Population recovery patterns of Southeast Asian ungulates after poaching

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ABSTRACT

Large ungulate populations in Southeast Asia have collapsed due to commercial poaching, but little is known about patterns of population recovery after poaching has been controlled. Using a sign-based index of abundance, we measured 6-year trends in abundance and habitat use of five ungulate species after poaching ceased at a site in Thailand. Regression slopes of annual indices against time indicated population growth rates (r) of 0.44 and 0.31 for muntjac (*Muntiacus muntjak*) and gaur (*Bos gaurus*), respectively—close to the intrinsic rates of natural increase for similarly-sized ungulates. Thus, muntjac and gaur can recover relatively rapidly from low population levels. In contrast, sambar (*Cervus unicolor*) remained consistently rare despite freedom from hunting, perhaps because prime males had been selectively targeted for trophies, disrupting the species mating system. Wild pigs (*Sus scrofa*) were already relatively abundant when monitoring started, illustrating their resilience to hunting and ability to quickly recolonize disturbed areas. Gaur herds (the key demographic unit of the population) and muntjac consistently selected deciduous over evergreen forest as their populations increased, revealing the importance of food-rich deciduous forest in driving recovery of these species. The unexpected failure of sambar to recover suggests that reproductive behavior may override seemingly positive interventions (i.e., stopping poaching) that reduce mortality. Small but well-protected recovery zones set within forested areas might help propel population recovery of ungulates and increase the prey base for endangered tigers.

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1. Introduction

Overexploitation is the second-most important threat to the survival of the world's mammals after habitat loss (Groom, 2006). Ungulates (Artiodactyla), in particular, are disproportionately threatened with extinction compared with most other mammals, largely due to massive overhunting (Mace and Balmford, 2000; Baillie et al., 2004). This crisis is well-advanced in Southeast Asia, where large ungulate (species > 5 kg) populations have been decimated in recent decades due to commercial poaching to supply local and regional markets with meat, antlers, horns, and other body parts (Srikosamatara and Suteethorn, 1994; Nooren and Claridge, 2001; Sodhi et al., 2004; Corlett, 2007). This trade has driven widespread declines in population abundance, and caused many site-level extirpations within intact forest, such that intact ungulate communities are now absent in the region. For example, only 39% (18 of 46) of protected areas assessed by Smith et al. (1999) in Thailand had all of the following (historically present) taxa: red muntjac (*Muntiacus muntjak*), wild pig (*Sus scrofa*), sambar (*Cervus unicolor*), and wild cattle (*Bos* spp.). Where these species still persist, their densities are often well below habitat carrying capacity,

even in the best protected sites (Rabinowitz, 1989; Srikosamatara, 1993; Srikosamatara and Suteethorn, 1995; Steinmetz, 2004; Lynam et al., 2006). Larger species (wild cattle, sambar) succumb to hunting pressure earlier and tend to be extirpated first whereas smaller or more resilient species (wild pig, muntjac) can sometimes persist at reduced densities (Pattanavibool and Dearden, 2002; Tungittiplakorn and Dearden, 2002).

The depletion of ungulates from tropical forests has many other harmful implications besides their own demise. Large ungulates such as deer and wild cattle participate in fundamental ecological processes, including dispersal of large seeds (Prasad et al., 2006), influencing spatial patterns of vegetation (Adler et al., 2001), and serving as the principal prey for endangered tigers (*Panthera tigris*) and other sympatric large carnivores (Karanth et al., 2004). Prey depletion reduces survival and lowers habitat carrying capacity for tigers (Karanth and Stith, 1999), and is a major threat to tiger persistence and recovery within otherwise intact forest (Sanderson et al., 2006).

Despite the crisis of overhunting in tropical forests and the important ecological role of targeted ungulates, little is known about the population ecology of large tropical herbivores (Gaillard et al., 2000), particularly in Southeast Asia, and research and monitoring are urgently needed to inform effective conservation interventions (Milner-Gulland and Bennett, 2003). Our goals in this

Table 1
Ecological and reproductive characteristics of ungulate species studied at Brong Dee, Thailand, 2000–2005. Information sources: Lekagul and McNeely, 1988; Nowak, 1999.

Species	Diet	Body mass (kg)[a]	Sexual maturity (years)	Litter size	Longevity (years)	Social structure	Mating system
Red Muntjac *Muntiacus muntjak*	Browser, frugivore	20–28	1	1	10	Solitary	Male–female pairing within already established territories
Southern Serow *Naemorhedus sumatraensis*	Browser	85–140	2.5	1	10	Solitary	Unknown; possibly similar to muntjac
Wild pig *Sus scrofa*	Omnivore	75–200	0.5–0.7	up to 12	10–12	Herds + bachelors	Female following: males wander, seek females (in herds)
Sambar *Cervus unicolor*	Browser, grazer,	185–260	2	1	26 (captive)	Solitary or small groups	Mating territories: males establish mating territories during the rut, await females
Gaur *Bos gaurus*	Grazer, browser	650–900	2–3	1	18–30	Herds + bachelors	Female following: males wander, seek females (in herds)

[a] Body masses are ranges of adult males and females.

study were to (a) describe patterns of population recovery for common Southeast Asian ungulate species after cessation of poaching, and (b) identify the influence of habitat selection on population growth rate and abundance. We made use of a natural experiment at a site in Thailand where ungulate populations (and their predators) had been reduced by poaching, but were subsequently protected through management intervention. Based on our results, we provide recommendations that protected area managers could employ to promote ungulate recovery. Our study focused on red muntjac, wild pig, sambar, gaur (*Bos gaurus*), and southern serow (*Naemorhedus sumatraensis*) (Table 1); these species comprise a large ungulate community that was historically common throughout Southeast Asia.

2. Study area and background

The study was conducted in Thung Yai Naresuan Wildlife Sanctuary (3600 km^2) from 1999 through 2005. Thung Yai is in western Thailand adjacent to Myanmar, and forms the core of the 18,000 km^2 Western Forest Complex. Major habitats are mixed deciduous and semi-evergreen forest (<1000 m elevation), and montane evergreen forest (>1000 m elevation). The sanctuary is characterized by rugged mountains with elevations up to 1811 m. Mean annual rainfall (±SD) from 1997–2005 was 1731 ± 217 mm (Thai Department of Meteorology, 2005). Mean annual maximum and minimum temperatures were 33.6 ± 0.2° C, and 20.5 ± 0.7° C, respectively. Annual rainfall is concentrated between May and October, with typically < 100 mm of rain per month in the dry season (November to April). Rainfall during our study, and in two of three preceding years, was consistent between years (±2 standard deviations of the 9-yr. mean from 1997–2005); thus, we expect the population dynamics we observed were not greatly influenced by exceptional climate variation.

The study area (15° 23′ N, 98° 43′ E), called Brong Dee, is a 20 km^2 undulating valley at 700 m elevation, encircled by mountains up to 1000 m. Two forest types occur, each approximately equally represented in area, and dispersed as a mosaic of patches of 5–20 ha. Mixed deciduous forest (MDF) has a relatively open canopy dominated by deciduous tree species that reach 15–30 m in height. Grass and bamboo are typically abundant in the understory; these are important foods for ungulates (Prayurasiddhi, 1997; Steinmetz, 2004). Semi-evergreen forest (SEF) is dominated by evergreen tree species that create a dense canopy at 30–40 m height; grass and bamboo are generally scarce.

From 1960 to 1995, the Brong Dee valley was the site of a small mining concession that was the base for an illegal commercial poaching operation (Nakhasathien and Stewart-Cox, 1990; R. Kittayapaisan, sanctuary ranger, pers. comm.). Mine operations resulted in limited habitat degradation or alteration (<2 ha). Hunters were employed to obtain meat (primates, ungulates), trophies (gaur horns, sambar antlers, elephant tusks), and body parts used in traditional medicine (tiger, bears, serow). In 1995, the Royal Forest Department raided the Brong Dee mine, confiscating guns and cable snares used to capture large mammals (M. Khaengkhetkarn, pers. comm). No quantitative baseline of wildlife abundance existed for the period prior to our study, but senior sanctuary rangers familiar with the area ranked the Brong Dee valley as the most heavily-hunted area in the sanctuary and described it as largely bereft of gaur, sambar, and muntjac by 1995 (when hunting ceased), compared with surrounding areas (Jomlong, pers. comm; R. Kittayapaisan, pers. comm.). As surrounding areas were also hunted, Brong Dee represented a site of locally severe population reduction, set within a landscape of overall population decline. Since 1995, Brong Dee and surrounding areas have received increased patrolling by rangers and village volunteers, and there has been just one known incident of hunting (of a gaur), in 2001. Thus, conditions for ungulates at Brong Dee switched dramatically from heavily hunted to almost completely secure.

3. Methods

3.1. Field methods

Ungulates in Brong Dee were difficult to observe directly because they occurred at low densities, inhabited dense forests with low visibility, and were often nocturnal. We expected few direct observations of animals under these conditions, so we used an index of relative abundance derived from animal signs to monitor change in population size (Caughley, 1977). We conducted a pilot survey in 1999 (*n* = 4 transects) to determine the sample size required to track changes in our index. Following Gibbs et al. (1998: 938), and employing the coefficient of variation in the index for wild pig (=45%; pigs were the only species commonly encountered at that time), we determined that 30 transects should provide adequate power (>80%) to detect a 25% trend in the population index over time at α < 0.1. Thirty straight strip transects (400 m long, 2 m wide, *n* = 15 in each habitat) were monitored each year (2000–2005), except in year 1 when fewer (*n* = 13), longer (750 m) transects were used. Transects were placed in each 1 km^2 cell of the study area, separated by at least 400 m. Transects were not permanent, and did not follow animal or human trails. Each transect was divided into eight contiguous 50 m segments. Two observers walked slowly (<1 km/hour) along transects, recording animal signs (tracks, dung) as present or absent (undetected) in each segment. Surveys were conducted in the same month each year (December) to avoid

environmental and seasonal variation that might affect substrate (i.e., tracking conditions) and animal activity. Data were recorded by the first three authors every year, so observer variation was also avoided. Species abundance and habitat use was inferred from the proportion of transect segments with signs. Transects were the sample units. Similar frequency-based indices have been used to study abundance, habitat use, and response to hunting pressure, of tropical ungulates elsewhere (Muchaal and Ngandjui, 1999; Bennett et al., 2000; Jenkins et al., 2002).

We distinguished tracks and dung of the focal species based on size and shape (van Strien, 1983; Thongnamchaima and Mather, 1997). Ambiguous signs, which occurred in 6% of transect segments overall, were omitted from analysis. Only recent signs (<2 weeks) were used; sign aging was based on 6 years of field experience at the time of the initial survey. Where contiguous segments were clearly traversed by the same animal or group of animals, we counted presence only in one segment.

Gaur and wild pig occur in mixed-sex herds of multiple age classes, and as single males or small bachelor groups (Bhumpakphan, 1997; Steinmetz et al., 2008). Herds are the key social group for reproduction in these species so we analyzed habitat use separately for herds and single males. We distinguished signs of herds from single animals by examining the area (5 m radius) around the initial sign observed. Groups of tracks of the same age but including different hind footprint sizes were considered evidence of a herd. Additionally, for wild pigs, soil-rooting signs along a broad front, or a riven path of movement with multiple sets of tracks, were considered to represent a herd. If uncertain, we recorded signs as a single individual.

3.2. Detection probability of animal signs

We were concerned that detectability of signs would differ between habitat types, thereby confounding comparisons of relative animal abundance between habitats. This potential bias was assessed in two ways. First, a tracking score was assigned to each transect segment, as follows: 1-ground mostly bare, signs easily observed where present; 2-ground moderately covered by grass or leaf litter (30–70%), signs difficult to observe; 3-ground densely covered, signs very difficult to spot. Differences between mean scores for each habitat were tested with Mann–Whitney U-tests for each year. We also used mean scores to look for changing patterns of tracking conditions within each habitat over time.

Second, in 2005, we estimated sign detection probability directly, through repeated surveys on a subset of transects in each habitat (Tyre et al., 2003). On every other transect ($n = 14$), the same observers resurveyed those segments in which no signs were found on the initial walk. These data (a matrix of 1s and 0s corresponding to presence or non-detection on the two sampling occasions in each transect segment, $n = 112$) were modeled as a problem of sign occupancy within transect segments, using the approach of MacKenzie et al. (2002), and software PRESENCE (Hines and MacKenzie, 2004). We thus obtained estimates of detection probability and occupancy (i.e., proportion of segments with signs, adjusted for imperfect detection), for trial transects. We compared unadjusted index values with occupancy estimates to assess the effect that imperfect detection had on our sign index. We applied this procedure to muntjac and gaur, which represent expected extremes of sign detectability among the focal species—gaur signs are largest and most obvious, whereas those of muntjac are smallest and least apparent.

3.3. Analysis of population growth

Population abundance trends were assessed with least-squares linear regression of mean annual population index against year (Hatch, 2003). We used resulting regression slopes as estimates of mean annual population growth rates (r) (Caughley, 1977). These rates should also be congruent with intrinsic rates of increase (r_{max}), since animals were at low density and resources presumably were not limiting (Caughley, 1977). Index values were natural log transformed prior to analysis to stabilize error variances, and because an exponential model was biologically appropriate since populations were expected to change by a constant rate (i.e., exponentially) rather than a constant amount (Thompson et al., 1998; Elzinga et al., 2001). Normality and equality of variances were assessed with plots of residuals against the predictor variable (Quinn and Keough, 2002). All species except serow met assumptions after transformation. There was evidence of serial correlation for pigs (Durbin-Watson statistic 3.66) and serow (2.80) but not for other species (1.86–2.15). Counts in a time series are not independent (van Strien et al., 1997), but this should not affect analysis of trends for low density populations such as ours, which should be free from density dependent effects on growth rate. Results were considered statistically significant when $\alpha < 0.05$.

We treated 95% confidence intervals (CIs) of regression slopes as measures of observed effect size, and used these to assess the power of statistical tests as well as the biological significance of results (Steidl et al., 1997; Thompson et al., 1998). Population abundance trends might not be detected if the statistical power of regression tests was low (i.e., Type II error), but CIs of effect size present information to help evaluate whether null hypotheses (of no trend) should be reliably accepted, as CI width is inversely related to power (Thomas, 1997; Thompson et al., 1998). To judge whether effect sizes were signaling a biologically meaningful change, we compared them with estimates of ungulate population growth rates from other studies. We could not find any data for Southeast Asian species, however (indeed, this was one motivation of our study), so we gathered published data on growth rates from rebounding populations of ungulate species elsewhere with similar body weight and life history characteristics (gestation, litter size, interbirth interval) as our focal species (Table 2). Based on this information, we chose $r = 0.2$ as the minimum rate of population increase to look for. This magnitude of change seemed biologically relevant for all size classes of ungulates being studied, and was close to the minimum rate of change that our sampling design would be able to detect with adequate power, based on our pilot survey (see 3.1 Field methods).

3.4. Analysis of habitat use

To assess trends in habitat use over time by each species, we used repeated measures analysis of variance (ANOVA), with year and habitat type as main effects. The response variable was the natural log transformed population index for each habitat. A constant (0.5) was added to avoid taking the logarithm of zero (Krebs, 1999). Different social groups (herds, single males) of gaur and wild pig were assessed separately.

For each species we asked three questions. First, did overall use of habitats differ (pooling data across years)? Second, were differences in habitat use consistent from year to year? A significant interaction in the ANOVA between habitat and year would indicate that habitat use differences did not follow a consistent pattern over time, perhaps due to environmental changes or lack of habitat preference. Third, were trends in use of each habitat similar over time? Significant linear contrasts of the year × habitat interaction after ANOVA would indicate divergent trends, perhaps due to effects of animal density on habitat selection. The main effect of year was of little interest since overall trends in abundance were already assessed with linear regression. When necessary, we report adjusted P values according to the Huynh-Feldt epsilon; this corrects biases from lack of sphericity in the variance–covariance ma-

Table 2
Intrinsic rates of increase of ungulate species used for comparison with observed growth rates of ungulates at Brong Dee, Thailand, 2000–2005.

Species	Body mass (kg) [a]	Intrinsic rate of increase (r_{max})	Source
Mazama gouazoubira	17	0.49[c]	Robinson and Redford, 1986
Mazama americana	26	0.40[c]	Robinson and Redford, 1986
Sus scrofa	75–200	0.69[d]	Choquenot and Dexter, 1996
Cervus elaphus	75–340	0.20[d]	McCorquodale et al., 1988
Cervus elaphus	75–340	0.28[d]	Eberhardt et al., 1996
Bison bison	700	0.32[d]	Larter, 1994[b]
Bison bison	700	0.30[d]	Singer and Norland, 1994

[a] Body masses are from the respective listed sources, except *Sus scrofa* (ranges from Lekagul and McNeely, 1988) and *Cervus elaphus* (Nowak, 1999).
[b] Cited in: Sinclair, 1996.
[c] r_{max} Calculated using Cole's equation.
[d] r_{max} Calculated from population abundance estimates.

trix that can otherwise inflate F statistics (Quinn and Keough, 2002).

Sample size in year 1 ($n = 16$ transects) was less than other years ($n = 30$). Unequal sample size renders ANOVA equations inappropriate in repeated measures designs (Quinn and Keough, 2002), so year 1 was omitted from the analysis. To determine the effect this might have on our conclusions, we substituted missing observations ($n = 14$) in year 1 with the respective habitat-specific means for that year, and conducted a second analysis with all years. P values were slightly different but overall conclusions were unchanged except in one case (main effect of habitat for gaur singles). Therefore, habitat use trends from years 2 to 6 are largely representative of the entire study period; we report statistical results for this 5-year data subset, but, graphically, show all 6 years.

4. Results

4.1. Detection probability

On the 14 trial transects used to assess sign detection error rates, we missed muntjac signs in four of 112 segments (3.6%), and gaur signs in two segments (1.8%). Detection probability in both habitats was thus very high for both small signs (muntjac: MDF, $p = 0.98$; SEF, $p = 0.97$) and large signs (gaur: MDF, $p = 1.0$; SEF, $p = 0.93$). We initially recorded muntjac signs in 70.3% of MDF segments and 64.6% of SEF segments; respective proportions after adjustment for imperfect detection were 70.4% (SE 5.8%) and 64.7% (SE 6.9%). Gaur signs were recorded in 47.5% of MDF segments and 33.3% of SEF ones; adjusted estimates were 47.5% (SE 7.9%) and 33.5% (SE 6.8%). Thus, proportions of transect segments with signs were nearly identical whether derived from raw values or adjusted for imperfect detection. We report unadjusted values. We believe these low error rates resulted from the consistent use of experienced observers, narrow width of transects, slow walking rate, and a field method dedicated solely to detecting sign presence (rather than detecting all signs).

Tracking conditions tended to be more challenging (higher tracking scores) in semi-evergreen forest (range of mean annual scores, 1.43–2.43) than deciduous forest (1.10–1.96) due to a combination of heavier leaf litter and dimmer light underneath the canopy. This was reflected also in slightly lower sign detection probabilities in SEF (above). This difference was statistically significant in 2004 ($U = 58$; $p = 0.007$), but this did not seem to bias our conclusions as habitat use of most species in 2004 tended to match overall patterns. No temporal trends in tracking conditions were apparent in either habitat.

4.2. Population trends

Gaur and muntjac population indices increased three and 10-fold, respectively, over the 6 year study (Fig. 1), and regression
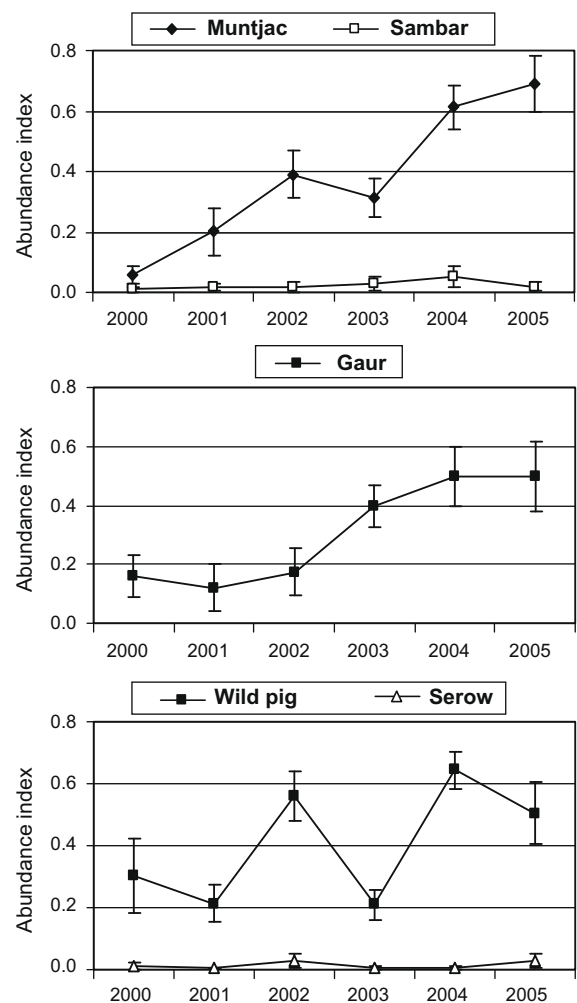

Fig. 1. Trends in population abundance of ungulates at Brong Dee, Thailand, 2000–2005, based on a relative abundance index derived from proportion of transect segments with signs ($n = 30$ transects, except 2000, when $n = 13$; each transect had 8, 50-m segments). Bars represent 90% confidence intervals.

slopes of annual indices were significantly greater than zero (Table 3). Gaur were uncommon in the first 3 years (index < 0.2), then increased in 2003 (index = 0.41) and thereafter remained relatively common (index > 0.5). Muntjac were initially scarce (index = 0.06) but increased steadily throughout the study (Fig. 1). We recalculated sign indices for gaur singles and herds to explore their respective relative contributions to overall population growth shown in Fig. 1: herds were absent, or nearly so, in the first 3 years but increased in 2003 and thereafter remained relatively common

Table 3
Results of linear regression of (log) abundance index against year ($n = 6$ years) for ungulates at Brong Dee, Thailand, 2000–2005. Bold P-values indicate slopes significantly greater than zero.

Species	Coefficient of determination (r^2)	Slope	F	P
Wild pig	0.27	0.139	1.48	0.29
Muntjac	0.83	0.440	19.72	**0.01**
Samber	0.51	0.215	4.13	0.11
Gaur	0.82	0.307	17.76	**0.01**
Serow	0.01	0.056	0.05	0.83

(index = 0.24–0.31); single males were uncommon for the first 4 years (index = 0.09–0.17) then increased in years 5 and 6 (index = 0.20–0.26). Thus, the overall population increase of gaur (Fig. 1) was driven mainly by increasing numbers (and perhaps sizes) of herds.

Population increases were not detected for wild pig, sambar, and serow, whose regression slopes were positive but not significantly different from zero (Table 3). Abundance of wild pigs was highly variable (Fig. 1): they were rare in years 1, 2, and 4 (index = 0.22–0.32), but relatively common in years 3, 5, and 6 (index > 0.5). Sambar and serow were consistently rare throughout the study, with signs in < 6% of segments each year.

Population growth rates for muntjac ($r = 0.44$) and gaur ($r = 0.31$) were well above 0.2, the minimum effect size that we hoped to detect. Additionally, 95% CIs barely descended below this threshold (Fig. 2); thus, these results seem significant biologically as well as statistically. Confidence intervals for other species included zero, hence, null hypotheses of no trend were not rejected. However, intervals for sambar were mostly above zero and included a wide range of biologically significant values (Fig. 2). Thus, the true slope was probably positive (i.e., sambar are actually increasing) but statistical power was too low to interpret the likely magnitude, and results should be regarded as biologically and statistically inconclusive (i.e., the null hypothesis of no trend may have been incorrectly rejected; Thompson et al., 1998). The slope interval for serow was narrow and centered on zero, suggesting the population, though small, may have been stable (Fig. 2). Effect size intervals for wild pig indicated that the population may be increasing, but erratic movements into and out of the study area by herds produced data too variable to make a determination.

4.3. Habitat use

Pooling across years, muntjac, wild pig herds, gaur singles, and gaur herds used MDF significantly more than SEF, whereas serow
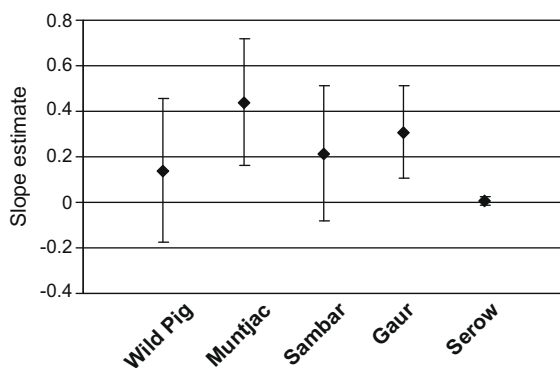

Fig. 2. Observed effect sizes of population growth rates for five ungulate species at Brong Dee, Thailand, 2000–2005, inferred from linear regression slopes of abundance indices on time. Bars represent 95% confidence intervals.

mainly occurred in SEF (Fig. 3; Table 4, habitat main effects). Selection for MDF was strongest for gaur herds ($F = 26.5$, $P < 0.0001$) and muntjac ($F = 11.3$, $P = 0.002$). Overall, 76% of segments with signs of gaur herds were in MDF. The majority of gaur signs in SEF were from single males. No patterns of habitat selection were detected for wild pig singles or sambar.

Patterns of habitat use for most species were consistent over time, indicated by non-significant year × habitat interactions (Table 4). For example, although muntjacs were relatively more abundant in MDF than SEF, they showed parallel trends in population growth in both habitats (Fig. 3, Table 4). The main exception was gaur singles, whose habitat use patterns varied each year (Fig. 3), although most signs occurred in mixed deciduous forest overall. Gaur herds consistently favored MDF (Fig. 3), but they also had a significant year × habitat interaction in the AN-OVA (Table 4), apparently caused by the large increase in MDF relative to SEF starting in year 4 (Fig. 3). Slopes of abundance for gaur herds in each habitat diverged significantly over time (Fig. 3; Table 4, year × habitat trend); thus, gaur herds increasingly used MDF over SEF as they increased in abundance. Divergent trends in habitat use over time were not detected for other species (Table 4).

5. Discussion

This study was limited to a single small study site in an uncontrolled experiment; thus, our results should be viewed as a preliminary case study. However, we collected a reasonably long time series of observations in a unique natural experiment, producing one of the first pictures of population dynamics of Southeast Asian ungulate species. Although we missed the first 3 years after poaching at Brong Dee, our pilot survey in 1999 suggested that animal abundance prior to monitoring was very low (except for pigs), so we believe our results capture the responses of low density populations released from poaching pressure. Also, the site was representative of common habitats in the region. Therefore, the results shed light on the process of population recovery of these little-known species, and might provide insights for recovery strategies for ungulates in Southeast Asian forests.

5.1. Patterns of population recovery

Ungulates tend to be limited by birth rate during initial stages of recovery from hunting, becoming food-limited later as ecological carrying capacity is reached (Coulson et al., 2004). By observing population growth from low density, we were able to estimate intrinsic rates of increase (r_{max}; the maximum a population can achieve), which are only observable for populations well below carrying capacity and freed from resource competition (Milner-Gulland and Akcakaya, 2001). A species' intrinsic rate of increase reflects its ability to recover from disturbance (Sutherland and Norris, 2003) and persist in the face of exploitation (Bodmer et al., 1997; Sinclair and Krebs, 2003).

Our estimates of population growth rate are rough reflections of true rates since they were derived from sign abundance rather than counts of animals themselves. Nonetheless, mean annual growth rates for muntjac (0.44) and gaur (0.31) were close to the estimated r_{max} for similarly-sized brocket deer (*Mazama* spp.) and bison (*Bison bison*) (Table 2). Thus, these estimates are biologically plausible, and suggest an average population growth of ($e^r =$) 55% and 36% per year for muntjac and gaur, respectively. Our index-based inferences also corresponded with our increasingly frequent direct observations of gaur and muntjac during field work: for example, our gaur sightings were zero in years 1 to 3, but averaged 6.3 per year (SD = 8.4) in years 4 to 6 (including single males,
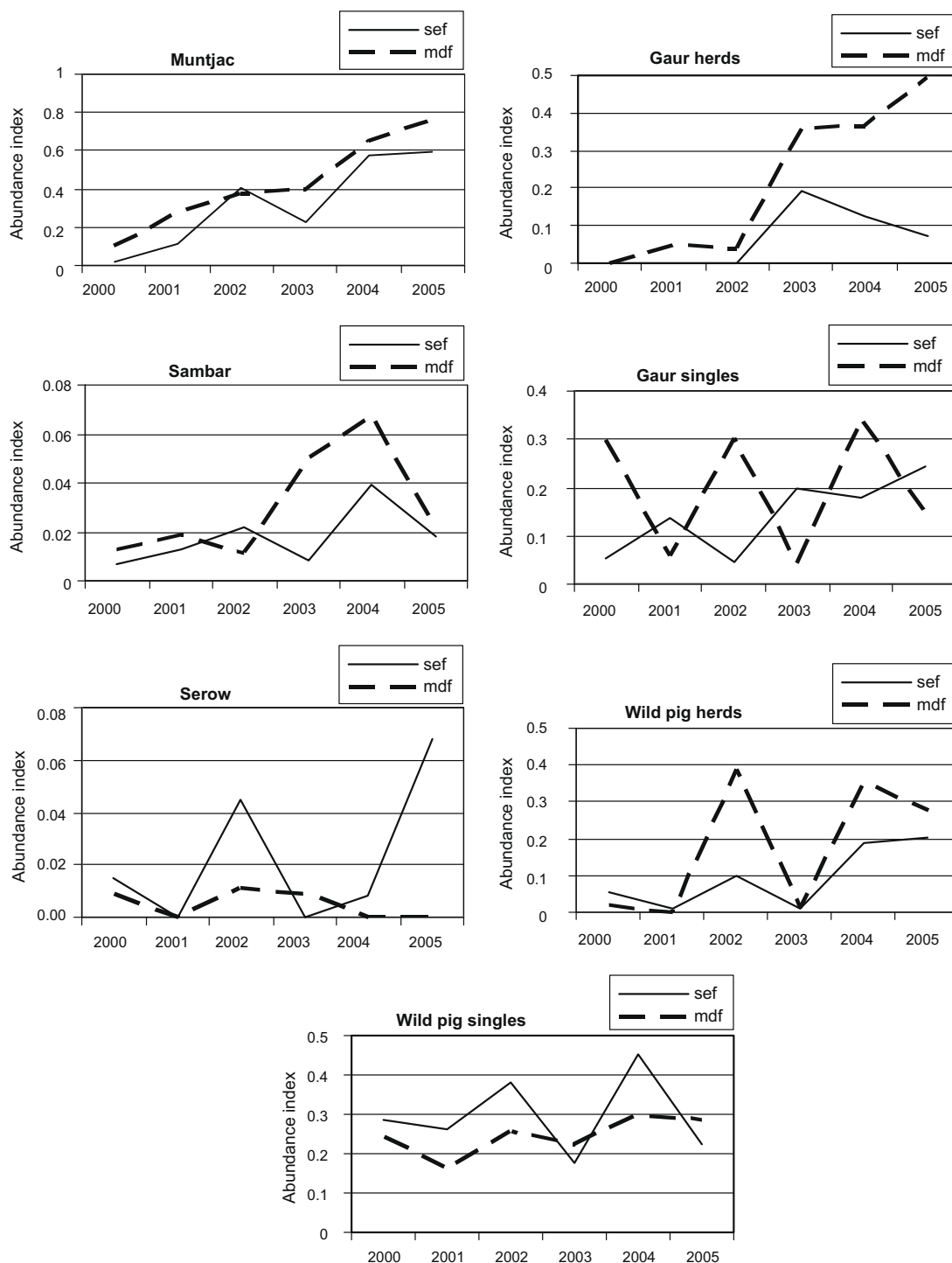
Fig. 3. Habitat use trends for recovering ungulates at Brong Dee, Thailand, 2000–2005, based on relative abundance indices derived from the proportion of transect segments with signs of a species (*n* = 30 transects per yr.). sef: semi-evergreen forest; mdf: mixed deciduous forest.

herds, and calves). We believe these rising sighting rates reflect higher densities, not increasingly confiding behavior, as all individuals that noticed us fled.

Muntjac in western Thailand attain densities of 1.0–3.1 individuals/km² in areas with minimal hunting (Srikosamatara, 1993; Steinmetz and Mather, 1996; Sukmasuang, 2001). Wild cattle (gaur and banteng [*Bos javanicus*] combined) have densities of 0.9–1.8 individuals/km² (Srikosamatara, 1993; Bhumpakphan, 1997). Abundances of muntjac and gaur were apparently still rising when our study ended, either in terms of overall abundance (muntjac: Fig. 1) or preferred habitat use (gaur herds: Fig. 3). This suggests that carrying capacity of the site was not yet reached for these species.

Our field method could not distinguish the relative contribution of reproduction and immigration to population growth. Immigration from source populations is important for replenishing overhunted populations of tropical ungulates (Fimbel et al., 2000; Hill and Padwe, 2000; Novaro et al., 2000). Srikosamatara (2000) observed that increasing gaur density at one site in adjacent Huay Kha Khaeng Wildlife Sanctuary followed reduced poaching pres-

Table 4
Repeated measures analysis of variance for effects of time (year) and habitat type on population abundance of ungulates at Brong Dee, Thailand, 2000–2005. SS: sum of squares. MS: mean square. Significant differences indicated with bold font.

Species	Source of variation	SS	df	MS	F-ratio	P
Wild pig singles	Habitat	0.154	1	0.154	1.930	0.176
	Residual	2.231	28	0.080		
	Year × habitat	0.454	4	0.114	1.360	0.252
	Residual	9.356	112	0.084		
	Year × habitat trend (linear)	0.112	1	0.112	1.626	0.213
	Residual	1.926	28	0.069		
Wild pig herds	Habitat	0.690	1	0.690	5.744	**0.023**
	Residual	3.365	28	0.120		
	Year × habitat	0.539	3	0.180	1.547	0.209
	Residual	9.757	84	0.116		
	Year × habitat trend (linear)	0.012	1	0.012	0.092	0.764
	Residual	3.645	28	0.130		
Muntjac	Habitat	0.674	1	0.674	11.328	**0.002**
	Residual	1.667	28	0.06		
	Year × habitat	0.453	4	0.091	1.777	0.125
	Residual	7.136	112	0.055		
	Year × habitat trend (linear)	0.005	1	0.005	0.199	0.392
	Residual	0.656	28	.023		
Sambar	Habitat	0.169	1	0.169	1.679	0.206
	Residual	0.281	28	0.001		
	Year × habitat	0.033	4	0.008	0.515	0.725
	Residual	1.810	112	0.016		
	Year × habitat trend (linear)	0.003	1	0.003	0.241	0.627
	Residual	0.357	28	0.001		
Gaur singles	Habitat	0.319	1	0.319	5.628	**0.025**
	Residual	1.588	28	0.057		
	Year × habitat	1.782	4	0.445	5.555	**<0.0001**
	Residual	8.982	112	0.080		
	Year × habitat trend (linear)	0.029	1	0.029	0.032	0.859
	Residual	2.527	28	0.090		
Gaur-herds	Habitat	1.906	1	1.906	26.542	**<0.0001**
	Residual	2.011	28	0.072		
	Year × habitat	1.209	4	1.209	5.897	**0.022**
	Residual	5.742	112	0.051		
	Year × habitat trend (linear)	1.03	1	1.03	10.073	**0.004**
	Residual	2.864	28	0.102		
Serow	Habitat	0.037	1	0.037	4.874	**0.036**
	Residual	0.213	28	0.008		
	Year × habitat	0.069	2	0.035	2.142	0.128
	Residual	0.898	55	0.016		
	Year × habitat trend (linear)	2.163	1	0.021	1.975	0.171
	Residual	0.307	28	0.011		

sure that allowed remnant animals to return. However, since ungulates in the landscape around Brong Dee were also hunted, potential immigrant populations would have required a period of growth themselves before expanding into Brong Dee.

Range expansion by other ungulate species, such as bison (Larter et al., 2000), muskox (Reynolds, 1998), and elk (Lemke et al., 1998), occurs after thresholds of local density are reached, followed by pulses of dispersal into new range. Subsequent population growth at the new site occurs primarily through reproduction by the colonizers (Larter et al., 2000). The gaur population trend at Brong Dee resembled this pattern, with an eruptive rather than gradual increase (Fig. 1), followed by increasing numbers of calves and juveniles in latter years. Thus, we hypothesize that Brong Dee was initially replenished through immigration by herds from surrounding areas, followed by on-site reproduction. In contrast, population growth of muntjac at Brong Dee may have been driven mostly by birth and recruitment of remnant resident animals. Red muntjac have small annual home ranges of < 4 km² in western Thai forests (Sukmasuang, 2001), which implies short dispersal distances and slow rates of expansion. For example, expansion into new areas by congener Reeve's muntjac (*Muntiacus reevesi*) is slow, about 1 km per year (Chapman et al., 1994). Rates of spread of sambar are apparently also slow: Caughley (1963) cal-

culated a maximum rate of 0.6 km per year for an expanding population introduced into New Zealand.

The wild pig population at Brong Dee suffered least from poaching. Pigs were already relatively abundant when monitoring began at Brong Dee, indicating their demographic resilience to hunting and behavioral ability to quickly recolonize disturbed areas. Wild pigs have much higher fecundity than other ungulates in this study (Table 1), and a correspondingly high intrinsic population growth rate (r_{max} = 0.69, Table 2). Species with high r_{max} are better able to resist decline than those with low growth (Bodmer et al., 1997; Sinclair and Krebs, 2003). Additionally, wild pigs are good colonizers after disturbance (Srikosamatara, 2000), and are generalists with respect to food and habitat (Lekagul and McNeely, 1988). Thus, demographic and behavioral attributes of wild pigs render them much more resilient to hunting pressure compared with other species in this study. The wide annual swings in pig abundance at Brong Dee (Fig. 1) reflect wide-ranging movements and attraction to unpredictable food sources (i.e., bamboo seeds; RS, pers. obs.), and match observations elsewhere in Thai forests (e.g., Sukmasuang, 2001).

Serow were encountered rarely at Brong Dee even though our transects covered slopes and cliff bases which are the species' preferred habitat (Lekagul and McNeely, 1988). They may have been

more common in inaccessible cliff areas, which we did not survey. For sambar, the scarcity of sign accurately reflects its very low abundance at Brong Dee. Elsewhere in Thung Yai, where hunting pressure has been much lower, the status of sambar is better and populations are increasing in some areas (Steinmetz et al., 2006a; M. Khaengkhetkarn, unpub. data).

5.2. Mating systems and population recovery

Sambar remained surprisingly rare at Brong Dee despite 10 years of freedom from hunting. Populations of similar-sized red deer (Cervus elaphus) can increase fairly rapidly (20–28% per year) from low numbers (McCorquodale et al., 1988; Eberhardt et al., 1996), and have doubled in 10 years following release from culling (Coulson et al., 2004). Hypothetically, even a tiny remnant population of, say, three sambar in 1995, and supposing annual $r = 0.2$, could increase to 22 animals in 10 years, or about $1/km^2$ in our study site. The failure of sambar to recover at Brong Dee might simply reflect a very low population that unluckily retains only one sex (i.e. demographic stochasticity). However, elsewhere in the region as well, sambar have been particularly slow to recover compared to other ungulates (Thailand: Steinmetz et al., 2009; Cambodia, Sumatra: B. Long, pers. comm., 2009), indicating that the effect at Brong Dee might be related to some intrinsic trait of sambar rather than a site-specific peculiarity of our study site.

An alternative explanation for the lack of sambar recovery is that the disproportionate loss of males, which were preferentially targeted for their commercially valuable antlers, has impaired reproduction. Most ungulates have polygynous breeding systems that usually are not limited by the number of males (Mysterud et al., 2002), but excessive hunting of males (e.g., for horns or antlers) can depress population growth by pushing sex ratios too far or disrupting social behavior (Milner et al., 2007). Saiga (Saiga tartarica) populations recently collapsed after sex ratios became highly skewed due to excessive hunting of males, which caused the proportion of breeding females to plummet (Milner-Gulland et al., 2003).

Removal of males might be particularly deleterious for sambar because, unlike other species at Brong Dee, their mating system appears to involve female selection for prime males (Table 1). During the rut, which in Thailand occurs in the cool season (Lekagul and McNeely, 1988; RS, pers. obs.), eligible sambar males (i.e., large and antlered) establish breeding territories delineated by antler-rubbed trees, scrapes, wallows, and scent-marking (Schaller, 1967; Lekagul and McNeely, 1988; RS, pers. obs.). Females explore these territories and mate with suitable males. In other deer species with functionally similar behavior, such as moose (Alces alces, Miquelle, 1991), Eld's deer (Cervus eldi; in Johansson and Liberg, 1996), and red deer (McComb, 1991), ovulation is induced by such stimuli, and a shortage of adult males can lead to delayed ovulation in females (Komers et al., 1999). For seasonal breeders, as sambar appear to be in Thailand, delayed calving can place newborns and their mothers outside periods of optimal environmental conditions (e.g., plant phenology and nutrition, cover for predator avoidance) resulting in reduced calf survival and recruitment (Aung et al., 2001; Mysterud et al., 2002). Although it is unlikely that female sambar at Brong Dee would forgo mating with remnant males whatever their status, it is plausible that the species' reproductive behavior renders it less resilient to the unnaturally low densities and disrupted population structure that result from commercial hunting. In contrast to sambar, the mating systems of gaur (female following) and muntjac (temporary pairing; Table 1), should function better after hunting, because a few males could find and fertilize many females. More research is needed on the role of behavior, and its interaction with human harvesting patterns, in the recovery of these once-common species.

5.3. Habitat selection

At low densities, animals are able to occupy the highest-quality habitat available, with the population expanding into lower quality habitat as numbers increase (Rosenzweig, 1991). This results in reduced fitness for an increasing proportion of animals as the population grows, and is an important mechanism of density-dependent population regulation (Sutherland and Norris, 2003). Muntjac and gaur at Brong Dee maintained significantly higher use of MDF than SEF as their populations increased from low numbers, suggesting a general preference for this habitat by both species. Gaur herds—the key demographic unit of the population that includes breeding females, calves, and juveniles—were consistently concentrated in MDF and used this habitat disproportionately more than SEF as the population increased (Fig. 3). Thus, MDF appears to underlie population recovery of gaur, supporting relatively fast population growth through increased fitness (reflected by breeding herds) at low density. This is probably related to the availability of nutritious grass (scarce in SEF) and abundant browse in MDF. For many large herbivore species, high forage quality and quantity increase survival of young animals (Gaillard et al., 2000). Muntjacs, perhaps for similar reasons, were also most abundant in MDF in most years (Fig. 3).

These results are consistent with habitat selection studies of gaur and muntjac based on other methods. In Huay Kha Khaeng, radio-collared muntjacs and gaur used MDF and other deciduous forest types more than SEF (Prayurasiddhi, 1997; Sukmasuang, 2001), and muntjac density in Thung Yai (determined from distance sampling) was twice as high in MDF (2.1 animals per km^2) as in SEF (Steinmetz and Mather, 1996). In general, deciduous forest types support higher densities of many Asian ungulate species (Eisenberg and Seidensticker, 1976).

5.4. Conservation implications

This research showed that muntjac, gaur, and wild pig can recover fairly rapidly from overhunting, given freedom from poaching. However, in most Southeast Asian protected areas, financial, staff, and logistical constraints impede high levels of protection across the entire area (Robichaud et al., 2001; Bruner et al., 2004). Given these constraints, it might be more effective and realistic to focus management effort in a network of small recovery zones, which could be given intensive and sustained protection until recovery goals were met, rather than rely on diffuse patrolling that implicitly seeks to protect all areas all the time. This research has shown that even small areas such as Brong Dee are practical for recovering some species. Larger zones would be better, however, by encompassing a larger initial source population to initiate recovery (Komers and Curman, 2000). This might be especially important for species with both low densities and very skewed sex and age structures, such as sambar, as larger areas would also encompass more remnant adults capable of breeding.

Replicating wildlife recovery zones across a protected area seems like a promising, practical way to promote landscape-wide recovery of ungulates. Marine reserves and no-take zones, which are similar conceptually, have successfully restored fish populations in overfished areas (Mosqueira et al., 2000; Roberts et al., 2001). Dispersal in most vertebrates is linked to density (Hansson, 1991), so recovery zones could eventually function as sources for recolonization of outlying lower-density areas. In this way, the value of recovery zones to population recovery efforts should actually increase with time. Recovery zones should encompass high quality habitat that generates the fastest-possible population growth and supports high densities of animals. Deciduous forest appeared to best meet these criteria for gaur and muntjac at Brong Dee. Managers should consider habitat improvement to promote population

growth within recovery zones, such as creating artificial mineral licks and grasslands (Bhumpakphan, 1997); at the same time, the risk that such improvements could create poaching hotspots by concentrating animals spatially should be recognized. Lastly, an advantage of recovery zones as a general approach to recovering large mammals is the link to community-based conservation. Recovery zones are geographically and conceptually focused interventions that are more likely to invite local support and participation than general bans which are poorly or unevenly enforced. Indeed, wildlife recovery at Brong Dee was achieved through collaborative action between Thung Yai management officials and village conservation groups who helped patrol and monitor the area (Steinmetz et al., 2006a,b).

Acknowledgements

References

Adler, P.B., Raff, D.A., Laurenroth, W.K., 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128, 465–479.

Aung, M., McShea, W.J., Htung, S., Than, A., Soe, T.M., Monfort, S., Wemmer, C., 2001. Ecology and social organization of a tropical deer (Cervus eldi thamin). Journal of Mammalogy 82, 836–847.

Baillie, J.E.M., Hilton-Taylor, C., Stuart, S. (Eds.), 2004. 2004 IUCN Red List of Threatened Species: A Global Species Assessment. IUCN, Gland, Switzerland.

Bennett, E.L., Nyaol, A.J., Sompud, J., 2000. Saving Borneo's bacon: the sustainability of hunting in Sarawak and Sabah. In: Robinson, J.G., Bennett, E.L. (Eds.), Hunting for sustainability in tropical forests. Columbia University Press, New York, pp. 305–324.

Bhumpakphan, N., 1997. Ecological characteristics and habitat utilization of gaur (Bos guarus H. Smith, 1827) in different climatic sites. Thesis, Kasetsart University, Bangkok, Thailand.

Bodmer, R.E., Eisenberg, J.F., Redford, K.T., 1997. Hunting and the likelihood of extinction of Amazonian mammals. Conservation Biology 11, 460–466.

Bruner, A.G., Gullison, R.E., Balmford, A., 2004. Financial costs and shortfalls of managing and expanding protected area systems in developing countries. BioScience 54, 1119–1126.

Caughley, G., 1963. Dispersal rates of several ungulates introduced into New Zealand. Nature 200, 280–281.

Caughley, G., 1977. Analysis of vertebrate populations. John Wiley, New York.

Chapman, N., Harris, S., Stanford, A., 1994. Reeves' Muntjac in Britain: their history, spread, habitat selection, and the role of human intervention in accelerating their dispersal. Mammal Review 24, 113–160.

Choquenot, D., Dexter, N., 1996. Spatial variation in food limitation: the effects of foraging constraints on the distribution and abundance of feral pigs in the rangelands. In: Floyd, R.B., Sheppard, A.W., De Barro, P.J. (Eds.), Frontiers of Population Ecology. CSIRO Publishing, Collingwood, Australia, pp. 531–546.

Corlett, R.T., 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39, 292–303.

Coulson, T., Guinness, F., Pemberton, J., Clutton-Brock, T., 2004. The demographic consequences of releasing a population of red deer from culling. Ecology 85, 411–422.

Eberhardt, L.E., Eberhardt, L.L., Tiller, B.L., Cadwell, L.L., 1996. Growth of an isolated elk population. Journal of Wildlife Management 60, 369–373.

Eisenberg, J.F., Seidensticker, J., 1976. Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. Biological Conservation 10, 293–305.

Elzinga, C.L., Saltzer, D.W., Wiloughby, J.W., Gibbs, J.P., 2001. Monitoring Plant and Animal Populations. Blackwell Science, Malden, Massachusetts, USA.

Fimbel, C., Curran, B., Usongo, L., 2000. Enhancing the sustainability of duiker hunting through community participation and controlled access in the Lobeke Region of southeastern Cameroon. In: Robinson, J.G., Bennett, E.L. (Eds.), Hunting for Sustainability in Tropical Forests. Columbia University Press, New York, pp. 356–374.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toïgo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31, 367–393.

Gibbs, J.P., Droege, S., Eagle, P., 1998. Monitoring populations of plants and animals. BioScience 48, 935–940.

Groom, M.J., 2006. Threats to biodiversity. In: Groom, M.J., Meffe, G.K., Carroll, C.R. (Eds.), Principles of conservation biology. Sinauer Associates, Sunderland, USA, pp. 63–109.

Hansson, L., 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42, 17–38.

Hatch, S.A., 2003. Statistical power for detecting trends with applications to seabird monitoring. Biological Conservation 111, 317–329.

Hill, K., Padwe, J., 2000. Sustainability of Ache hunting in the Mbaracayu Reserve, Paraguay. In: Robinson, J.G., Bennett, E.L. (Eds.), Hunting for Sustainability in Tropical Forests. Columbia University Press, New York, pp. 79–105.

Hines, J.E., MacKenzie, D.I., 2004. PRESENCE, version 2.0. .

Jenkins, R.K.B., Corti, G.R., Fanning, E., Roettcher, K., 2002. Management implications of antelope habitat use in the Kilombero Valley, Tanzania. Oryx 36, 161–169.

Johansson, A., Liberg, O., 1996. Functional aspects of marking behavior by male roe deer (Capreolus capreolus). Journal of Mammalogy 77, 558–567.

Karanth, K.U., Stith, B.M., 1999. Prey depletion as a critical determinant of tiger population viability. In: Seidensticker, J.S., Christie, S., Jackson, P. (Eds.), Riding the Tiger: Tiger Conservation in Human Dominated Landscapes. Cambridge University Press, Cambridge, pp. 100–113.

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. Proceedings of the National Academy of Science 101, 4854–4858.

Komers, P., Birgersson, B., Ekvall, K., 1999. Timing of estrus in fallow deer is adapted to the age of available mates. American Naturalist 153, 431–436.

Komers, P.E., Curman, G.P., 2000. The effect of demographic characteristics on the success of ungulate re-introductions. Biological Conservation 93, 187–193.

Krebs, C.J., 1999. Ecological Methodology, second ed. Addison Wesley Longman, Inc., Menlo Park, California, USA.

Larter, N.C., 1994. Plant–Herbivore Dynamics Associated with an Erupting Ungulate Population: A Test of Hypotheses. PhD. Dissertation, University of British Columbia, Vancouver, Canada.

Larter, N.C., Sinclair, A.R.E., Ellsworth, T., Nishi, J., Gates, C.C., 2000. Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. Animal Conservation 4, 299–309.

Lekagul, B., McNeely, J.A., 1988. Mammals of Thailand, second ed. Association for the Conservation of Wildlife, Bangkok.

Lemke, T.O., Mack, J.A., Houston, D.B., 1998. Winter range expansion by the northern Yellowstone elk herd. Intermountain Journal of Science 4, 1–9.

Lynam, A.J., Round, P.D., Brockelman, W.Y., 2006. Status of Birds and Large Mammals in Thailand's Dong Phayayen-Khao Yai forest Complex. Biodiversity Research and Training Program (BRT) and Wildlife Conservation Society, Bangkok.

Mace, G.M., Balmford, A., 2000. Patterns and processes in contemporary mammalian extinctions. In: Entwistle, A., Dunstone, N. (Eds.), Priorities for the Conservation of Mammalian Diversity: Has the Panda had its Day? Cambridge University Press, Cambridge, UK, pp. 27–52.

MacKenzie, D.I., Nichols, J.D., Lachmann, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less then one. Ecology 83, 2248–2255.

McComb, K.E., 1991. Female choice for high roaring rates in red deer, Cervus elaphus. Animal Behavior 41, 79–88.

McCorquodale, S.M., Eberhardt, L.L., Eberhardt, L.E., 1988. Dynamics of a colonizing elk population. Journal of Wildlife Management 52, 309–313.

Milner, J.M., Nilsen, E.B., Andreassen, H.P., 2007. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21, 36–47.

Milner-Gulland, E.J., Akcakaya, H.R., 2001. Sustainability indices for exploited populations. Trends in Ecology and Evolution 16, 686–692.

Milner-Gulland, E.J., Bennett, E.L., 2003. Wild meat: the bigger picture. Trends in Ecology and Evolution 18, 351–357.

Milner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B., Grachev, I.A., 2003. Reproductive collapse in saiga antelope harems. Nature 422, 135.

Miquelle, D.G., 1991. Are moose mice? The function of scent urination in moose. American Naturalist 138, 460–477.

Mosqueira, I., Cote, I.M., Jennings, S., Reynolds, J.D., 2000. Conservation benefits of marine reserves for fish populations. Animal Conservation 3, 321–332.

Muchaal, P.K., Ngandjui, G., 1999. Impact of village hunting on wildlife populations in the western Dja Reserve, Cameroon. Conservation Biology 13, 385–396.

Mysterud, A., Coulson, T., Stenseth, N.C., 2002. The role of males in the dynamics of ungulate populations. Journal of Animal Ecology 71, 907–915.

Nakhasathien, S., Stewart-Cox, B., 1990. Nomination of the Thung Yai-Huai Kha Khaeng Wildlife Sanctuary to be a UNESCO World Heritage Site. Royal Forest Department, Bangkok.

Nooren, H., Claridge, G., 2001. Wildlife Trade in Laos: The End of the Game. Netherlands Committee for IUCN, Amsterdam.

Novaro, A.J., Redford, K.H., Bodmer, R.E., 2000. Effect of hunting in source-sink systems in the Neotropics. Conservation Biology 14, 713–721.

Nowak, R.M., 1999. Walker's Mammal of the World, sixth ed. Johns Hopkins University Press, Baltimore, USA.

Pattanavibool, A., Dearden, P., 2002. Fragmentation and wildlife in montane evergreen forests, northern Thailand. Biological Conservation 107, 155–164.

Prasad, S., Krishnaswamy, J., Chellam, R., Goyal, S.P., 2006. Ruminant-mediated seed dispersal of an economically valuable tree in Indian dry forests. Biotropica 38, 679–682.

Prayurasiddhi, T., 1997. The Ecological Separation of Gaur (*Bos gaurus*) and Banteng (*Bos javanicus*) in Huai Kha Khaeng Widlife Sanctuary, Thailand. PhD. Thesis. University of Minnesota.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Rabinowitz, A., 1989. The density and behavior of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary Thailand. Natural History Bulletin of the Siam Society 37, 235–251.

Robinson, J.G., Redford, K.H., 1986. Intrinsic rate of natural increase in Neotropical forest mammals: relationship to phylogeny and diet. Oecologia 68, 516–520.

Reynolds, P.E., 1998. Dynamics and range expansion of a reestablished muskox population. Journal of Wildlife Management 62, 734–744.

Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. Science 294, 1920–1923.

Robichaud, W., Marsh, C.W., Southammakoth, S., Khounthikoummane, S., 2001. Review of the national protected area system in Lao PDR. Lao-Swedish Forestry Programme. Department of Forestry, Vientiane.

Rosenzweig, M.L., 1991. Habitat selection and population interactions: the search for mechanism. American Naturalist 137 (supplement), S5–S28.

Sanderson, E., Forrest, J., Loucks, C., Ginsberg, J., Dinerstein, E., Seidensticker, J., Leimgruber, P., Songer, M., Heydlauff, A., O'Brien, T., Bryja, G., Klenzendorf, S., Wikramanayake, E., 2006. Setting Priorities for the Conservation and Recovery of Wild Tigers: 2005-2015. The Technical Assessment. WCS, WWF, Smithsonian, and NFWF-STF, New York and Washington DC.

Schaller, G.B., 1967. The Deer and the Tiger. University of Chicago Press, Chicago, USA.

Sinclair, A.R.E., 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. In: Floyd, R.B., Sheppard, A.W., De Barro, P.J. (Eds.), Frontiers of Population Ecology. CSIRO Publishing, Collingwood, Australia, pp. 127–154.

Sinclair, A.R.E., Krebs, C.J., 2003. Complex numerical responses to top-down and bottom-up processes in vertebrate populations:. In: Sibly, R.M., Hone, J., Clutton-Brock, T.H. (Eds.), Wildlife Population Growth Rates. Cambridge University Press, Cambridge, UK, pp. 127–147.

Singer, F.J., Norland, J.E., 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Canadian Journal of Zoology 72, 1383–1394.

Smith, J.L.D., Tunhikorn, S., Tanhan, S., Simcharoen, S., Kanchanasaka, B., 1999. Metapopulation structure of tigers in Thailand. In: Seidensticker, J.S., Christie, S., Jackson, P. (Eds.), Riding the Tiger: Tiger Conservation in Human Dominated Landscapes. Cambridge University Press, Cambridge, UK, pp. 166–175.

Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L., 2004. Southeast Asian biodiversity: an impending disaster. Trends in Ecology and Evolution 19, 654–660.

Srikosamatara, S., 1993. Density and biomass of large herbivores and other mammals in a dry tropical forest, western Thailand. Journal of Tropical Ecology 9, 33–43.

Srikosamatara, S., Suteethorn, V., 1994. Wildlife conservation along the Lao-Thai border. Natural History Bulletin of the Siam Society 42, 3–21.

Srikosamatara, S., Suteethorn, V., 1995. Populations of gaur and banteng and their management in Thailand. Natural History Bulletin of the Siam Society 43, 55–83.

Srikosamatara, S., 2000. Monitoring densities and distributions of large mammals: Huai Kha Khaeng Wildlife Sanctuary, Thailand. In: Galt, A., Sigaty, T., Vinton, M. (Eds.), The World Commission on Protected Areas 2nd Southeast Asia Regional Forum. IUCN, Vientiane, pp. 390–395.

Steidl, R.J., Hayes, J., Schauber, E., 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61, 270–279.

Steinmetz, R., Mather, R., 1996. Impact of Karen villages on the fauna of Thung Yai Naresuan Wildlife Sanctuary: a participatory research project. Natural History Bulletin of the Siam Society 44, 23–40.

Steinmetz, R., 2004. Gaur (*Bos gaurus*) and banteng (*B. javanicus*) in the lowland forest mosaic of Xe Pian Protected Area, Lao PDR: abundance, habitat use, and conservation. Mammalia 68, 141–157.

Steinmetz, R., Chutipong, W., Seuaturien, N., Chirgsaard, E., 2006a. Collaborative Monitoring and Recovery of Large Mammals in Thung Yai Naresuan Wildlife Sanctuary, Thailand. WWF-Thailand and Department of National Parks, Wildlife, and Plant Conservation, Bangkok.

Steinmetz, R., Chutipong, W., Seuaturien, N., 2006b. Collaborating to conserve large mammals in Southeast Asia. Conservation Biology 20, 1391–1401.

Steinmetz, R., Chutipong, W., Suaturien, N., Chirgsaard, E., 2008. Community structure of large mammals in tropical montane and lowland forest in the Tenasserim-Dawna Mountains, Thailand. Biotropica 40, 344–353.

Steinmetz, R., Seuaturien, N., Chutipong, W., Poonnil, B., 2009. The Ecology and Conservation of Tigers and their Prey in Kuiburi National Park, Thailand. WWF Thailand and Department of National Parks, Wildlife, and Plant Conservation, Bangkok, Thailand.

Sukmasuang, R. 2001. Ecology of Barking Deer (*Muntiacus* spp.) in Huai Kha Khaeng Wildlife Sanctuary. Thesis, Kasetsart University, Bangkok.

Sutherland, W.J., Norris, K., 2003. Behavioral models of population growth rates: implications for conservation and prediction. In: Sibly, R.M., Hone, J., Clutton-Brock, T.H. (Eds.), Wildlife Population Growth Rates. Cambridge University Press, Cambridge, UK, pp. 225–248.

Thompson, W.L., White, G.C., Gowan, C., 1998. Monitoring Vertebrate Populations. Academic Press, San Diego, USA.

Thomas, L., 1997. Retrospective power analysis. Conservation Biology 11, 276–280.

Thongnamchaima, B., Mather, R. 1997. Mammals in Huai Kha Khaeng Wildlife Sanctuary. WWF-Thailand Project Office. Bangkok. (in Thai).

Tungittiplakorn, W., Dearden, P., 2002. Hunting and wildlife use in some Hmong communities in northern Thailand. Natural History Bulletin of the Siam Society 50, 57–73.

Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K., Possingham, H.P., 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications 13, 1790–1801.

van Strien, N.J., 1983. A guide to the tracks of mammals of western Indonesia. School of Environmental Conservation Management, Ciawi, Indonesia.

van Strien, A.J., van de Pavert, R., Moss, D., Yates, T.J., van Swaay, C.A.M., Vos, P., 1997. The statistical power of two butterfly monitoring schemes to detect trends. Journal of Applied Ecology 34, 817–828.