Is the clouded leopard *Neofelis nebulosa* extinct in Taiwan, and could it be reintroduced? An assessment of prey and habitat

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Abstract During 1997–2012 we conducted a nationwide camera-trapping survey and assessed the availability of prey and habitat for the clouded leopard *Neofelis nebulosa* in Taiwan. We surveyed 1,249 camera-trap sites over 113,636 camera-trap days, from the seashore to an altitude of 3,796 m and covering various types of vegetation. No clouded leopards were photographed during 128,394 camera-trap days, including at 209 sites in other studies, confirming the presumed extinction of clouded leopards in Taiwan. Assessment of the prey base revealed altitudinal distribution patterns of prey species and prey biomass. Areas at lower altitudes and with less human encroachment and hunting supported a higher prey biomass and more of the typical prey species of clouded leopards. Habitat analysis revealed 8,523 km² of suitable habitat but this was reduced to 6,734 km² when adjacent areas of human encroachment were subtracted. In the absence of hunting and large mammalian carnivores the major prey of clouded leopards in Taiwan, such as Formosan macaques *Macaca cyclopis*, Reeves's muntjacs *Muntiacus reevesi*, Formosan serow *Capricornis swinhoei* and sambar *Rusa unicolor*, could become over-abundant. Thus, it is important to address the cascading effect of the disappearance of top-down predator control. Our assessment indicated that, with proper regulation of hunting, habitat restoration and corridor improvement, it may be possible to reintroduce the clouded leopard.

Keywords Camera-trapping, extinct, habitat assessment, *Neofelis nebulosa*, prey distribution, reintroduction, Taiwan

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Introduction

The clouded leopard *Neofelis nebulosa* is categorized as Vulnerable on the IUCN Red List and is listed on Appendix I of CITES (2014). It is the largest felid in Taiwan and has been categorized as Endangered under the Wildlife Conservation Act since 1989. Lee & Lin (1992) suggested that clouded leopards were nearly or already extinct in Taiwan; no direct records of occurrence (e.g. sightings, photographs, carcasses) had been reported since 1983 and pre-1983 records were based on interviews. However, for a species to be categorized as Extinct, IUCN stipulates that exhaustive surveys must be conducted in its range over a time frame appropriate to the taxon's life cycle (IUCN, 2001). No field surveys of clouded leopards have been conducted in Taiwan and information from local people is anecdotal and unsubstantiated (Rabinowitz, 1988). The population status of the species cannot be ascertained without field surveys but if any clouded leopards remain they can only be in very small numbers and in remote areas.

The clouded leopard's prey species have experienced pressure from habitat loss as a result of human encroachment and from hunting, although commercial hunting was banned in 1973 (Lee & Lin, 1992). However, populations of some prey species, including Formosan macaques *Macaca cyclopis* and some mammalian herbivores, have reportedly increased, causing conflict on farmlands and in forests. Although these increases could be a result of the hunting ban, reduced predation pressure from the disappearance of clouded leopards cannot be ruled out (Crooks &

Soule, 1999; Chiang et al., 2012). Disappearance of large apex predators can impose trophic cascades on an ecosystem, with effects on biodiversity (Terborgh et al., 2001; Estes et al., 2011). Thus, it is important to assess the population status of the clouded leopard and locate any surviving individuals. Reintroduction of clouded leopards to Taiwan could be considered if extirpation is confirmed.

The success of any conservation action and/or reintroduction of clouded leopards would depend on the availability of suitable prey and habitat. The discovery of clouded leopards would necessitate conservation actions such as habitat improvement and/or restocking the population to increase genetic diversity (Roelke et al., 1993). If it were confirmed that no clouded leopards remain, suitable reintroduction sites should be identified and habitat quality and connectivity improved. Our objectives were (1) to investigate whether there are any remaining clouded leopards in Taiwan, (2) to document the altitudinal distribution patterns of major potential prey species, (3) to assess the abundance of prey species, (4) to test whether prey populations are being reduced by anthropogenic hunting, and (5) to identify suitable habitat for restoration and for the reintroduction of clouded leopards.

Study area

Taiwan is an orogenic island of c. 36,000 km², with a large altitudinal range and a maximum altitude of c. 4,000 m. The vegetation gradient changes from coastal plains and lowland tropical and subtropical rainforest to temperate coniferous forest and alpine grassland at the highest altitudes. The Tawu Mountain area in southern Taiwan (Fig. 1) encompasses two protected areas: Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area. It contains the largest remaining lowland primary forest and is the location in which, if clouded leopards still occur on the island, they are most likely to be found (Rabinowitz, 1988). There is minimal human disturbance in the area and it is primarily covered by pristine *Ficus–Machilus, Machilus–Castanopsis* and *Quercus* forests and *Tsuga* rainforests along the altitudinal gradient 130–3,100 m over 922 km².

Methods

Camera-trap surveys

We conducted camera-trap surveys in national parks, protected areas and fragmented lowlands throughout Taiwan during 1997–2012, mostly using film cameras developed in Taiwan. Film camera-traps were set at c. 2 m height and tilted at 40–60° to face the trail or intersection of trails. In 2009 we started using digital camera-traps from Cuddeback (Wisconsin, USA), Reconyx (Wisconsin, USA) and Bushnell (Kansas, USA) in some of the surveys, and by 2011 film camera-traps had been replaced completely by digital. The digital camera-traps were set at c. 0.5 m height for horizontal detection, to accommodate their sensor design. Such horizontal detection may result in higher variations in the detection range, given the variable terrain. With film camera-traps tilted downwards, the detection area was more consistent for prey comparison across sites. Thus, only film camera-traps were used to assess the prey base, to reduce bias from the variable detection areas at sites with digital cameras.

A more extensive camera-trap survey was conducted in the Tawu Mountain area during 2001–2004 to study prey populations under the most natural conditions, without human disturbance and hunting, using stratified sampling according to altitude (Chiang et al., 2012). Several camera-trap sites were baited with live chickens and other olfactory, visual or auditory lures to increase the chances of photographing clouded leopards.

Prey assessment

We used the number of photographic events per camera-trap day (O'Brien et al., 2003) as an index of relative abundance of prey because of its correlation with population densities of mammalian herbivores (O'Brien et al., 2003; Rowcliffe et al., 2008; Rovero & Marshall, 2009). Consecutive photographs of the same species within 1 hour were counted as one event and multiple consecutive pictures of groups of animals (e.g. Formosan macaques) were also counted as single events. The relative abundance index of each prey species was multiplied by the edible percentage of mean adult body weight (g) and summed across all prey species, for use as a prey biomass index. Edible percentage was determined as 65% for prey >25 kg, 80% for prey >4 kg and 90% for prey <4 kg (Emmons, 1987; Pedersen et al., 1999; Mills et al., 2004). However, we estimated that the maximum amount of meat a clouded leopard could obtain from large prey (assuming multiple feeding events) was 50 kg, based on the daily meat consumption and kill rates of other wild felids.

To investigate altitudinal patterns of prey distribution and abundance under natural conditions, without hunting, we compared relative abundance indices for each prey and carnivore species and prey biomass indices between four altitudinal zones in the Tawu Mountain area (150–1,200, 1,200–2,000, 2,000–2,500 and 2,500–3,100 m). These four zones reflect the four major vegetation types in the area. We used Kruskal–Wallis tests to identify if there were significant differences between relative abundance indices and prey biomass indices between the zones. We used Jonckheere–Terpstra tests to identify if there were monotonic patterns of relative abundance indices and prey biomass indices along the altitudinal gradient. We performed

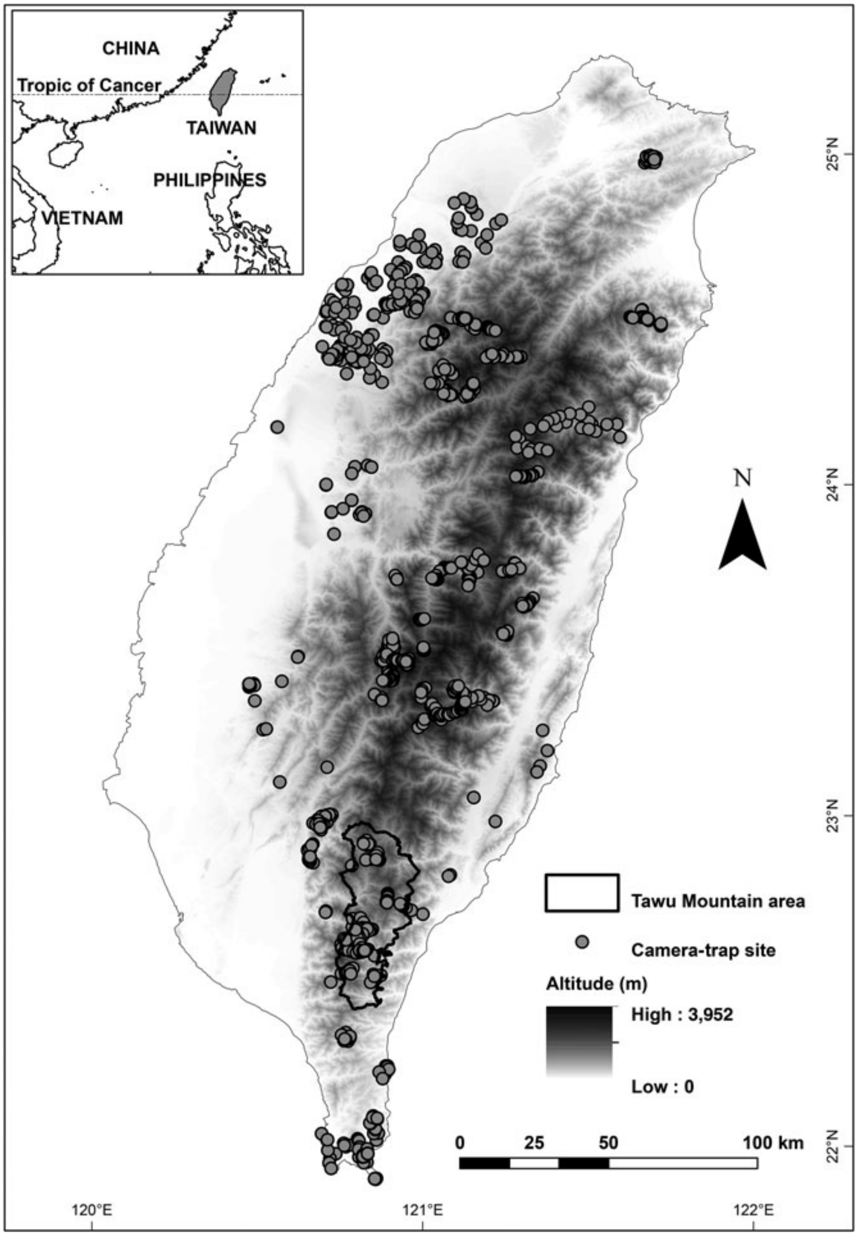

FIG. 1 Locations of camera-trap sites across Taiwan. The inset shows the location of Taiwan off the coast of China.

one-sided Wilcoxon rank–sum tests to examine the effects of hunting on relative abundance indices and prey biomass indices in hunted and non-hunted areas at altitudes $<$2,000 m in the Tawu Mountain area. We used *R v. 2.15* (R Development Core Team, 2009) to conduct statistical analysis. Jonckheere–Terpstra tests were performed in *SPSS v.16* (SPSS, Chicago, USA).

We also conducted a meta-analysis of prey biomass index, including data from other camera-trap studies in Taiwan (Wang, 2004, 2008; Wu et al., 2004; Wang & Hsu, 2005; Wang & Huang, 2005; Hwang & Chian, 2007), to understand factors influencing prey biomass across the country. The prey biomass index used in this meta-analysis was based on the five largest prey species (macaques and ungulates) because limited data were available for some areas. These five species accounted for almost 99% of the prey biomass index. We hypothesized that prey biomass could be influenced by human activity, distance to central Taiwan and altitude. We used multiple linear regression and the information-theoretic approach (Akaike information criterion, AIC_c) to compare the full model with three independent variables and models with each variable removed in turn.

In our models the value for human activity was based on three factors: accessibility from roads and villages (0 or 1), hunting pressure (0–3), and history of forest practices or agricultural use (0–5). These three factors were each scaled to 10 and summed to give an overall score for human activity (0–30). Accessibility from roads and villages was assigned a value of 1 if the area was within 5 km of major roads or well-maintained logging roads or within 3 km of aboriginal villages, and a value of 0 if the area was outside these ranges. Hunting pressure was assigned a value of 0 if there was no hunting, 1 if there was occasional hunting, 2 if there was persistent seasonal hunting (i.e. every year during October–April) and 3 if there was persistent hunting all year round. The history of forest practices was determined from literature and field observations and was based on the estimated percentages of forest alteration for agriculture, plantations and clear-cutting.

Habitat assessment

We identified areas of suitable habitat for clouded leopards based on the species' habitat requirements (Nowell & Jackson, 1996; Grassman et al., 2005). Natural broadleaf forest, mixed broadleaf–conifer forest (primary or secondary) and old-growth cypress forest were considered potential suitable habitats. We excluded coniferous forest, which usually occurs at >2,500 m in Taiwan, non-forested areas, agricultural land, bamboo forest and clear-cut plantation forest (mostly conifers). We identified potentially suitable habitat using a digitized vegetation map produced by Taiwan Forestry Bureau in 1995. Based on data from other studies (home-range and core-area sizes and distances covered daily; Grassman et al., 2005; Austin et al., 2007) we included in our analyses forest patches >40 km^2 and fragmented patches 4–40 km^2 that were within 1 km of contiguous primary habitat. Given that clouded leopards may hunt at forest edges (Grassman et al., 2005) we considered a 500 m buffer along the boundaries of areas of suitable habitat. Human encroachment and hunting are common and persistent near villages and along roads, and therefore we considered that suitable habitat must be at least 5 km from villages and 3 km from major roads. If clouded leopards used areas adjacent to villages and major roads they would probably have been observed.

Results

Camera-trap surveys

During 1997–2012 we established 1,249 camera-trap sites over 113,646 camera-trap days in various parts of Taiwan, from the coast to 3,796 m altitude. These included 377 sites (13,354 camera-trap days) in the Tawu Mountain area. The total effort, including 209 sites from other surveys, was 1,458 sites (Fig. 1) and 128,394 camera-trap days. No camera traps recorded clouded leopards.

Prey assessment

Our camera-trap survey yielded a comprehensive record of potential mammalian and avian prey. Twelve mammal species and two phasianid bird species identified as potential prey were photographed (Table 1). We excluded other carnivores as prey because clouded leopards have not been observed killing carnivores, nor have carnivores been found in clouded leopard scats (Griffiths, 1993; Nowell & Jackson, 1996; Grassman et al., 2005).

In the Tawu Mountain area we identified a significant decreasing trend in prey biomass index with increasing altitude (Jonckheere–Terpstra test, $P < 0.0001$; Table 1). Reeves's muntjacs *Muntiacus reevesi* had the highest relative abundance index (Table 1) at <2,500 m and accounted for >50% of the prey biomass index at <1,200 m. Formosan macaques were the second most important contributor to the relative abundance index at <2,500 m but contributed less than Formosan serow *Capricornis swinhoei* and sambar *Rusa unicolor* to the prey biomass index because they are not as heavy. Although wild pigs *Sus scrofa* were the second largest prey, because of their low relative abundance index their contribution to the prey biomass index was lower than that of the other four prey species at <2,500 m. Macaques and the four ungulates contributed >99% of the total prey biomass index.

We detected significant decreasing trends in relative abundance index with increasing altitude for macaques, muntjacs, Chinese pangolins *Manis pentadactyla*, Swinhoe's pheasants *Lophura swinhoii*, red-bellied tree squirrels *Callosciurus erythraeus*, and spinous country rats *Niviventer coninga* (Jonckheere–Terpstra test, all $P < 0.003$; Table 1). Although there were significant altitudinal differences, no monotonic linear trends were observed for serow and sambar. Only Taiwan white-faced flying squirrels *Petaurista alborufus lena*, Formosan white-bellied rats *Niviventer culturatus* and Taiwan partridges *Arborophila crudigularis* showed increasing relative abundance indices along the altitude gradient (Jonckheere–Terpstra test, all $P < 0.003$; Table 1); however, these are not important prey species nor do they weigh > 0.5 kg.

At altitudes <2,000 m in the Tawu Mountain area the prey biomass index was significantly lower in hunted than non-hunted areas ($P < 0.0001$; Table 2) because of the significantly reduced abundance of ungulate and primate species (except wild pigs) in hunted areas (Table 2). In contrast, none of the smaller prey species, which were not targeted by hunters, had significantly lower relative abundance indices in hunted areas than in non-hunted areas (Table 2).

Based on camera-trap data from across the country, the prey biomass indices of the five largest prey species decreased as human activity increased ($F_{1,26} = 32.08$, $P < 0.0001$). The full model, which included all three variables (human activity, distance to central Taiwan and mean altitude), best explained countrywide variations in the prey biomass indices of these five species (Table 3) and all three factors were significant. In summary, reduced hunting pressure and human encroachment, lower altitudes and closer proximity to

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TABLE 1 Prey species in descending order by weight, with maximum edible weight, mean adult weight, relative abundance index (no. of photographic events per camera-trap day) in four zones of altitude in Tawu Mountain area, Taiwan, during 2001–2004 (Fig. 1), P for Kruskal–Wallis test for altitudinal differences, and P for Jonckheere–Terpstra test for monotonic patterns among the four zones.

			Relative abundance index					
Prey species	Maximum edible weight (g)[1]	Mean adult weight (kg)[2]	150–1,200 m (n = 72)	1,200–2,000 m (n = 49)	2,000–2,500 m (n = 43)	2,500–3,100 m (n = 22)	Kruskal–Wallis P	Jonckheere–Terpstra P
Prey > 4 kg								
Sambar *Rusa unicolor*	50,000	165	0.0251	0.0342	0.0291	0.0016	0.0032	0.1594
Wild pig *Sus scrofa*	28,470	43.8	0.0093	0.0040	0.0074	0.0089	0.1644	0.4988
Formosan serow *Capricornis swinhoei*	18,200	28	0.0792	0.0868	0.0403	0.0858	0.0040	0.5522
Reeves's muntjac *Muntiacus reevesi*	8,000	10	0.6006	0.1962	0.1200	0.0069	< 0.0001	< 0.0001
Formosan macaque *Macaca cyclopis*	7,200	9	0.0931	0.0984	0.0532	0.0374	0.0087	0.0023
Chinese pangolin *Manis pentadactyla*	3,600	4.5	0.0056	0.0046	0.0000	0.0000	0.0025	0.0003
Prey < 2 kg								
White-faced flying squirrel *Petaurista alborufus lena*	1,370	1.522	0.0002	0.0000	0.0016	0.0105	< 0.0001	0.0004
Swinhoe's pheasant *Lophura swinhoii*	990	1.1	0.0244	0.0363	0.0069	0.0027	0.0007	0.0007
Red-bellied tree squirrel *Callosciurus erythraeus*	324	0.36	0.0107	0.0157	0.0000	0.0000	0.0007	0.0002
Long-nosed tree squirrel *Dremomys pernyi owstoni*	324	0.36	0.0024	0.0028	0.0010	0.0044	0.5639	0.8893
Taiwan partridge *Arborophila crudigularis*	281	0.312	0.0048	0.0083	0.0134	0.0115	0.0694	0.0132
Striped tree squirrel *Tamiops maritimus*	63	0.07	0.0000	0.0000	0.0013	0.0017	0.2222	0.0697
Formosan white-bellied rat *Niviventer culturatus*	61	0.068	0.0000	0.0062	0.0182	0.0088	< 0.0001	< 0.0001
Spinous country rat *Niviventer coninga*	61	0.068	0.0650	0.0949	0.0004	0.0000	< 0.0001	< 0.0001
Total relative abundance index			0.9204	0.5879	0.2926	0.1801		
Total prey biomass index			8491.1	5750.0	3758.8	2241.7		< 0.0001

[1]Minimum of 65% of body weight and 50 kg for large prey and 90% of body weight for small prey

[2]Based on our own field data or literature

TABLE 2 Prey species in descending order by weight, relative abundance indices for non-hunted and hunted areas at altitudes <2,000 m in the Tawu Mountain area, Taiwan (Fig. 1), during 2001–2004, and Wilcoxon rank-sum P for hunting impacts.

	Relative abundance index		
Prey species	Non-hunted area (n = 121)	Hunted area (n = 22)	Wilcoxon rank-sum P
Prey > 4 kg			
Sambar	0.0288	0.0011	0.0004
Wild pig	0.0071	0.0151	0.8334
Formosan serow	0.0823	0.0374	0.0082
Reeves's muntjac	0.4368	0.1452	<0.0001
Formosan macaque	0.0953	0.0703	0.0385
Chinese pangolin	0.0052	0.0000	0.0479
Prey <2 kg			
White-faced flying squirrel	0.0001	0.0000	0.3420
Swinhoe's pheasant	0.0292	0.0196	0.3276
Red-bellied tree squirrel	0.0128	0.0088	0.4832
Long-nosed tree squirrel	0.0026	0.0000	0.1095
Taiwan partridge	0.0062	0.0125	0.9200
Striped tree squirrel	0.0000	0.0011	0.9910
Formosan white-bellied rat	0.0025	0.0024	0.7050
Spinous country rat	0.0771	0.1344	0.4261
Prey biomass index	7381.1	2871.2	<0.0001

central Taiwan supported higher biomass of clouded leopard prey.

Habitat assessment

The total area of suitable habitat for clouded leopards, excluding small, isolated fragments, was c. 8,523 km² (24% of the total land area of Taiwan). After applying the 500 m buffer and excluding areas around roads and villages the area of potential high-quality habitat was reduced to 6,734 km² (Fig. 2a). The largest continuous block is 2,555 km², in central/eastern Taiwan and the second largest block, which encompasses the Tawu Mountain area in southern Taiwan, is 2,022 km² (Fig. 2a). However, a larger portion of the Tawu Mountain area is at altitudes <2,000 m compared to other patches (Fig. 2b). Areas of suitable habitat that are unencroached by humans are fragmented and isolated by roads, agricultural lands and coniferous plantation forests, particularly at altitudes <2,000 m and more so at altitudes <1,500 m (Fig. 2c), where the most abundant prey are found. In summary, the most suitable habitat for the clouded leopard is concentrated in southern and eastern Taiwan.

TABLE 3 Linear-regression models of prey biomass index, based on data for macaques, sambar, Reeves's muntjacs, Formosan serow and wild pigs from camera-trapping studies conducted at 28 sites across Taiwan during 2000–2010.

Model*	ΔAIC_c	Akaike weight	R^2
HA + DCT + ALT	0.00	0.887	0.714
HA + DCT	5.48	0.057	0.604
HA + ALT	5.51	0.056	0.604
ALT + DCT	27.18	0.000	0.141

*HA, index of human activity; DCT, distance to central Taiwan; ALT, mean altitude

Discussion

The mean number of camera-trap days required to record a clouded leopard or Sunda clouded leopard *Neofelis diardi* in other South-east Asian countries is 113–879, with as few as 8–24 camera-trap sites (Lynam et al., 2001; Kawanishi & Sunquist, 2004; Rao et al., 2005; Azlan & Lading, 2006; Azlan & Sharma, 2006; Johnson et al., 2006; Cheyne & Macdonald, 2011). Carbone et al. (2001) suggested that 1,000 camera-trap days was sufficient time to detect tigers *Panthera tigris* at low population densities (0.4–0.7 per 100 km²). The area of suitable habitat for clouded leopards in Taiwan is c. 8,523 km². If there were only one tiger in this area the predicted camera-trapping effort to detect its presence would be c. 85,000 trap days. Given our camera-trapping effort of 128,394 camera-trap days without success, it is unlikely that clouded leopards still exist in Taiwan.

Carbone et al. (1999) suggested that carnivores weighing <21.5 kg feed mostly on prey that is ≤45% of their own weight. Adult Formosan macaques and Reeves's muntjacs have a mean weight of 9.5 kg, which is c. 41–86% of a clouded leopard's body weight (11–23 kg) and is approximately equal to the mean weight of confirmed prey of clouded leopards, based on scat analyses and field observations (Griffiths, 1993; Grassman et al., 2005). Formosan serow, which are similar in weight to clouded leopards, could also be an important prey species as clouded leopards have been observed feeding on goats cached in trees (Hazarika, 1996). Although clouded leopards are reportedly capable of killing sambar weighing 165 kg (Swinhoe, 1862; Kano, 1930; Nowell & Jackson, 1996), a skull analysis suggested that large prey need to be partially restrained for clouded leopards to deliver a powerful bite at the nape of the neck (Therrien, 2005). Eurasian lynx *Lynx lynx* regularly prey on reindeer *Rangifer tarandus* up to 4–8 times their body weight but the reindeer are generally those in poor body condition (Pedersen et al., 1999). We speculate that sambar preyed upon by clouded leopards are mostly

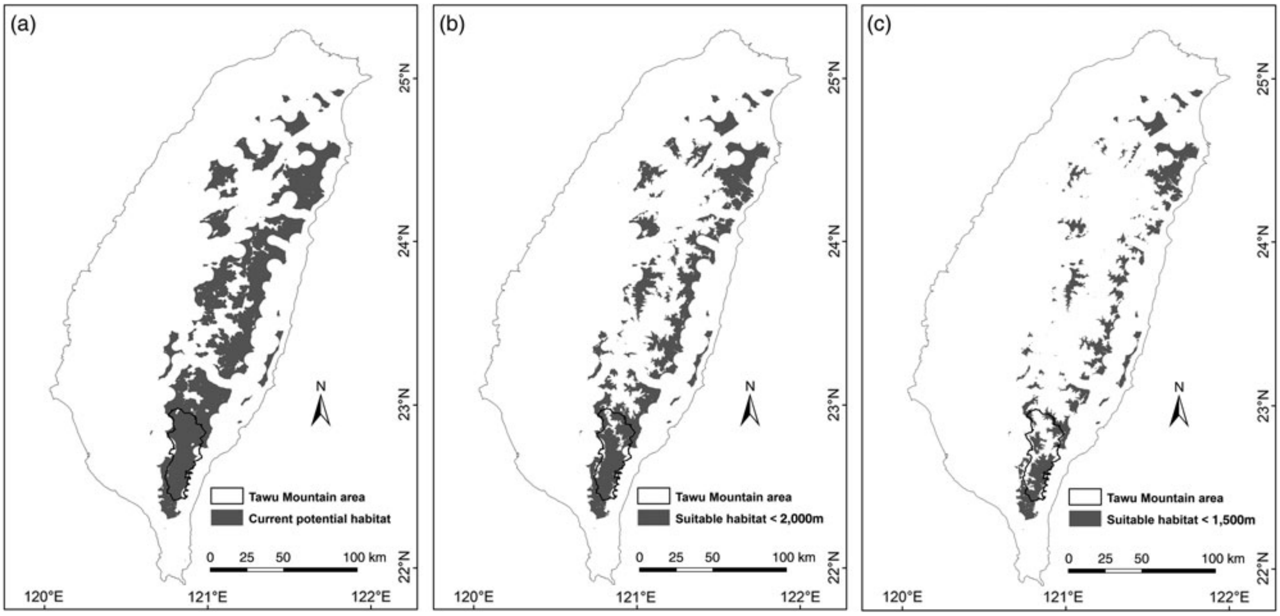

FIG. 2 (a) Distribution of suitable habitat for the clouded leopard *Neofelis nebulosa* in Taiwan, excluding areas close to roads and villages, (b) suitable habitat at < 2,000 m altitude, and (c) suitable habitat at < 1,500 m altitude.

smaller, weaker or younger individuals. Thus, the importance of sambar in terms of prey biomass index may be inflated. Wild pigs had low relative abundance indices and may be too aggressive to be targeted even by large felids such as leopards (Hayward et al., 2006).

Potential clouded leopard prey in Taiwan can be divided into two categories by weight (Table 1): ≥ 9 kg (macaques and ungulates) and ≤1 kg (birds and rodents). Chinese pangolin, arboreal flying squirrels and smaller carnivores are excluded because they had low relative abundance indices or there were no confirmed records of them being preyed upon by clouded leopards (Griffiths, 1993; Nowell & Jackson, 1996; Grassman et al., 2005). For prey in the ≤1 kg category only Swinhoe's pheasant weighs c. 1 kg; all the others weigh <0.4 kg. Their contributions to the total prey biomass index was, on average, <0.8% of that of the five largest prey species for all altitudes in the Tawu Mountain area. Clouded leopards may not spend much time travelling in rugged and steep terrain to search for prey <0.4 kg as this would not be optimal for maximizing their energy intake (Griffiths, 1980). Therefore, larger prey species, particularly macaques, muntjacs and serow, would be of greatest importance to the survival of clouded leopards in Taiwan.

However, these major prey species are targeted by hunters. The prey biomass index of hunted areas at altitudes of <2,000 m could be as low as that at the highest altitudes, where there is no hunting and clouded leopards would rarely occur. Therefore, hunting could reduce the prey base to an unfavourable level for clouded leopards. The five largest prey species, plus Chinese pangolins and flying squirrels, were hunted both extensively and intensively in the past for commercial purposes, and hunting was widespread before the Wildlife Conservation Act of 1989 was enforced. Prey depletion would have been a threat to the survival of clouded leopards in Taiwan over the past decades or even centuries (Karanth & Stith, 1999).

Three of the larger prey species (muntjacs, macaques and pangolins) were more abundant at lower altitudes. Sambar, serow and wild pig did not show altitudinal differences in abundance. However, as altitude increased, the three largest prey species (i.e. heavier than a clouded leopard) comprised a higher percentage of total available prey (Table 1). This may not be good for clouded leopards because these larger prey may be difficult to catch (Griffiths, 1980; Carbone et al., 1999). As the prey base showed a decreasing trend with altitude, we suggest that the primary habitat for clouded leopards is at lower altitudes, particularly <2,000 m. However, both clouded leopards and their major prey populations have suffered habitat loss and hunting pressure as a result of timber harvesting and human encroachment. Thus, habitat loss and prey depletion are the two main factors driving the extinction of the clouded leopard in Taiwan.

As a result of increasing awareness of the need for environmental protection, logging of natural forests in Taiwan was halted in 1991. Forests have been undergoing regeneration and succession, becoming suitable habitats for clouded leopards and their prey again. If habitat around areas of human encroachment could be better managed and/or restored to a less fragmented condition, the best-quality habitat for clouded leopard in Taiwan could cover c. 8,500 km^2 or more. Such an area could be inhabited by 500–600 clouded leopards, based on population density estimates from Thailand (> 6 per 100 km^2; Austin & Tewes, 1999), or up to 760 (9 per 100 km^2, 95% CI 8–17; Wilting et al., 2006), based on density estimates for the Sunda clouded leopard in Borneo. However, these are conservative estimates, because leopards would also utilize nearby areas in addition to the best-quality habitat assessed.

Populations of the clouded leopard's prey species are also recovering as a result of the ban on commercial hunting, and thus, given also the recovery and protection of habitat, the reintroduction of clouded leopards in Taiwan may potentially be considered. The Tawu Mountain area, where vegetation coverage and prey levels are suitable and human activities are limited, would be the ideal place for initiating the re-establishment of the clouded leopard in Taiwan. As genetic (Buckley-Beason et al., 2006; Wilting et al., 2011) and morphological research (Kitchener et al., 2006) did not identify clouded leopards in Taiwan as a distinct subspecies, animals from mainland Asia could be utilized for reintroduction. As wildlife conservation is a priority issue there, and considering the ongoing recovery of habitat and prey, Taiwan could become a global refuge for clouded leopards.

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References

Austin, S.C. & Tewes, M.E. (1999) Ecology of the clouded leopard in Khao Yai National Park, Thailand. *Cat News*, 31, 17–18.

Austin, S.C., Tewes, M.E., Grassman, Jr, L.I. & Silvy, N.J. (2007) Ecology and conservation of the leopard cat *Prionailurus bengalensis* and clouded leopard *Neofelis nebulosa* in Khao Yai National Park, Thailand. *Acta Zoologica Sinica*, 53, 1–14.

Azlan, J.M. & Lading, E. (2006) Camera trapping and conservation in Lambir Hills National Park, Sarawak. *Raffles Bulletin of Zoology*, 54, 469–475.

Azlan, J.M. & Sharma, D.S.K. (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. *Oryx*, 40, 1–6.

Buckley-Beason, V.A., Johnson, W.E., Nash, W.G., Stanyon, R., Menninger, J.C., Driscoll, C.A. et al. (2006) Molecular evidence for species-level distinctions in clouded leopards. *Current Biology*, 16, 2371–2376.

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

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. (1999) Energetic constraints on the diet of terrestrial carnivores. *Nature*, 402, 286–288.

Cheyne, S.M. & Macdonald, D.W. (2011) Wild felid diversity and activity patterns in Sabangau peat-swamp forest, Indonesian Borneo. *Oryx*, 45, 119–124.

Chiang, P.J., Pei, K.J.C., Vaughan, M.R. & Li, C.F. (2012) Niche relationships of carnivores in a subtropical primary forest in southern Taiwan. *Zoological Studies*, 51, 500–511.

CITES (2014) *Convention on International Trade in Endangered Species of Wild Fauna and Flora. Appendices I, II and III.* Http://cites.org/eng/app/appendices.php [accessed 7 November 2014].

Crooks, K.R. & Soule, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400, 563–566.

Emmons, L.H. (1987) Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology*, 20, 271–283.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. et al. (2011) Trophic downgrading of planet earth. *Science*, 333, 301–306.

Grassman, L.I., Tewes, M.E., Silvy, N.J. & Kreetiyutanont, K. (2005) Ecology of three sympatric felids in a mixed evergreen forest in north-central Thailand. *Journal of Mammalogy*, 86, 29–38.

Griffiths, D. (1980) Foraging costs and relative prey size. *American Naturalist*, 116, 743–752.

Griffiths, M. (1993) *Management of Large Mammals*. Unpublished report. WWF International, Gland, Switzerland.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. (2006) Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, 270, 298–313.

Hazarika, A.A. (1996) Goat predation by clouded leopard (*Neofelis nebulosa*) in Kakoi Reserve Forest of Assam. *Journal of the Bombay Natural History Society*, 93, 584–585.

Hwang, M.-H. & Chian, Y.Y. (2007) Monitoring larger mammals in the Nanzihshian logging road area, Yushan National Park, Taiwan. *Taiwan Journal of Forest Science*, 22, 135–147.

IUCN (2001) *IUCN Red List Categories and Criteria (version 3.1).* IUCN Species Survival Commission, IUCN, Gland, Switzerland.

Johnson, A., Vongkhamheng, C., Hedemark, M. & Saithongdam, T. (2006) Effects of human–carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. *Animal Conservation*, 9, 421–430.

Kano, T. (1930) The distribution and habit of mammals of Formosa (2). *Zoological Magazine*, 42, 165–173.

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* (eds J. Seidensticker, P. Jackson & S. Christie), pp. 100–113. Cambridge University Press, Cambridge, UK.

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

Kitchener, A.C., Beaumont, M.A. & Richardson, D. (2006) Geographical variation in the clouded leopard, *Neofelis nebulosa*, reveals two species. *Current Biology*, 16, 2377–2383.

Lee, L.L. & Lin, L.K. (1992) Status and research of mammals in Taiwan. In *The Biological Resources of Taiwan: A Status Report.*

Academia Sinica Monograph Series No. 11 (ed. C.I. Peng), pp. 245–267. Institute of Botany, Taiwan, and Academia Sinica, Taipei, Taiwan.

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. *Natural History Bulletin of the Siam Society*, 49, 61–75.

Mills, M.G.L., Broomhall, L.S. & du Toit, J.T. (2004) Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? *Wildlife Biology*, 10, 177–186.

Nowell, K. & Jackson, P. (1996) *Wild Cats: Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland.

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. *Animal Conservation*, 6, 131–139.

Pedersen, V.A., Linnell, J.D.C., Andersen, R., Andren, H., Linden, M. & Segerstrom, P. (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. *Wildlife Biology*, 5, 203–211.

R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rabinowitz, A. (1988) The clouded leopard in Taiwan. *Oryx*, 22, 46–47.

Rao, M.H., Myint, T., Zaw, T. & Htun, S. (2005) Hunting patterns in tropical forests adjoining the Hkakaborazi National Park, north Myanmar. *Oryx*, 39, 292–300.

Roelke, M.E., Martenson, J.S. & O'Brien, S.J. (1993) The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Current Biology*, 3, 340–350.

Rovero, F. & Marshall, A.R. (2009) Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, 46, 1011–1017.

Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008) Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45, 1228–1236.

Swinhoe, R. (1862) On the mammals of the island of Formosa. *Proceedings of the Zoological Society of London*, 23, 347–365.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G. et al. (2001) Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923–1926.

Therrien, F. (2005) Mandibular force profiles of extant carnivorans and implications for the feeding behaviour of extinct predators. *Journal of Zoology*, 267, 249–270.

Wang, Y. (2004) *Zone Planning and Wildlife Resource Monitoring at Danda Important Wildlife Habitat (II)*. Taiwan Forestry Bureau, Council of Agriculture, Executive Yuan, Taipei, Taiwan.

Wang, Y. (2008) *Alpine Ecosystem of Toroko National Park—Study on the Habitat Use of Sambar Deer (I)*. Toroko National Park, Hualien, Taiwan.

Wang, Y. & Hsu, Y.F. (2005) *A Survey on Formosan Black Bear and Other Wildlife in Beech Forest at Tunshan Area (II)*. Taiwan Forestry Bureau, Council of Agriculture, Executive Yuan, Taipei, Taiwan.

Wang, Y. & Huang, H.Y. (2005) *A Study on Wildlife Resource at Danda Important Wildlife Area (1/2)*. Taiwan Forestry Bureau, Council of Agriculture, Taipei, Taiwan.

Wilting, A., Christiansen, P., Kitchener, A.C., Kemp, Y.J.M., Ambu, L. & Fickel, J. (2011) Geographical variation in and evolutionary history of the Sunda clouded leopard (*Neofelis diardi*) (Mammalia: Carnivora: Felidae) with the description of a new subspecies from Borneo. *Molecular Phylogenetics and Evolution*, 58, 317–328.

Wilting, A., Fischer, F., Bakar, S.A. & Linsenmair, K.E. (2006) Clouded leopards, the secretive top-carnivore of South-East Asian rainforests: their distribution, status and conservation needs in Sabah, Malaysia. *BMC Ecology*, 6, 16.

Wilting, A., Mohamed, A., Ambu, L.N., Lagan, P., Mannan, S., Hofer, H. & Sollmann, R. (2012) Density of the Vulnerable Sunda clouded leopard *Neofelis diardi* in two commercial forest reserves in Sabah, Malaysian Borneo. *Oryx*, 46, 423–426.

Wu, H.Y., Wu, Y.H. & Wu, S.H. (2004) *Monitoring the Status of Large Mammals at the Eastern Area in Yushan National Park (2)*. Yushan National Park, Nantou, Taiwan.

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