0.00
(3) Nam Ngao	25	1271 ± 140 (1012–1576)	370 ± 328 (0–1109)	8.1 ± 2.1 (4–12)	0.12
(4) Phou Jae	25	951 ± 227 (543–1263)	748 ± 291 (300–1467)	6.8 ± 2.3 (2.2–10)	1.21
(5) Thamla	25	1439 ± 140 (1194–1706)	673 ± 721 (0–1641)	9.6 ± 2.3 (5.9–13.6)	0.36

CTD, trap days per camera; RAI, relative abundance index.

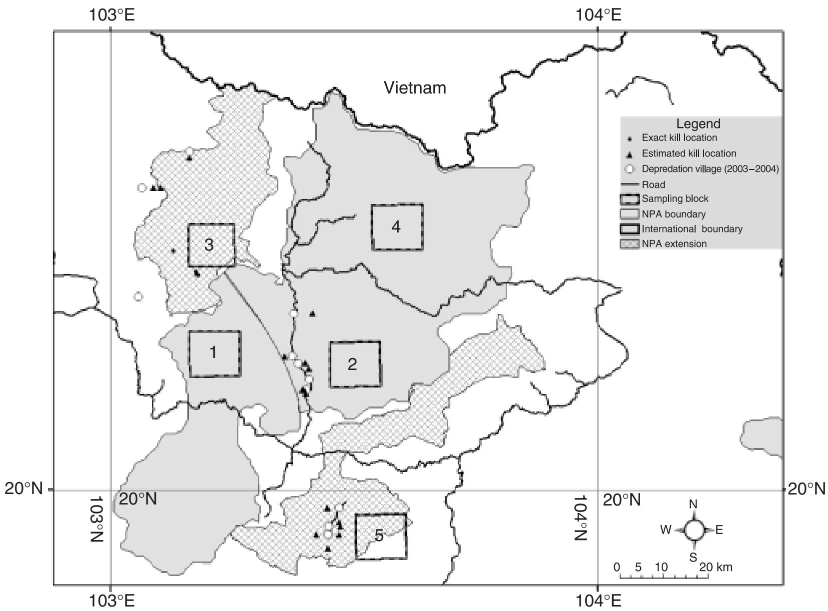

Figure 3 Location of villages reporting tiger *Panthera tigris* depredation of livestock from April 2003 to June 2004 with actual and estimated kill sites relative to camera-trap sampling blocks, Nam Et-Phou Louey National Protected Area, Laos.

(Spearman rank correlation $r = -0.95$, $n = 5$, $P = 0.01$). The relative abundance of large prey was not significantly different between camera locations at varying levels of human population (Kruskal–Wallis $\chi = 0.6$, d.f. = 2, $n = 124$, $P = 0.75$), suggesting that large prey was relatively scarce across the entire area.

Survey teams recorded hunting evidence in every block, including active trip-wire explosive traps across game trails for large mammals. Cameras recorded 10 times more independent photos of humans in blocks 4 and 5 (mean 0.79 IP/100 CTD; range 0.0–16.6, $n = 100$) than in other blocks (Table 5; mean 0.08 IP per 100 CTD; range 0.0–3.7, $n = 147$). In these highly disturbed blocks (4 and 5), mean human RAI was significantly higher than in other blocks (Mann–Whitney U, $Z = -2.69$, $n = 124$, $P = 0.007$) and mean human population was greater (Table 5). District police reports of tiger poaching during the study period were also from highly disturbed blocks (C. Vongkhamheng, unpubl. data): six tigers killed by explosive traps set in livestock carcasses near block 4 from June to September 2003 and one tiger shot near block 5 in April 2004.

Historical depredation reports came from 28 villages (Fig. 1) that reported losing 583 livestock (mean = 2.1 livestock per village per year; range 0–8.3) from 1993 to 2002. Seventy-three per cent of attacks were 1 h or more (walking distance) from the village (mean = 1.2, range 0–5) and 57% were full-size adults (3 + years old; estimated minimum weight of 250–350 kg). During the study period, 11 villages reported tiger attacks on 28 livestock (Fig. 3), representing 1.7% of their total herd ($n = 1679$): a mean of 2.1 livestock per village per year (range 1–7). Most kills (79%) were over 1 h (mean = 1.2, range 0.3–2.5) from the village and 75% occurred during the rice cropping season (May–October) when cattle graze outside the village (Phensavanh *et al.*, 1999). GPS data from kill sites indicated that reports of 1 h walking were equivalent to a mean straight-line distance of 1.6 km ($n = 7$, range 1.2–2.2). Extrapolating this to all reports indicated that livestock were on average 2.7 km from a village ($n = 28$, range 0.4–9.7) and 4.5 km from the nearest sampling block ($n = 25$, range 1.1–9.5) when attacked (Fig. 3). Cameras did not record livestock within sampling blocks. Most livestock (69%) were full-size adults and most kill sites investigated ($n = 21$) were less than 25 m from grasslands (86%) and water (62%), factors that are reliable predictors of large carnivore kills (Karanth, 1995; Karanth & Sunquist, 2000).

Although evidence suggested that the attacks were by tigers, in 69% of cases officers could not obtain fresh evidence to confirm predator identification, given an average lag of 60 days (range 12–132) between the attack and kill site inspection that resulted from delayed farmer reporting. Only 12% of households ($n = 607$) in villages reporting attacks during the study expressed interest in a program to insure cattle against depredation. Lack of interest was attributed to (1) inexperience with insurance programs, (2) lack of forage to keep livestock near the village as required by the program and (3) the lucrative market for tiger bone trade, which delayed the reporting of kills by farmers who engaged in opportunistic tiger poaching using explosives in freshly killed livestock carcasses as bait.

Discussion

The NEPL NPA contains a tiger population with densities as high as or exceeding that of areas surveyed in neighboring Cambodia (Wildlife Conservation Society – Cambodia, unpubl. data), north-east Thailand (Lynam, Kreetiyutanont & Mather, 2001; Lynam, Kanwatanakid & Suckaseam, 2003) and parts of Myanmar (Myanmar Forestry Department, 2003; Lynam, Khaing & Zaw, 2006). The results from this study indicate that three major factors stemming from human–tiger conflict are likely affecting tiger abundance and distribution.

The first factor is prey depletion. The abundance of large prey was consistently low such that tigers are now largely dependent on small prey or livestock, resembling a ‘muntjac-only scenario’ (Sunquist, Karanth & Sunquist, 1999) where tigers exist at low densities as the prey base supports only occasional reproduction. Although small prey remain relatively common, abundance varied according to human density and our results suggest that hunting was likely responsible for this pattern. One study estimated that each household annually consumed 141 kg of wild meat, of which 20% was deer and pig (ICEM, 2003*b*), the principal prey of tiger (Sunquist & Sunquist, 2002; Kawanishi & Sunquist, 2004). Given an average of 35 households per village in 98 NPA villages (Schlemmer, 2002), this is a minimum estimated offtake of 96 000 kg of ungulates annually (2840 kg per 100 km^2), which is equivalent to the meat required to sustain a tiger population at a density of 1 per 100 km^2 (Sunquist & Sunquist, 2002). This offtake does not account for additional harvest by outside hunters or animals traded commercially. In 2005, 42% of respondents in a survey of NPA villages indicated that outsiders also hunt in village areas (A. Johnson, unpubl. data). In recent years, villages reported weekly commerce in wildlife products with Vietnamese traders (Davidson, 1998), with gaur gall bladders and sambar deer antlers among the products commonly sold (Vongkhamheng, 2002).

The second, and likely most critical, factor affecting tigers is commercial poaching. Although overall prey abundance did not vary between sampling blocks, tiger abundance did. Assuming prey abundance is a reliable predictor of tiger abundance (Karanth *et al*., 2004), our results suggest that tiger abundance varied because of direct human-caused mortality rather than a relative lack of prey. This resembles north-eastern Thailand (Lynam *et al*., 2001, 2003) and parts of Myanmar (Lynam *et al*., 2006), where tiger abundance is depressed by poaching despite relatively abundant prey. In NEPL, tiger poaching appears closely linked to cattle grazing, with farmers opportunistically using livestock to bait tigers more so than as retaliation for livestock attacks. Contrary to previous predictions that livestock loss was a widespread problem (Davidson, 1998, 1999; Schlemmer, 2002), we found that depredation affected only 12% of NPA villages and a small fraction of the total herd. Given the opportunity to report attacks in return for possible compensation, farmers lagged in both reporting and removing livestock to villages. Similarly in Russia, farmers were uninterested in insurance when the risk of livestock loss to tigers was relatively low (Miquelle *et al*., 2005). Likewise, NEPL farmers appear willing to accept livestock loss given traditional cropping systems plus opportunities for tiger poaching to offset loss that encourage grazing in close proximity to tigers.

The tiger trade from NEPL has become increasingly lucrative in recent years. Prices ranged from US$ 550 for a tiger carcass in 1997 to US$ 11 528 in 2004 (Davidson, 1998; Nooren & Claridge, 2001; Vongkhamheng, 2002; K. Souvanphone, unpubl. data). In neighboring Vietnam, carcasses sold for US$ 1000–33 357 in the late 1990s and up to US$ 70 000 in China (Nowell, 2000). Laos’ annual per capita income is only US$ 293 (UNDP, 2002) and NEPL districts are among the poorest in the country (GoLPDR, 2004); therefore, the enticement to supplement income with trade in tigers and other large mammals is considerable. Loss of livestock valued at US$ 100–700 is a risk that some farmers appear willing to take in return for potentially killing a tiger, especially as incidents of prosecution are rare (Nooren & Claridge, 2001).

Although livestock husbandry practices may be driving tiger attacks in NEPL, the extent of livestock loss to tigers remains unclear because predation evidence disappears quickly (Nyhus *et al*., 2003). When officers did access relatively fresh kills, measurements of drag distance, tracks as well as livestock size provided evidence that tigers were likely responsible (see Karanth & Sunquist, 2000). Attacks were within 10 km of sampling blocks and tigers photographed ranged over 8 km within blocks. Given the depressed NEPL prey base, tiger ranges are likely comparatively large (>200 km^2) to provide adequate food (Sunquist & Sunquist, 2002) and livestock may support tiger densities in the absence of wild prey (Karanth *et al*., 2004). While possibly sustaining the current tiger population, livestock also increase the susceptibility of tigers to poaching as the demand for tiger bone escalates.

A final factor affecting tiger abundance may be prey competition between large carnivores sharing similar dietary niches. Camera trapping revealed that NEPL harbors an exceptionally diverse carnivore community containing six felid species including leopard as well as dhole, two bear species and 11 species of small carnivores. Cameras recorded 35 independent photos of leopard ($n = 25$) and dhole ($n = 10$) relative to nine independent photos of tiger. Although leopards typically take smaller and more diverse prey species (Sunquist & Sunquist, 1989), where several species of large carnivores co-exist in conjunction with an over-harvested prey base, competition for prey between large carnivores may be linked to depressed tiger populations (Rabinowitz, 1989; Ramakrishnan, Coss & Pelkey, 1999). More research is needed to understand prey selection and partitioning by large carnivores in NEPL.

NEPL NPA is characteristic of Laos' multiple-use protected areas, which are largely under-staffed and poorly funded (Robichaud *et al*., 2001) relative to the challenge of managing resource extraction by thousands of human residents. Our results indicate that conservation of tigers in Laos' protected areas will be dependent on spatially separating large carnivores and prey from humans by modifying livestock husbandry practices and enforcing protected area zoning. Altering husbandry practices and behavior of livestock producers is typically resisted for reasons of economy or inertia (Treves & Karanth, 2003). Fortunately, successful models developed by the Center for Tropical Agriculture now allow farmers to grow sufficient livestock forage near villages (Horne *et al*., 1999). With proactive agriculture extension, farmers no longer need to graze livestock in close proximity to tiger populations. Tiger attacks may decline when livestock is moved to villages if hunting of tiger prey is also reduced.

National regulations mandate demarcation of core and managed zones in protected areas (MAF, 2003), although zoning and enforcement have been sporadically funded since the system was established in 1993 (Robichaud *et al*., 2001). Regulations state that hunting is prohibited in core zones, and harvest of tigers, gaur and serow is illegal throughout the country. Tiger survival is dependent on establishing sizable core zones ($>3000\,km^2$) where tiger and prey are not hunted (Rabinowitz, 1999; Karanth & Nichols, 2002). Although small tiger populations of six to 12 breeding individuals may be demographically viable in a 100-year time frame (Dinerstein *et al*., 1997; Karanth & Stith, 1999), the likelihood of extirpation resulting from conflict increases in small fragments (Woodroffe & Ginsberg, 1998). In Malaysia, tiger and prey were largely absent from forest fragments smaller than $100\,km^2$ (Laidlaw, 2000). Protected areas that may contain viable tiger populations in Laos are relatively large for Indochina ($1516–3532\,km^2$) with suitable habitat also remaining outside of protected areas, providing opportunities to demarcate sizable core areas as well as connectivity corridors between them. Without this zoning, it will likely become increasingly difficult to maintain tigers and their prey within Laos' multiple-use protected area system.

Acknowledgements

This study was conducted under the Endangered Species MoU between the Department of Forestry and the Wildlife Conservation Society with funding from the Save the Tiger Fund, a special project of the National Fish and Wildlife Foundation in partnership with Exxon Mobil Corporation (No. 2002-0301-007 and No. 2003-0087-025), and the United States Fish and Wildlife Service Rhinoceros and Tiger Conservation Fund (No. 98210-3-G546). We thank T. O'Brien, M. Kinnaird, A. Lynam, D. Miquelle, K. U. Karanth, S. Strindberg, J. Ginsberg and M. Rao for advice and assistance. We are especially grateful to B. Xayavong, depredation officers from five districts and camera-trap survey team members from nine villages that assisted with data collection and to government authorities in Houaphan and Luang Prabang provinces for the invitation to work in the protected area. Two anonymous reviewers provided valuable comments on an earlier draft of this manuscript.

References

Berkmuller, K., Evans, T., Timmins, R. & Vongphet, V. (1995). Recent advances in nature conservation in the Lao PDR. *Oryx* **29**, 253–260.

Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993). *Distance sampling: estimating abundance of biological populations*. London: Chapman & Hall.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T.O., Seidensticker, J., Smith, D.J.L., Sunquist, M., Tilson, R. & Shahruddin, W.N.W. (2001). The use of photographic rates to estimate densities of tiger and other cryptic mammals. *Anim. Conserv*. **4**, 75–79.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T.O., Seidensticker, J., Smith, J.L.D., Tilson, R. & Shahruddin, W.N.W. (2002). The use of photographic rates to estimate densities of tiger and other cryptic mammals: response to Jennelle et al. *Anim. Conserv*. **5**, 121–123.

Davidson, P. (1998). *A wildlife and habitat survey of Nam Et Phou Louey national biodiversity conservation areas, Houaphanh province*. Vientiane: Wildlife Conservation Society (WCS) and Centre for Protected Areas and Watershed Management (CPAWM).

Davidson, P. (1999). *A wildlife and habitat survey of Nam Et and Phou Louey National Biodiversity conservation areas, Houaphanh province, Lao PDR: Addendum*. Vientiane: Wildlife Conservation Society (WCS) and Centre for Protected Areas and Watershed Management (CPAWM).

Dinerstein, E., Wikramanayake, E., Robinson, J., Karanth, U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Connor, M., Hemley, G. & Bolze, D. (1997). *A framework for identifying high priority areas and actions for the conservation of tigers in the wild*. Washington, DC: World Wildlife Fund – US and Wildlife Conservation Society.

Duckworth, J.W. & Hedges, S. (1998). *Tracking tigers: a review of the status of tiger, Asian elephant, gaur and banteng in Vietnam, Lao, Cambodia and Yannan province (China) with recommendations for future conservation action*. Hanoi: WWF Indochina Programme.

Duckworth, J.W., Salter, R.E. & Khounboline, K. (1999). *Wildlife in Lao PDR: 1999 status report*. Vientiane: The World Conservation Union (IUCN), Wildlife Conservation Society (WCS) and Centre for Protected Areas and Watershed Management (CPAWM).

EIU (2003). *Country profile 2003. Cambodia, Laos*. London: The Economist Intelligence Unit.

Frank, L., Woodroffe, R. & Ogada, M.O. (2005). People and predators in Laikipia district, Kenya. In *People and wildlife: conflict or co-existence?*: 286–304. Woodruffe, R., Thirgood, S. & Rabinowitz, A. (Eds). Cambridge: Cambridge University Press.

GoLPDR (2004). *National growth and poverty eradication strategy*. Vientiane: Prime Minister's Office.

Horne, P.M., Magboo, E., Kerridge, P.C., Tuhulele, M., Phimphachanhvongsod, V., Gabunada Jr. F., Binh, L.H. & Stur, W.W. (1999). Participatory approaches to forage technology development with smallholders in Southeast Asia. In *Working with farmers: the key to adoption of forage technologies*: 23–31. Stur, W.W., Horne, P.M., Hacker, J.B. & Kerridge, P.C. (Eds). Oro City, Mindanao, Philippines: Australian Centre for International Agricultural Research.

ICEM (2003*a*). *Lao PDR national report on protected areas and development*. Indooroopilly, Queensland: International Centre for Environmental Management.

ICEM (2003*b*). *Economic benefits of protected areas: field studies in Cambodia, Lao PDR, Thailand and Vietnam*. Indooroopilly, Queensland: International Centre for Environmental Management.

IUCN (1994). *Guidelines for protected area management categories*. Gland, Switzerland: IUCN.

Jennelle, C.S., Runge, M.C. & MacKenzie, D.I. (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Anim. Conserv*. **5**, 119–120.

Johnson, A., Singh, S. & Duongdala, M. (2005). Wildlife hunting and use in Luang Namtha Province: implications for rural livelihoods and biodiversity conservation in the uplands of the Lao PDR. In *Poverty reduction and shifting cultivation stabilisation in the uplands of Lao PDR: technologies, approaches and methods for improving upland livelihoods*: 195–208. Bouahom, B., Glendinning, A., Nilsson, S. & Victor, M. (Eds). Luang Prabang, Lao PDR: National Agriculture and Forestry Research Institute.

Karanth, K.U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. *Biol. Conserv*. **71**, 333–338.

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

Karanth, K.U. & Nichols, J.D. (Eds). (2002). *Monitoring tigers and their prey: a manual for researchers, managers and conservationists in tropical Asia*. Bangalore, India: Centre for Wildlife Studies.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *Proc. Natl. Acad. Sci. USA* **101**, 4854–4858.

Karanth, K.U. & Stith, B.M. (1999). Prey depletion as a critical determinant of tiger population viability. In *Riding the tiger: tiger conservation in human-dominated landscapes*: 100–113. Seidensticker, J., Christie, S. & Jackson, P. (Eds). Cambridge: Cambridge University Press.

Karanth, K.U. & Sunquist, M.E. (1995). Prey selection by tiger, leopard, and dhole in tropical forests. *J. Anim. Ecol*. **64**, 439–450.

Karanth, K.U. & Sunquist, M.E. (2000). Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. *J. Zool. (Lond.)* **250**, 255–265.

Kawanishi, K. & Sunquist, M.E. (2004). Conservation status of tigers in a primary rainforest of peninsular Malaysia. *Biol. Conserv*. **120**, 329–344.

Laidlaw, R. (2000). Effects of habitat disturbance and protected areas on mammals of peninsular Malaysia. *Conserv. Biol*. **14**, 1639–1648.

Lynam, A.J., Kanwatanakid, C. & Suckaseam, C. (2003). *Ecological monitoring of wildlife at Khao Yai National Park, Thailand*. Bangkok: Wildlife Conservation Society-Thailand Country Program Office.

Lynam, A.J., Khaing, S.T. & Zaw, K.M. (2006). Developing a national tiger action plan for the Union of Myanmar. *Environ. Mgmt*. **37**, 30–39.

Lynam, A.J., Kreetiyutanont, K. & Mather, R. (2001). Conservation status and distribution of the Indochinese tiger (*Panthera tigris corbetti*) and other large mammals in a forest complex in northeastern Thailand. *Nat. Hist. Bull. Siam Soc*. **49**, 61–75.

Madhusudan, M.D. & Karanth, K.U. (2002). Local hunting and the conservation of large mammals in India. *Ambio* **31**, 49–54.

MAF. (2003). *National biodiversity conservation areas, aquatic and wildlife management regulations*. No. 0360/AF.2003. Vientiane: Ministry of Agriculture and Forestry.

Miquelle, D., Nikolaev, I., Goodrich, J., Litvinov, B., Smirnov, E. & Suvorov, E. (2005). Searching for the co-existence recipe: a case study of conflicts between people and tigers in the Russian Far East. In *People and wildlife: conflict or co-existence?*: 305–322. Woodruffe, R., Thirgood, S. & Rabinowitz, A. (Eds). Cambridge: Cambridge University Press.

Myanmar Forestry Department (2003). *A national tiger action plan for the Union of Myanmar*. Vol. 57. Yangon: Myanmar Forest Department and Wildlife Conservation Society.

Nichols, J.D. & Karanth, K.U. (2002). Statistical concepts: estimating absolute densities of tigers using capture–recapture sampling. In *Monitoring tigers and their prey: a manual* *for researchers, managers and conservationists in tropical Asia*: 121–138. Karanth, K.U. & Nichols, J.D. (Eds). Bangalore, India: Centre for Wildlife Studies.

Nooren, H. & Claridge, G. (2001). *Wildlife trade in Laos: the end of the game*. Amsterdam: Netherlands Committee for IUCN.

Nowell, K. (2000). *Far from a cure: the tiger trade revisited*. Kuala Lampur: TRAFFIC International.

Nyhus, P., Fischer, H., Madden, F. & Osofsky, S. (2003). Taking the bite out of wildlife damage: the challenges of wildlife compensation schemes. *Conserv. Practice* **4**, 37–40.

O'Brien, T.G., Kinnaird, M.F. & Wibisono, H.T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Anim. Conserv.* **6**, 131–139.

Otis, D.L., Burnam, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* **107**, 1–97.

Phensavanh, P., Sukan, Phimmasan, H., Phimphachanh-vongsod, V., Phenvichith, V. & Novaha, S. (1999). Forage options for smallholder farmers in shifting cultivation farming systems of Lao PDR. In *Working with farmers: the key to adoption of forage technologies*: 287–289. Stur, W.W., Horne, P.M., Hacker, J.B. & Kerridge, P.C. (Eds). Oro City, Mindanao, Philippines: Australian Centre for International Agricultural Research.

Rabinowitz, A. (1989). The density and behaviour of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Nat. Hist. Bull. Siam Soc.* **37**, 235–251.

Rabinowitz, A. (1999). The status of the Indochinese tiger: separating fact from fiction. In *Riding the tiger: tiger conservation in human-dominated landscapes*: 148–165. Seidensticker, J., Christie, S. & Jackson, P. (Eds). Cambridge: Cambridge University Press.

Rabinowitz, A. (2005). Jaguars and livestock: living with the world's third largest cat. In *People and wildlife: conflict or co-existence?*: 278–285. Woodruffe, R., Thirgood, S. & Rabinowitz, A. (Eds). Cambridge: Cambridge University Press.

Ramakrishnan, U., Coss, R.G. & Pelkey, N.W. (1999). Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biol. Conserv.* **89**, 113–120.

Robichaud, W., Marsh, C.W., Southammakoth, S. & Khounthikoummane, S. (2001). *Status review of protected areas in Lao PDR*. Vientiane: Lao–Swedish Forestry Programme.

Roder, W. (2001). *Slash-and-burn rice systems in the hills of northern Lao PDR: description, challenges, and opportunities*. Los Banos, Philippines: International Rice Research Institute.

Sandewall, M., Ohlsson, B. & Sawathvong, S. (2001). Assessment of historical land-use changes for purposes of strategic planning – a case study in Laos. *Ambio* **30**, 55–61.

Schlemmer, G. (2002). *Community livelihoods analysis, Nam Et Phou Louey National Biodiversity Conservation Areas*. Vientiane: World Conservation Union (IUCN) and Ministry of Agriculture and Forestry (MAF).

Soisaloa, M.K. & Cavalcanti, S.M.C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biol. Conserv.* **129**, 487–496.

Sunquist, M., Karanth, K.U. & Sunquist, F. (1999). Ecology, behaviour and resiliance of the tiger and its conservation needs. In *Riding the tiger: tiger conservation in a human-dominated landscape*: 5–18. Seidensticker, J., Christie, S. & Jackson, P. (Eds). Cambridge: Cambridge University Press.

Sunquist, M.E. & Sunquist, F.C. (1989). Ecological constraints on predation by large felids. In *Carnivore behavior, ecology, and evolution*: 283–301. Gittleman, J.L. (Ed.). Ithaca: Cornell University Press.

Sunquist, M. & Sunquist, F. (2002). *Wild cats of the world*. Chicago: University of Chicago Press.

Terborgh, J. & Peres, C.A. (2002). The problem of people in parks. In *Making parks work*: 307–319. Terborgh, J., Schaik, C.v., Davenport, L. & Rao, M. (Eds). Washington, DC: Island Press.

Treves, A. & Karanth, K.U. (2003). Human–carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* **17**, 1491–1499.

UNDP. (2002). *National human development report for Lao PDR 2001*. Vientiane: United Nations Development Programme (Laos).

Vongkhamheng, C. (2002). *Participatory wildlife diversity monitoring with different ethnic groups in Nam Et-Phou Loey National Biodiversity Conservation Areas, Northern Lao PDR*. MSc thesis, Mahidol University, Bangkok.

WCS/WWF/SI (2006). *Tiger conservation landscape: classifiation and prioritization*. New York: Wildlife Conservation Society, Worldwide Fund for Nature, Smithsonian Institution.

White, G.C., Anderson, D.R., Burnam, K.P. & Otis, D.L. (1982). *Capture–recapture and removal methods for sampling closed populations*. Los Alamos, NM: Los Alamos National Laboratory Publication LA-9787-NERP.

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

Woodroffe, R. (2000). Predators and people: using human densities to interpret carnivore declines. *Anim. Conserv.* **3**, 165–173.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.

