Ecology and conservation of Formosan clouded leopard, its prey, and other sympatric carnivores in southern Taiwan

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Abstract

During 2000-2004 I studied the population status of the Formosan clouded leopard (*Neofelis nebulosa brachyurus*) and the ecology of its prey and other sympatric carnivores in the largest remaining lowland primary forest in southern Taiwan. My research team and I set up 232 hair snare stations and 377 camera trap sites at altitudes of 150-3,092m in the study area. No clouded leopards were photographed in total 13,354 camera trap days. Hair snares did not trap clouded leopard hairs, either. Assessment of the prey base and available habitat indicated that prey depletion and habitat loss, plus historical pelt trade, were likely the major causes of extinction of clouded leopards in Taiwan.

Using zero-inflated count models to analyze distribution and occurrence patterns of Formosan macaques (*Macaca cyclopis*) and 4 ungulates, we found habitat segregation among these 5 herbivore species. Formosan macaques, Reeve's muntjacs (*Muntiacus reevesi micrurus*), and Formosan serows (*Nemorhaedus swinhoei*) likely were the most important prey species of Formosan clouded leopards given their body size and high occurrence rates in lower altitudes. In contrast, sambar deer (*Cervus unicolor swinhoii*) tended to occur more frequently as altitude increased. Formosan macaques exhibited seasonal differences in occurrence rates and were absent at altitudes > 2,500m in winter.

Only Formosan serows showed preference for cliffs and rugged terrain, while the other 4 species, except wild boars (*Sus scrofa taivanus*), avoided these areas. Habitat segregation in forest understory and structure were more pronounced among the 4 ungulates. Forest structure rarely affected occurrence rates of Formosan macaques on the ground.

Niche relationships of the other sympatric carnivores were studied through habitat, diet, and temporal dimensions. Resource partitioning by carnivores was observed. Altitude was the strongest factor explaining the composition of the carnivore community in the local study-area scale and in the landscape scale across Taiwan. Carnivores could be divided into 2 groups: low-mid altitude consisting of Formosan ferret badgers (*Melogale moschata subaurantiaca*), gem-faced palm civets (*Paguma larvata taivana*), lesser oriental civets (*Viverricula indica taivana*), crab-eating mongooses (*Herpestes urva formosanus*), leopard cats (*Prionailurus bengalensis chinensis*), and feral cats (*Felis catus*), and the mid-high altitude group consisting of yellow-throated martens (*Martes flavigula chrysospila*), Siberian weasels (*Mustela sibirica taivana*), and Asiatic black bears (*Ursus thibetanus formosanus*). Carnivore richness was higher at mid altitudes where these 2 groups overlapped (i.e. mid-domain effect). The low-mid altitude carnivores were more nocturnal and tolerant of human activity and forest alteration except crab-eating mongooses, which were diurnal and avoided human encroachment. Similar to crab-eating mongooses, the mid-high altitude carnivores also avoided human encroachment and were diurnal except for Siberian weasels, which were more nocturnal. Diet summary based on their major food items for all sympatric carnivores revealed 3 groups of foragers which foraged on: invertebrates, small mammals, and plant fruits. Felidae, yellow-throated martens, and Siberian weasels preyed on small mammals. Asiatic black bears and gem-faced palm civets ate mostly plant fruits. The other 3 carnivores were mainly invertebrate foragers. These 9 carnivores partitioned resource uses in the 3 niche dimensions except for some overlap in resource use by leopard cats and feral cats.

Prey base for Formosan clouded leopards and the carnivore richness in Taiwan were found to be lower in areas with higher levels of human activity. On the other hand, Formosan macaques and ungulates could become over-abundant without human hunting and top carnivore predation. Mesopredator release may occur because of vanishing top carnivores, causing reduction of the lower trophic level prey species. It is important to assess the cascading impacts of the loss of the Formosan clouded leopards and Eurasian otters (*Lutra lutra chinensis*) and the declining Asiatic black bears and to consider reintroduction of Formosan clouded leopards, as well as active management of the other larger mammals. These results provided baseline information for reintroduction of clouded leopards and management of their prey and generated new hypotheses regarding the ecology of these large mammals for future investigation.

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Chapter 1: Background information, study area and general methods

Introduction

The clouded leopard (*Neofelis nebulosa*) is listed as vulnerable by the IUCN (Baillie et al. 1996), endangered in the U. S. Endangered Species Act (McMahan 1982, USFWS 1987) and is under Appendix I of CITES (Drollinger 1985). Clouded leopards are distributed in Southeast Asia (Guggisberg 1975, Nowell and Jackson 1996, Fig. 1.1). Having behavioral and body characteristics of both large cats and small cats (Guggisberg 1975, Gao 1987, Rabinowitz et al. 1987), they have intrigued many wildlife biologists. However, little is known about this species because of its elusiveness, arboreality, and forest habitat, making it a difficult cat species to study (A. Rabinowitz per. comm. in Santiapillai and Ashby 1988, Nowell and Jackson 1996). Most information about clouded leopards is anecdotal and comes from local interviews and surveys, casual sightings, and captive individuals (Nowell and Jackson 1996). Until recently there were only 2 radio telemetry studies on clouded leopards, both in Thailand (Austin 2002, Grassman et al. 2005b).

The Formosan clouded leopard (*N. n. brachyurus*) is a subspecies of clouded leopards and occurs only in Taiwan (Ellerman and Morrison-Scott 1951, Guggisberg 1975). It is listed as endangered under the "Wildlife Conservation Law" in Taiwan (Council of Agriculture, COA, 1989). Information about the Formosan clouded leopard is less than for the other subspecies and comes primarily from interviews with native Taiwanese tribesmen (Kano 1929;1930, McCullough 1974, Rabinowitz 1988). Rabinowitz (1988) interviewed 70 indigenous hunters in 1986 and reported that the latest confirmed record of a clouded leopard in Taiwan was from the Tawu Mountain area in

1983. Because there are no recent officially substantiated records by biologists, some suspect that it may be virtually extinct now. However, this speculation may be inappropriate since no field survey on clouded leopards in Taiwan has ever been conducted. Some suspected pugmark records have been reported in recent years (Lue et al. 1992, Wang et al. 1996), and some captures and sightings of clouded leopards by aborigines (indigenous peoples in Taiwan) were reported as late as 2005 (Liu and ChangChien 2004, Wang and Huang 2005, personal unpublished interview data) in Taiwan. Wang et al. (1995) also reported discovery of a pelt of a young clouded leopard in eastern Taiwan in 1989-1990. But, none of these records could be substantiated. The Formosan clouded leopard may still exist, but the current population status is unknown, controversial, and in need of field investigation to obtain more affirmative and persuasive evidence.

Cross-island roads and human encroachment have fragmented and isolated the suitable habitats of clouded leopards in Taiwan (see chapter 2). This may divide the existing clouded leopard population into several smaller isolated populations, which likely would make them susceptible to inbreeding depression (Soule 1980, Roelke et al. 1993, Lacy 1997). Moreover, demographic reduction and subsequent depletion of genetic variation has been observed in many studies (Gilbert et al. 1991, Hoelzel et al. 1993, Roelke et al. 1993, Corbet et al. 1994, Hartl and Pucek 1994) and is known to be detrimental to endangered species (Lande and Barrowclough 1987, O'Brien 1994b;a, Frankham 1995). Therefore, it is urgently important to determine whether any small populations of clouded leopards still exist in Taiwan before they go extinct.

Rabinowitz (1988) concluded that the Tawu Mountain area is where clouded leopards are most likely to occur. In 1988, the Tawu Mountain area was established as a nature reserve to preserve the largest remaining low-to-mid-elevation primary forests in Taiwan. Taiwan has 23 million people living within 36,000km^2 (634 people/ km^2). Most of the low-to-mid-elevation primary forests have been encroached upon by humans, timber-harvested, or converted to agricultural lands. Thus, Tawu Mountain Nature Reserve is a particularly valuable reserve to Taiwan. The reserve covers an elevation range from 130m to 3,097m within 470 km^2. Various evergreen forest types occur along the altitude gradient within a small area. Moreover, Taiwan is located between 2 zoogeographic regions so that species from both Oriental and tropical Philippines occur simultaneously in the reserve (Kuroda 1952, Liu and Lio 1981, Chen 1995). Finally, Tawu Mountain Nature Reserve preserves many different habitat types and diverse species, which may rival or equal tropical rainforests of a similar size. However, prior to being designated a nature reserve, a cross-island freeway construction was proposed to cut through the heart of Tawu Mountain Nature Reserve. Although the plan is postponed due to the conflict of crossing a nature reserve, which prohibits any construction plan, it has not been canceled. The highway plan would fragment the habitat in half making the current situation even worse. Constructing a road in such rugged and steep terrain likely would cause landslides, which ultimately would result in forest destruction. In addition, the convenient access brought by the road would allow people to easily convert forests to agricultural lands, settle there, and introduce poaching on many prey species of clouded leopards. Such events have occurred along all the other existing cross-island freeways and more than likely will occur again along any new road. This is of great concern to the conservation of Formosan clouded leopards and preserving the biodiversity of Tawu Mountain Nature Reserve.

The Formosan clouded leopard was the largest true carnivore in Taiwan and its prey was heavily hunted before and even after the hunting ban in 1973 (Wang and Lin 1986;1987). Habitat degradation, urbanization and poaching also may have decreased the prey base of clouded leopards in Taiwan. Karanth and Stith (1999) suggested that prey depletion is an overlooked factor which drives the current decline of wild tigers in addition to poaching and habitat loss and "…sustaining small but productive tiger populations depends primarily on maintaining high prey densities." Similarly, many other studies concluded that prey distribution and abundance, at least in part, is associated with the densities and home range sizes of larger wild felids (Muckenhirn and Eisenberg 1973, Seidensticker 1976, Sunquist 1981, Emmons 1987, Crawshaw and Quigley 1991, Karanth and Sunquist 1995, Baillie et al. 1996, Miquelle et al. 1996, Karanth and Nichols 1998, Karanth et al. 2004, Kawanishi and Sunquist 2004). Thus, it will also be important to understand the current population status and ecology of the prey species for the conservation of clouded leopards in Taiwan. Rabinowitz (1988) recommended that "Detailed forest surveys to look for more conclusive evidence of the clouded leopard, and to assess the status of other large species and their remaining habitat, should be carried out in the Tawu Mountain area…" However, there has not been any management/monitoring effort or wildlife research to investigate the clouded leopard, its prey and other sympatric carnivores in Tawu Mountain Nature Reserve since its establishment. Large mammal research is very rare in other areas of Taiwan, too. Baseline information for large mammals regarding their ecology, habitat use and distribution is especially lacking, making conservation and management of these large mammals (e.g., sambar deer *Cervus unicolor*, Formosan serow *Nemorhaedus swinhoei*, clouded leopard, yellow-throated marten *Martes flavigula*, etc.) ineffective.

Conservation of large carnivores is an important issue. Carnivores, which depend on a higher proportion of meat, tend to have larger home ranges than insectivores and frugivores (Gittleman and Harvey 1982), and large carnivores often occupy more extensive home ranges. Conducting studies on umbrella species, such as the Formosan clouded leopard, may benefit other smaller sympatric species because conservation of large carnivores usually involves preserving greater areas (Noss 1990, Launer and Murphy 1994, Gittleman et al. 2001). Effective conservation and management plans of large carnivores also require information on the population status, movement pattern, diet, habitat requirement, as well as population status and ecology of prey species. Extensive variation in the ecology of large felids has been documented in many studies; therefore, site-specific information is required for effective conservation efforts. This project investigated the current status of Formosan clouded leopards and collected baseline information on its prey and other sympatric carnivores for their conservation and management in the Tawu Mountain Nature Reserve and other areas in Taiwan. Given that the altitude range covers almost 3/4 of Taiwan's whole altitude range and diverse pristine forest types exist in the study area, this will be the first and most thorough research conducted on the ecology and conservation of larger mammals in Taiwan.

Literature Review on the Clouded Leopard

Distribution, subspecies recognition, and population status

The clouded leopard ranges from the south-eastern Himalayas, southern China, and Taiwan, to Peninsular Malaysia, Sumatra, and Borneo (Fig. 1.1, Swinhoe 1862, Guggisberg 1975, Nowell and Jackson 1996, Sunquist and Sunquist 2002). Originally, the clouded leopard was classified as the single member of the genus *Neofelis* (Ewer 1973) and consisted of 4 subspecies (Nowell and Jackson 1996). However, the latest genetic and morphometric research suggested that the subspecies *N. n. diardi* in Sumatra and Borneo should be classified as a distinct species (i.e. *N. diardi*) because of distinct haplotypes (Buckley-Beason et al. 2006), smaller cloud markings, more cloud spots, and greyer fur (Kitchener et al. 2006). But, little is known about the ecological differences between these two clouded leopard species except genetic and morphological differences. For simplicity, I still refer to them as "clouded leopards" in general.

The Formosan clouded leopard (*Neofelis nebulosa brachyurus*) was first introduced to scientists by Swinhoe and was described as a distinct species, *Leopardus brachyurus*, based on a shorter tail length (Swinhoe 1862). But, Swinhoe (1870) revised it to an insular race of the continental clouded leopards after acquiring more specimens. Horikawa (1930) and Pocock (1939) maintained that tail length is not a consistent criterion. Kuroda (1938;1940) even suggested that it is unnecessary to classify the Formosan clouded leopard as a distinct subspecies. Using clouded leopard samples from the National Taiwan Museum (7 specimen, but DNA was successfully extracted from only 1 sample), the latest genetic analysis showed that Taiwan clouded leopards diverged from the other mainland subspecies in haplotypes, but not to the level of a distinct species (Buckley-Beason et al. 2006).

Although clouded leopards are widespread in Southeast Asia, they are nowhere abundant, and usually exist in relatively low population densities (Rabinowitz et al. 1987). In Taiwan, there are only sighting and capture reports from indigenous tribesmen (Kano 1929;1930, Rabinowitz 1988). Kano (1929) conducted biological surveys throughout Taiwan and suggested that clouded leopards are more abundant in eastern and southern Taiwan based on interviews with indigenous tribesmen. This agrees with the fact that jackets made from clouded leopard pelts occur only in southern tribes (per. obs.).

Rabinowitz (1988) interviewed indigenous hunters and reported that the latest capture record was in 1983. No field survey had been conducted on clouded leopards in Taiwan before this study. Only pugmarks, sightings, and captures by indigenous hunters are reported sporadically (Lue et al. 1992, Wang et al. 1996, Liu and ChangChien 2004, Wang and Huang 2005).

Body characteristics

Although belonging to Pantherinae, the clouded leopard is in fact a medium-sized cat, weighing between 11-23 kg (Pocock 1939, Banks 1949, Prater 1965, Lekagul et al. 1977, Nowell and Jackson 1996). It has distinctive large dark, cloud-shape markings, a tail typically as long as its head-body length (up to 80-90 cm: Pocock 1939, Lekagul et al. 1977, Metha and Dhewaju 1990), and relatively the longest canines of any felid relative to skull size (3.8-4.5cm: Guggisberg 1975) reminiscent of the saber-toothed tiger (Sterndale 1884). Although the skull of the clouded leopard does not reach pantherine size, it has attained pantherine cranial proportions (especially large teeth) (Werdelin 1983). The clouded leopard has not only body, but also behavioral characteristics that fall between those of large and small cats (Guggisberg 1975, Gao 1987, Rabinowitz et al. 1987). Like a small cat species, it purrs, and cannot roar; its method of eating food, grooming, and its body postures, however, are closer to those of the larger species of cats (Gao 1987, Mellen 1991).

Home range and movement patterns

Recently, researchers placed radio collars on a few free-ranging clouded leopards in Thailand, the first ever to be radio tracked (Austin 2002, Grassman et al. 2005b).

Austin (2002) tracked 2 adult clouded leopards and reported that they occupied similarly large home ranges (39.5km^2 for 1 female and 42.2km^2 for 1 male, 95% fixed kernel). Grassman et al.'s (2005b) results also showed no obvious differences of home range size (95% fixed kernel) between 2 adult males (35.5 and 43.5 km^2) and 2 adult females (33.6 and 39.7 km^2) in another area in Thailand.

Although there is a positive correlation between home range size (HRS) and body size (Harestad and Bunnell 1979, Gittleman and Harvey 1982, Mace et al. 1983), the HRS reported for clouded leopards in Thailand (Austin 2002, Grassman et al. 2005b) are larger than male leopard (*Panthera pardus*) home ranges (18 km^2) reported elsewhere in Thailand (Austin and Tewes 1999). However, large variation of HRS has been observed in many wild cat species. HRS for bobcats (*Lynx rufus*), which are slightly smaller than the clouded leopard, range from <4 km^2 in Alabama (Miller 1980) to 9-108 km^2 in Idaho (Bailey 1974), while the home ranges of ocelots (*Leopardus pardalis*) can be 0.8 km^2 in Brazil (Schaller 1984), 8.1 km^2 in Peru (Emmons 1988) to as high as 21 to 33 km^2 for ocelots in Belize (Dillon 2005). A similar 10-fold variation or more also has been reported for felids larger than the clouded leopard. Jaguars (*P. onca*) have HRS between 10 and 168.4 km^2 (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991). Leopards' HRS also vary from 8-10 km^2 to 100 km^2 (Schaller 1967, Muckenhirn and Eisenberg 1973, Seidensticker 1976, Bertram 1982, Rabinowitz 1989, Bailey 1993, Mizutani and Jewell 1998) and can be as large as several hundreds of square km (reviewed in Mizutani and Jewell 1998). Greater variation occurs in Mountain lions (*Puma concolor*) and tigers (*P. tigris*). Mountain lion HRS range from 55 km^2 to 1,454 km^2 (Hemmer 1968, Spreadbury et al. 1996). HRS for tigers, the largest wild cats of the world, may be as small as 16-17 km^2 for females in Nepal (Sunquist 1981) to as large as 1,000 km^2 in Siberia (Matjushkin et al. 1977). Many of these studies have concluded that prey distribution and abundance, at least in part, is associated with home range size and dynamics (Muckenhirn and Eisenberg 1973, Bailey 1974, Seidensticker 1976, Sunquist 1981, Emmons 1988, Crawshaw and Quigley 1991, Mizutani and Jewell 1998).

Austin (2002) tracked 2 radio-collared clouded leopards and reported that the female had a mean daily movement distance of 976.8m; the male had a mean daily movement distance of 1,167.6m, while Grassman et al. (2005b) reported an average 1,932m for 4 radio-tracked clouded leopards (range 122-7,724m). These are based on straight line measurements and the distance moved could be higher when animals meandered between sampling locations.

No dispersal data about clouded leopards are available. One subadult male clouded leopard was caught by local villagers in Nepal . It was radio-collared and translocated 100 km east of the original capture site. The first 8 days of tracking indicated only terrestrial behavior and occupancy of an area less than 1 km^2. It then moved west toward where it was originally captured. However, it was radio tracked for only 10 days (Dinerstein and Mehta 1989).

Arboreal behavior

The clouded leopard has arboreal talents which rival those of the margay (*Leopardus wiedi*) of South America (Nowell and Jackson 1996). Its relatively short, but powerful legs, large feet, and long tail are adaptations for arboreal life, giving the animal a low center of gravity and a good grip on tree branches (Gonyea 1976, Lekagul et al. 1977, Gonyea 1978, Taylor 1989, Griffiths 1993). In captivity, it has been observed to climb about on horizontal branches with its back to the ground, and hang upside down from branches by its hind feet (Hemmer 1968). Such behavior has been related to the hunting method of the clouded leopard by which it hangs over tree branches and jumps down upon passing prey (Lekagul et al. 1977). It also has been seen to run down tree trunks headfirst in captivity (Hemmer 1968), and once in the wild was observed to be hunting among a troop of pigtail macaques (*Macaca nemestrina*) (Davies 1990).

Because of its arboreal talents, most literature describes the clouded leopard as mainly arboreal based on local surveys and captive observation (Rafles 1821, Tickell 1843, Renshaw 1905, Banks 1931, Prater 1965, Lekagul et al. 1977, Payne et al. 1985, Humphrey and Bain 1990, Choudhury 1993;1997). Selous and Banks (1935), however, speculated that clouded leopards are more terrestrial in Borneo based on their experiences in baying clouded leopards on the ground with dogs twice and snaring some in secondary growth where no climbing is possible. In addition, clouded leopards have been documented to travel on the ground in selectively logged forest (Payne et al. 1985, Rabinowitz et al. 1987, Santiapillai and Ashby 1988) or in primary forests (Rabinowitz et al. 1987). Radio telemetry also suggested that clouded leopards may travel on the ground more often than in the trees (Dinerstein and Mehta 1989, Austin and Tewes 1999). Austin and Tewes (1999) contended that it could be difficult for clouded leopards to travel long distances through the trees. Grassman et al. (2005b) also suggested that clouded leopards traveled on the ground more than reported in the literature. However, comparing the ratio of the sighting records in trees, clouded leopards in Taiwan use trees more often (54%, Rabinowitz 1988) than in Malaysian Borneo (18%, Rabinowitz et al. 1987). The clouded leopard is likely not strictly arboreal and uses trees as resting and hunting sites (Guggisberg 1975, Rabinowitz et al. 1987, Davies 1990, Lloyd et al. 2006); variations may occur in different habitats or regions.

Activity pattern

Most accounts describe the clouded leopard as nocturnal due to rare observation (Swinhoe 1862, Renshaw 1905, Pocock 1939, Lekagul et al. 1977, Payne et al. 1985, Humphrey and Bain 1990, Choudhury 1993, Kanchanasakha et al. 1998). Since clouded leopards were sometimes seen traveling or hunting during daytime (Selous and Banks 1935, Banks 1949, Gibson-Hill 1950, Payne et al. 1985, Rabinowitz et al. 1987, Davies 1990), the clouded leopard may not be as strictly nocturnal as previously assumed. Radio telemetry studies in Thailand showed that clouded leopards have arrhythmic activity patterns (Austin 2002, Grassman et al. 2005b) with slightly higher activity near crepuscular hours. The camera trap study in Peninsular Malaysia also demonstrated similar results, but with a higher level of nocturnal activity (75%, Azlan and Sharma 2006). Since camera trapping takes photos while animals are traveling and radio telemetry studies usually associate movement with radio signal variations, results from the camera trapping study suggests that clouded leopards may travel on the ground more at night. Curio (1976) proposed that predators track the activity periods of their prey. Emmons (1987) studied the feeding ecology of ocelots, jaguars and pumas in southeastern Peru and concluded that the activity patterns of these felid predators are related to those of their prey. This also agrees with the idea that clouded leopards take both diurnal and nocturnal prey.

Food habits

Like many other big cats, clouded leopards consume a variety of animals, including birds, mammals, and sometimes fish, snakes and domestic animals (Jerdon 1874, Guggisberg 1975, Lekagul et al. 1977, Rabinowitz et al. 1987, Nowell and Jackson 1996, Grassman et al. 2005b). Although Grassman et al. (2005b) reported small mammals such as the Indochinese ground squirrel (*Menetes berdmorei*) and Muridae species in the diet, the stocky build, large canines and the large post canine space make the clouded leopard capable of killing relatively large prey (Pocock 1939, Lekagul et al. 1977, Therrien 2005a), which includes pangolin (*Manis* species), porcupines (Hystricidae), various deer species, wild boars (*Sus scrofa*), loris (*Nycticebus coucang*), macaques (*Macaca* species), orangutans (*Pongo pygmaeus* or *P. abelii*), goats and cattle (Banks 1931, Gibson-Hill 1950, Prater 1965, Guggisberg 1975, Payne et al. 1985, Rabinowitz et al. 1987, Davies 1990, Griffiths 1993, Hazarika 1996, Nowell and Jackson 1996, Grassman et al. 2005b). These data are based on interviews with tribesmen, finding kills, direct observation and fecal analysis. In Taiwan, however, only information from interviews with indigenous tribesmen is available. Reported prey consists of poultry, Formosan macaque (*Macaca cyclopis*), Reeve's muntjac (*Muntiacus reevesi micrurus*), Formosan serow (*Naemorhedus swinhoei*), sambar deer (*Cervus unicolor swinhoei*), and wild boars (*Sus scrofa taivanus*) (Swinhoe 1862, Kano 1930, McCullough 1974). Based on accounts in other countries, potential prey of clouded leopards in Taiwan could also include Swinhoe's pheasant (*Lopura swinhoii*), Chinese pangolins (*Manis pentadactyla*), squirrels and other smaller mammals and birds as well. Kano (1930) reported that clouded leopards like to eat macaques. This primate food preference agrees with other local surveys (Santiapillai and Ashby 1988, Choudhury 1997), sighting accounts (Banks 1931, Gibson-Hill 1950, Davies 1990, Nowell and Jackson 1996) and fecal analysis of which 4 out of 7 scats were primates (Griffiths 1993). That the prey consists of both terrestrial and arboreal species suggests that the clouded leopard could hunt both on the ground and in trees where it lies in ambush (Banks 1949, Lekagul et al. 1977, Davies 1990, Nowell and Jackson 1996). It is said that the clouded leopard will return to unfinished kills (Kano 1930, Selous and Banks 1935, Lekagul et al. 1977). Hazarika (1996) discovered a dead domestic goat cached on a tree branch 4m above the ground and saw a clouded leopard return to the kill the next day.

Habitat use

Although early literature indicates that clouded leopards occur in dense primary forests (Tickell 1843, Renshaw 1905, Pocock 1939, Prater 1965), recent available information based on limited observations or tracks shows that the clouded leopard is versatile and could occur in many different habitats, including grassland (Dinerstein and Mehta 1989), mangrove or coastal swamp (Gibson-Hill 1950, Payne et al. 1985), secondary or selectively logged forests (Banks 1931;1949, Rabinowitz et al. 1987, Choudhury 1997), evergreen rain forests (Rabinowitz et al. 1987, Rabinowitz 1988, Choudhury 1997) and coniferous forests (Rabinowitz 1988). However, these accounts are based on local interviews and some hunting, pugmark and direct observation records. Radio telemetry studies in Thailand showed variations in forest use comparing close primary forest and more open secondary forest-grassland habitat (Austin 2002, Grassman et al. 2005b). Three of the 6 clouded leopards tracked used vegetation types proportionally and 2 preferred closed primary forest. One occurred more in the open forest-grassland, which led Grassman et al. (2005b) to suggest that this particular clouded leopard used edges as hunting sites. Their results provided support for the generally held belief that clouded leopards occur in primary evergreen forest (Nowell and Jackson 1996, Sunquist and Sunquist 2002). Clouded leopards occur most often in lowlands (Renshaw 1905, Pocock 1939, Rabinowitz et al. 1987, Rabinowitz 1988, Davies 1990, Choudhury 1993;1997), but, they could occur as high as 2,585m in northeastern India (Choudhury 1997) and maybe up to 3,000m (Jerdon 1874, Rabinowitz 1988). However, occurrences of clouded leopards at these higher altitudes were extremely rare in the literature and were mostly indirect records based on interviews except a sighting by biologists at altitude 2,157m in northeastern India (Ghose 2002).

Population genetics

Heterozygosity within clouded leopards has been examined in a population of 20 captive animals from U.S. zoos using allozymes only. The percent average heterozygosity (H) of clouded leopards was 2.3 (Wang et al. 1995), which is similar to 2.3 for free ranging lions (*Panthera leo*) in Kruger National Park (Newman et al. 1985, O'Brien et al. 1987, Miththapala et al. 1991). However, the clouded leopard had the fewest number of allozyme polymorphisms compared to 9 other felid species, with only the cheetah (*Acinonyx jubatus*), a known bottleneck species (O'Brien and Johnson 2005), showing less heterozygosity (Newman et al. 1985, Wang et al. 1995).

Larger mammals in Taiwan

There are nearly 80 species of wild terrestrial mammals documented in Taiwan so far. Although new species, especially small mammals, are still being discovered or reclassified, larger terrestrial mammals (excluding Chiroptera, Insectivora and Muridae of Rodentia) in Taiwan currently consist of 1 primate, 5 ungulates, 11 carnivores, 6 Sciuridae (3 tree squirrel species and 3 flying squirrel species), 1 Leporidae (hare), and 1

Manidae (pangolin) (Table 1.1). Among these 25 species, primates, ungulates, tree squirrels, and pangolin could be considered potential major mammalian prey of the Formosan clouded leopard based on the literature and their size and ecology, although clouded leopards may opportunistically prey upon flying squirrels and other smaller carnivores. The other 10 carnivores are considered to be sympatric to the Formosan clouded leopard.

The Eurasian otter (*Lutra lutra chinensis*) has not been officially found in the wild in Taiwan for nearly 20 years and might be extinct (Lin 2000). The Taiwan high mountain least weasel (*Mustela formosana*) is a newly discovered species and few locations have been documented for its occurrence (Lin 2000). The Formosan sika deer (*Cervus nippon taiouanus*) became extinct in the wild in 1969 due to commercial hunting for its pelt and loss of lowland habitats by agricultural land expansion (Lee and Lin 1992). The Formosan hare (*Lepus sinensis formosus*) is not a forest species and is distributed only in small parts of the study area near the boundary close to aborigines' agricultural lands. It is mostly allopatric to Formosan clouded leopards and is unlikely to be a potential prey. Since no systematic field data were obtained on these 4 species and only data of direct observations of the 3 flying squirrel species were available throughout this study, these 7 species will not be discussed in this dissertation.

McCullough's survey in 1973 (McCullough 1974) could be considered the first scientific field survey of larger mammals in Taiwan after World War II, which ended Japanese's rule in Taiwan. McCullough's results had found the endangered situations of Formosan clouded leopards and sika deer. He also suggested that Chinese pangolins, Asiatic black bears (*Ursus thibetanus formosanus*), Eurasian otters, lesser oriental civets (*Viverricula indica taivana*), leopard cats (*Prionailurus bengalensis chinensis*), Formosan hares, sambar deer and yellow-throated martens (*Martes flavigula chrysospila*) need complete protection. Many other larger mammals also were threatened by heavy commercial hunting pressure and habitat loss and needed active management for a sustainable yield.

Hunting was banned in 1973. In 1989, the new Wildlife Conservation Law replaced the previous Hunting Law. Wildlife seemed to be recovering to some degree and the government began to support more wildlife surveys and research. However, in the beginning most of these were simply basic distribution surveys and obtained only presence/absence or species inventory data in some protected areas. Although more and more in depth research has been conducted for various wildlife species thereafter, research on larger mammals has been getting more attention only in the past decade. Nevertheless, research on larger mammals related to habitat selection, distribution patterns, population ecology or other conservation and management issues is still rare (Lee and Lin 1992, Lin 2000). For some species, e.g. Formosan clouded leopards, leopard cats, yellow-throated martens, lesser oriental civets, Eurasian otters, Asiatic black bears, Chinese pangolins, Formosan serows and sambar deer, scientific research is extremely rare or non existent. Data for the management and conservation of larger mammals are generally lacking (Lee and Lin 1992).

Study Area

The study area consists of two adjacent protected areas in southern Taiwan, i.e. Tawu Mountain Nature Reserve (TMNR, 48,000 ha) and Twin-ghost Lake Important Wildlife Area (TGLIWA, 45,000 ha) (Fig. 1.2). TMNR preserves the largest lowland primary forest remaining in Taiwan. Over 55 percent of the forest is below 1,200m.

Since the clouded leopard prefers lowland and the last confirmed record of Formosan clouded leopard occurred here (Rabinowitz 1988), TMNR was chosen as the major study area.

Tawu Mountain Nature Reserve is located in southeastern Taiwan, between 22°50’ – 22°25’ N latitude and 120°43’ – 120°57’ E longitude. It encompasses 5 watersheds, which support water use of towns to the east of the reserve. The altitude ranges from 130 m to 3,100 m, making the reserve consist of various vegetations including tropical and subtropical rainforests in the lowland, followed by temperate rainforests including mixed broad-leaved and conifer forests and temperate coniferous forests at higher elevations. Four major vegetation zones occur along altitude gradients (Su 1984) from altitude 150m to 3,100m. At the mountain foothill (<500m) is the tropical *Ficus-Machilus* forest zone, which is dominated by Lauraceae and Moraceae. In the low altitude (500-1,500m) is the subtropical *Machilus-Castanopsis* forest zone comprised of Lauraceae and Fagaceae. In the middle altitude (1,500-2,500m) is the temperate *Quercus* forest zone consisting of acer species, oaks and conifers like the Formosan red cypress (*Chamaecyparis formosensis*), which is similar to the redwood (*Sequoia* sp.) along the Pacific coast of North America, and Taiwan hemlock (*Tsuga chinensis* var. *formosana*). Within this vegetation zone, the physiognomy gradually turns into a mixture of hardwood and softwood at altitude around 2,000m, i.e. mixed broad-leaved and coniferous forests. The cool-temperate *Tsuga* forest zone at the highest altitude (2,500m-3,100m) within the study area is dominated by Taiwan hemlock and sometimes mixed with a few Taiwan armand pine (*Pinus armandii* var. *mastersiana*) and Taiwan spruce (*Picea morrisonicola*). All the forests are evergreen. However, the change of vegetation zones is gradual and the boundary of different zones is difficult to define clearly. In addition to the above 4 major vegetation types, Rhododendron (*Rhododendron formosanum*) forests occur sporadically along rides or in steep terrain at altitudes 1,000m-2,500m. The altitude ranges of different vegetation zones were based on studies around central Taiwan and may shift a little in the study area. Moreover, the Wallace line passes the southeast part of the reserve so that floral species from both Mainland Asia and tropical Philippines occur simultaneously within the reserve (Liu and Lio 1981, Chen 1995), which may make the tree species composition slightly different from central Taiwan.

There were no weather stations within the study area, but average precipitation and temperature were collected at the nearest weather station in the same climate zone at seashore (altitude 8m, approximate 30 km south-southeast of the study area) from 2001 to 2004 (Fig. 1.3). Because of the large altitude range (130m to 3,092m), temperature varies along altitudinal gradients. The average temperature ranges from 21°C at 500m to 7.5°C at 3,000m, as recorded in southern Taiwan. Since the altitude of the weather station was only 8m and temperature generally decreases as altitude increases (approximate 6.5°C per 1,000m), temperature at the highest altitude could drop below freezing 0°C during winter time. As typhoon and monsoon prevailing winds hit the mountain slopes causing more rainfall, the precipitation within the study area is usually higher than recorded at the seashore. The average annual precipitation is 4,400-4,800 mm within the study area. The dry season from October to April has a low average precipitation of 51 mm/month and a cooler average temperature 22.7°C; while the wet season from May to September has a higher average 340mm/month of rainfall and a hotter average temperature 27.7°C. Although the winter and spring months are drier, the forests are still evergreen throughout the whole reserve. Depending on altitude, slope, and other terrain factors, the precipitation may be more or less than the nearest Tawu weather station.

Although TMNR consists of diverse habitats, less than 10% of the reserve (< 4,500 ha) is above 1,900m. To increase sampling of habitats above 1,900m, we expanded our study area to include TGLIWA, which has 12,600 ha of forests above 1,900m. In addition, the mid-altitude of TGLIWA comprises several mountain lakes and herbivores are relatively more abundant there because of edges and gentler terrain. Moreover, areas above 1,900m in TMNR are usually steep and rugged. Some of the gentler mid-altitude terrain in TGLIWA complement the sampling of diverse habitat types for further habitat study. The vegetation types and climate of TGLIWA were basically similar to those of TMNR. But, altitudes1,900m-2,500m in TGLIWA consists of more giant coniferous trees such as Formosan red cypress and Taiwania (*Taiwania cryptomerioides*) than TMNR. TGLIWA is adjacent to TMNR to the north and the two protected areas could be considered a single unit (Fig. 1.2).

There are few logging roads within the study area and no research facilities. Backpacking on foot was the only way to access the study area. Because of the remoteness and ruggedness, researchers carried equipment and food on their own and spent weeks to venture into the depth of the forests to conduct research. Human disturbance is minimal within the study area except the southern and eastern parts near the boundary of TMNR and southwestern parts of TGLIWA, which are more accessible from nearby aboriginal villages. Despite hunting being illegal, poaching is still practiced in these more accessible areas. To avoid the influence of human disturbance on data collection, 4 survey zones (Table 1.2, Fig. 1.2) were chosen in the central and more remote parts of TMNR and TGLIWA, making it more time-consuming to collect data. These areas, with barely any hunting, were likely to have more abundant prey and thus might be more likely to have clouded leopards. Taimali watershed (survey zone 1) is the largest watershed of TMNR, and Chiben watershed (survey zone 2) is the second largest. Survey zones 3 and 4, Big Ghost Lake and Wahshan God Pond in the TGLIWA, were included to supplement habitats in the mid-to-high altitude range. These 4 survey zones cover an altitude range from 200m to 3,092m and have little to no human disturbance. Therefore, they host abundant prey and include all the vegetation types within the study area. Thus, habitat use and distribution patterns could be studied for all the other sympatric larger mammals, including clouded leopards' prey, under natural conditions. For the purpose of understanding the influence of hunting and to cover wider areas to search for clouded leopards, Jinlun watershed and Danan watershed (survey zones 5 and 6) of TMNR, which has persistent hunting pressure, were chosen for comparison with undisturbed areas. Hunting is banned except for indigenous ceremonial use. Therefore, poaching activity could be easily identified by observing hunters' traps, trails, and camps during field work. All camera trap sites in zones 5 and 6 were classified as hunted areas. Three other camera trap sites not in zones 5 and 6 with hunting activity observed nearby were also regarded as hunted areas.

More details about TMNR and TGLIWA can be found in Wang et al. (1987;1988), Rabinowitz and Lee (1990), Lu (1991), Ou (1994) and Yeh (1997).

General Methods

Camera trapping was the major method used to document the occurrence of the Formosan clouded leopard and to study the ecology (e.g. relative abundance, spatial distribution, species diversity, activity patterns, habitat use, and distribution patterns) of its prey and other sympatric carnivores. In addition, hair snares were utilized to search for clouded leopards and leopard cats. Direct observations of tracks and signs, and sporadic interviews of aborigines were used as auxiliaries.

Hair snares

Hair snaring targeted clouded leopards. The method of hair snaring basically followed the protocol of McDaniel et al. (2000) with some modifications. Each hair snare station was set up along animal trails. Two 10cm x 10cm Velcro pads were nailed onto the trunk of a suitable size tree at heights of 30cm and 50cm respectively. Catnip imitation oil and dried catnip leaves were spread over the surfaces of Velcro pads. Cotton balls soaked with catnip imitation oil were put behind the Velcro pads and also were hung at 2m high to increase the lures effective distance. An aluminum pan also was hung with the cotton balls as a visual lure. This protocol was tested in two clouded leopard enclosures at Taipei Zoo and it successfully snagged hairs from the captive clouded leopards in one night. Three to 5 hair snare stations, each separated 100m apart, were treated as a transect line to increase encounter rates. Individual hair snare stations also were set up wherever the habitats looked promising for clouded leopards. Hair snare stations were checked and lures were refilled during each field trip every 3 to 6 weeks. Depending on the area of field work, new hair snare stations were set up and some old hair snare stations were removed if field work at that particular site ended.

Camera trap types

The camera traps used were developed locally in Taiwan by M. C. Teng at the Department of Plant Industry in National Pintung University of Science and Technology (Pingtung, Taiwan). The camera trap unit used a passive infra-red sensor to detect animal motion and the camera connected to the sensor was either a Pentax PC-606W or an

Olympus µ2 autofocus rangefinder 35mm film camera. It is not species-specific and has a detection range of approximately 3 to 5 m. Another 10 Trailmaster camera trap units (Goodson & Associates Inc., Kansas, U.S.A.), which consist of TM-1500 active infra-red trail monitors and TM35-1 camera kits were used in more open areas and to target larger species, especially clouded leopards, by adjusting the transmitters and receivers' triggering heights and blocking pulse time. Both systems are capable of imprinting photographic events' dates and times onto the film. Two hundred or 400 ISO color print film was used to save battery power from frequent flashes for longer working time.

Approximately 60 passive infra-red units were used as the main tool to study the ecology, distribution, and habitat use of all the larger mammals, including Formosan clouded leopards. Camera traps were fixed to a tree trunk at about 2m height and tilted downward facing the animal trail or intersection of trails at around 40-60 degree (Fig. 1.4). This was different from most camera trapping studies (Lynam et al. 2001, O'Brien et al. 2003, Silver et al. 2004, Azlan and Sharma 2006), which set up cameras at a height around 0.5m along roads or trails and the detection is parallel to the ground. Horizontal detection is more suitable to larger animals or in gentler terrain. In Taiwan, we wanted to collect information on small carnivores and other smaller mammals as well, and the terrain is often too steep to set up camera traps for horizontal detection. With cameras aimed downward, the detection area was more consistent so that bias was significantly reduced for comparison and for habitat use study across sites. In addition, birds in bushes within detection range often falsely trigger cameras positioned for horizontal detection. This bird triggering issue is even worse for lowlands in winter in Taiwan as altitudinal migration results in many more bird species and larger numbers (tens to hundreds) flying and foraging in flocks in forest understory. Facing cameras downward avoids possible false triggers from distant birds in bushes. The “downward” protocol has been applied for over a decade in Taiwan’s camera trapping studies (Pei et al. 1997, Pei 1998, Pei and Sun 1999, Pei 2004b, discussions in Pei and Chiang 2004), and therefore the results from this study were comparable across Taiwan with other studies.

Camera traps were mostly straight trail sets, without any lures, to reduce bias from different reactions to lures among individuals and species. In addition to trail sets, different types of camera traps were set up to increase the chances of “trapping” clouded leopards. Various camera traps were baited with olfactory (commercial feline hunting lures and/or catnip imitation oil) and visual (aluminum pans and fake chicken feathers) lures, or live chickens. We also used call boxes, which periodically playback clouded leopard sounds and distress sounds of its prey, (e.g. Reeve’s muntjacs). Some hair snare stations had camera traps to determine which animals visited. A few camera traps were set up near cavities, which looked like good resting sites, and along logs crossing creeks, drainages or dry river/creek beds. Since clouded leopards are extremely arboreal (Guggisberg 1975, Nowell and Jackson 1996), several camera traps were placed in trees at heights ranging from 3m to 20m facing tree trunks or the intersection of tree trunks and branches. Trailmaster camera trap units were put mainly along wider trails, dried river/creek beds, drainages, ridge lines, or more open habitats because many larger cats, including clouded leopards, frequently have been observed to travel along available forest roads, larger trails, or dried river/creek beds (Rabinowitz et al. 1987, Karanth and Nichols 1998, Austin and Tewes 1999). The Trailmaster units were adjusted to photograph only larger species (50 cm height of transmitters and receivers and longer blocking pulse time), and were programmed not to take another picture within 2 minutes of the previous trigger to save film and increase the working time.

Sampling of camera trap sites

Because of the ruggedness, steepness and remoteness of the study area, random or systematic sampling was not feasible. To sample all altitudes, slopes, and habitat types systematically would have required an inordinate number of sites, and since there was no road in the study area and backpacking was the only way to gain access, it may take days to check just one randomly or systematically selected camera trap location. This made random and systematic sampling time and personnel consuming, and impossible to conduct in this area.

In the study area, altitude ranged from 130m to 3,092m and vegetation types changed along the altitude gradient. Sampling of camera trap sites was based on transects along altitude gradient and stratified by altitude, which implies different vegetation types, within the 6 survey zones. Camera trap sites within each altitude range (e.g. every 300m) were selected ad hoc to cover environmental characteristics (e.g. slope, aspect, distance to river, and slope position etc) as differently as possible. I put camera trap sites mostly in zones 1 to 4 for analysis of habitat use and distribution patterns because these areas were basically free of human hunting and forest disturbances. Habitats which did not look suitable for most larger mammals, e.g. steep terrain, or where few signs were observed, were still sampled with camera traps as the purpose was to understand habitat use and distribution patterns. To understand the effect of hunting on clouded leopard prey populations, camera traps were placed both in areas with and without persistent hunting pressure.

Field work was conducted by organizing field trips to the study area 1 to 2 times per month (i.e., backpacking was the only way of accessing the study area). Each field trip lasted 1 to 2 weeks, up to 4 weeks. Field work started in January, 2001 and ended in May, 2004. The core study zones 1 and 2, which cover nearly the whole altitude range (200m - 3,092m), were surveyed for the entire study period, others were surveyed for 1 to 2 years (Fig. 1.2).

Camera traps were checked during each field trip to replace film and batteries. Because of the remoteness and number of camera trap sites (50-70), it was impossible to check all cameras within one month. Furthermore, typhoons or torrential rains during wet seasons often raised river water levels or caused landslides along roads making the study area inaccessible. Therefore, the interval for checking each camera trap site ranged from 3 to 6 weeks and sometimes up to two months. Each film usually lasted 3 to 5 weeks depending on animal abundance. It could last as short as 1 week in the low altitudes or as long as 2-3 months in the high altitudes. To increase the sample size of camera trap sites to cover more diverse habitats (e.g., different altitudes, slopes, and aspects etc) and the chance of photographing clouded leopards, each camera trap was switched to a new site after the site had at least 2 rolls of film or 10 camera trap days.

The coordinates and altitudes of each camera trap site were obtained with a field Trimble GeoExplorer III GPS receiver (Trimble Navigation Limited, 645 North Mary Ave., Post Office Box 3642, Sunnyvale, CA 94088-3642, USA) using the local TWD67 Transverse Mercator coordinate system. Coordinates and altitudes were differentially post corrected using the Trimble Pathfinder software with data from the nearest base-station, which is approximate 19 km west of the center of the study area, located in the Department of Forestry of National Pingtung University of Science and Technology. At least 100 positions (one per 5 seconds) above precision level 3 were collected for each camera trap site to increase the precision of the final averaged coordinates. Precision was within several meters and more often within 1 to 2 meters based on the statistics from the Trimble Pathfinder software.–

Habitat measurement at camera trap sites

Habitat attributes associated with each camera trap site (trail sets) were measured on site after the removal of the camera traps or determined with the help of a digital elevation model of the study area through ArcGIS 9.2 and satellite images.

Habitat attributes were determined in 2 scales. Micro-habitat variables were mainly associated with vegetation and topography and were measured on site within 0.1ha of each camera trap site (trail sites), i.e. 17.84m radius circle from the center of the photographic area. These included altitude, slope, aspect, canopy cover, tree densities, canopy cover, herb/shrub/rock cover, ruggedness, average canopy height, average tree DBH/height, visual obscurity, and vegetation types, etc. (Table 1.3). Variables in the final analysis of micro-habitat use were divided into the following 7 categorizes: altitude and vegetation types, terrain shapes and ruggedness, forest understory and ground cover, forest structures, moisture gradient and wetness (distance to nearest river), seasonality (dry or wet season), and the size of the photographic area, which was not related to habitat use, but may influence the probability of being photographed. However, vegetation was correlated with altitude, which changed gradually from broad-leaved to coniferous forest along the altitudinal gradient and was often difficult to characterize the type accurately (e.g. forests in transition between *Machilus-Castanopsis* and *Quercus* forest zones). Therefore, I only used a binary variable to indicate whether the vegetation type is Rhododendron forest. I mainly used plotless point center quarter (PCQ) for forest structure and a systematic radial design for cover and terrain attributes to sample habitats based on the center of the photographic area (details see Table 1.3). Distance and height were measured with a Leica Geosystems (St. Gallen, Switzerland) DISTO™ Basic laser distance meter having <1cm precision. A clinometer and a densitometer were used to measure slopes and canopy cover, respectively.

A digital elevation model (DEM) was used to derive various meso-habitat variables. This was achieved with the help of GIS using coordinates of the camera traps. The grid size of the DEM model used was 40mX40m. Variables derived could be classified into 2 categories: temperature/wetness/vegetation types and terrain shape/ruggedness. The first includes altitude, slope position, distance to nearest river, moisture gradient (derived from aspect), solar radiation, and terrain wetness index. Variables related to terrain shape/ruggedness consisted of slope and its derivatives, and terrain shape index (Mcnab 1993) (Table 1.4). NDVI (normalized difference vegetation index), which was used as an index of the canopy reflectance, biomass, and productivity of the vegetation (Goward et al. 1991, Hsieh and Cheng 1995), was calculated using a SPOT 4 satellite image photographed on 6/28/2003. However, two camera trap sites were under clouds during the time of photograph and their NDVI were obtained from another SPOT 4 satellite image photographed on 12/2/2002 (this image has too much cloud and shadow area to be useful).

Table 1.1. Twenty-five large terrestrial mammals of Taiwan (mammals excluding Chiroptera, Insectivora, and Muridae of Rodentia)

Order	Family	English name	Scientific name	Documented occurrence in study area
Rodentia	Sciuridae	Red-bellied tree squirrel	*Callosciurus erythraeus*	★
		Long-nosed tree squirrel	*Dremomys pernyi owstoni*	★
		Striped tree squirrel	*Tamiops marutimus*	★
		White-faced flying squirrel	*Petaurista alborufus lena*	★
		Indian giant flying squirrel	*Petaurista philippensis*	★
		Hairy-footed flying squirrel	*Belomys pearsonii kaleensis*	★
Primates	Cercopithecidae	Formosan macaque	*Macaca cyclopis*	★
Pholidota	Manidae	Chinese pangolin	*Manis pentadactyla pentadactyla*	★
Lagomorpha	Leporidae	Formosan hare	*Lepus sinensis formosus*	★
Carnivora	Ursidae	Asiatic black bear	*Ursus thibetanus formosanus*	★
	Mustelidae	Taiwan high mountain least weasel	*Mustela formosana*	
		Siberian weasel	*Mustela sibirica taivana*	★
		Yellow-throated marten	*Martes flavigula chrysospila*	★
		Formosan ferret-badger	*Melogale moschata subaurantiaca*	★
		Eurasian otter	*Lutra lutra chinensis*	
	Viverridae	Gem-faced civet	*Paguma larvata taivana*	★
		Lesser oriental civet	*Viverricula indica taivana*	★
	Herpestidae	Crab-eating mongoose	*Herpestes urva formosanus*	★
	Felidae	Formosan clouded leopard	*Neofelis nebulosa brachyurus*	
		Leopard cat	*Prionailurus bengalensis chinensis*	
Artiodactyla	Cervidae	Reeve's muntjac	*Muntiacus reevesi micrurus*	★
		Sambar deer	*Cervus unicolor swinhoii*	★
		Formosan sika deer	*Cervus nippon taiouanus*	
	Bovidae	Formosan serow	*Nemorhaedus swinhoei*	★
	Suidae	Wild boar	*Sus scrofa taivanus*	★

Table 1.2. Altitude ranges, vegetation types (Su 1984), and human activity in the 6 survey zones (different watersheds) in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

No.	Zone	Altitude Range	Vegetation types				Human disturbance
			Ficus-Machilus	*Machilus-Castanopsis*	*Quercus*	*Tsuga*	
1	Taimali watershed	200m | 3,092m	X	X	X	X	Almost none
2	Chiben watershed	1,000m | 2,735m		X	X	X	Almost none
3	Big Ghost Lake	1,800m | 2,500m			X		Occasional backpackers
4	Wanshan God Pond	1,900m | 2,500m			X		Occasional backpackers
5	Jinlun watershed	150m | 1,800m	X	X	X		Persistent hunting
6	Danan watershed	500m | 1,100m		X			Persistent hunting

Table 1.3. List of micro-habitat variables and measurement methods used for habitat analysis in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

Category	**Habitat variable**	**Method of measuring and calculation**
Altitude/ vegetation	altitude	GPS receiver, differentially post processed with >100 GPS points
	Rhododendron forest	Yes/No.
Terrain shape/ Ruggedness	field slope	measured from downslope 10m to upslope 10m from the center with a Sunnto clinometer in percentage.
	cliff nearby	Yes/No. By observation within 100m.
	ruggedness	angles (i.e. slopes) from the center to 8 radial neighboring points (every 45° from north) at 3 different distances (2m, 4m, and 8m). Angles could be positive (inclination) or negative (declination).
	terrain shape index	Terrain shape indices were calculated in 3 different scales (2m, 4m, and 8m) using the previous 8 angles from the center to 8 radial neighboring points following McNab (1989), i.e. sum of 8 tangent(angle). Positive values indicate concave surface, negative values indicate convex surface, 0 indicate linear (not necessarily level) surface.
Forest understory/ ground cover	herb cover	10m line transect in the 8 radial directions (every 45° from north) from the center of the photographic area. Each transect line sampled 10 points (every 1 meter) totaling 80 points. Calculated as percentage.
	shrub cover	
	rock cover	
	shrub density	plotless PCQ: $1/d^2$ where d is the average distance of 4 nearest shrubs in the 4 quadrants (defined by E, S, W, N).
	shrub height	plotless PCQ: average shrub height of 4 nearest shrubs in the 4 quadrants.
	visual obscurity	Use a cover board at 5m and 10m from the four E, S, W, N directions. VO is estimated in 6 classes (0%, 1-20%, 20-40%, 40-60%, 60-80%, 80-100%) at 4 heights (0.5m, 1m, 1.5m, 1.5m, 2m) in each sampled direction (total 8 values) looking outward from the center to the cover board at 5m and 10m. Calculated as average percentage.
Forest structures	Nearest tree distance	Laser meter and DBH tape were used. Plotless PCQ in categories of different sizes of tree DBH: 1-3cm, 3-5cm, 5-10cm, 10-20cm, 20-40cm, >40cm to obtain averages at each category. Every two categories were combined to form small, medium, and large tree classes. Tree densities, basal area, average tree height, and average branch height were calculated for these 3 classes. Coefficient of variation (CV) was also calculated.
	Nearest tree DBH	
	tree height	
	branch height	
	forest stratum	2 to 5 stratum (include the herbaceous strata) by observation
	average canopy height	Height of the general canopy range, i.e. the highest forest strata, but not the single highest tree.
	canopy cover (average and CV)	8 measurements using a densiometer: facing east(E), south(S), west(W), north(N) at the center and 5m from the center respectively. Calculated as average percentage and CV for canopy patchiness (gaps).
Moisture gradient /wetness	aspect	Compass. For moisture gradient calculation.
	moisture gradient	10 levels: 1 (wettest) - 10 (driest) following Whittaker (1960) and Su (1987) based on field aspect and proximity to river and valley.
	distance to nearest river/lake	River is derived using a DEM hydrology model, calculated in ArcGIS 9.2.

Table 1.4. List of meso-habitat variables and the method of calculation for habitat analysis in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

Category	Variable	Method of calculation
Temperature wetness vegetation	NDVI	SPOT 4 satellite image, calculated in ERDAS Imagine 9.1.
	Altitude	GPS receiver, differentially post processed with >100 GPS points
	slope position (elevation)	0(valley)-100(ridge), ratio of elevation difference to the valley and ridge
	slope position (distance)	0(valley)-100(ridge), ratio of distance difference to the valley and ridge
	distance to nearest river/lake	River is derived using a DEM hydrology model.
	annual solar radiation (ASR)	Solar radiation of a whole year based on Fu and Rich (2002), which considered atmospheric conditions, altitude, aspect, and influences of surrounding topography. Calculated in ArcGIS 9.2.
	moisture gradient	10 levels: 1 (wettest) - 10 (driest) following Whittaker (1960) and Su (1987) based on DEM aspect and proximity to river and valley.
Ruggedness / terrain shape index	slope	From DEM in percentage (ArcGIS 9.2)
	slope standard deviation	standard deviations of slopes (percentage) within neighboring 3x3 cells
	cliff distance	Distance to nearest cliff. Cliff is defined as slope>45° with area>1.44ha (i.e., 3x3 cells, 120mX120m)
	cliff percentage	Proportion of cliff cells (slope>45°) within 25x25 cells (i.e., 1kmX1km or 100ha)
	Terrain shape index	Sum of altitude differences between 8 neighboring cells (3x3 grids in DEM, i.e. 120mX120m) divided by distance to neighboring cells following McNab (1989). Positive values indicate concave surface, negative values indicate convex surface, 0 indicate linear (not necessarily level) surface.

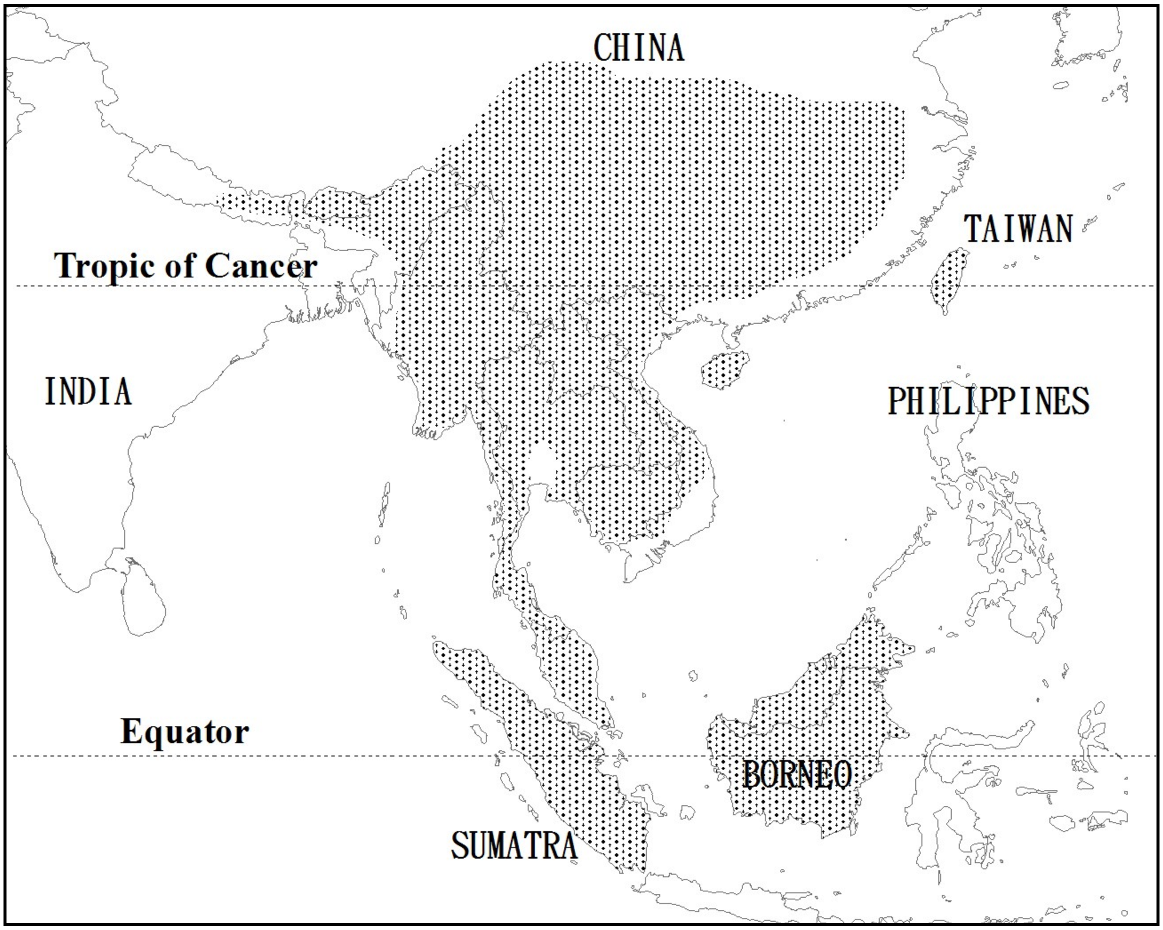

Figure 1.1 Distribution range (dotted area) of clouded leopards adapted from Nowell and Jackson (1996). The subspecies in Borneo and Sumatra is now recognized as a new species (*Neofelis diardi*) based on latest genetic (Buckley-Beason et al. 2006) and morphometric (Kitchener et al. 2006) differences.

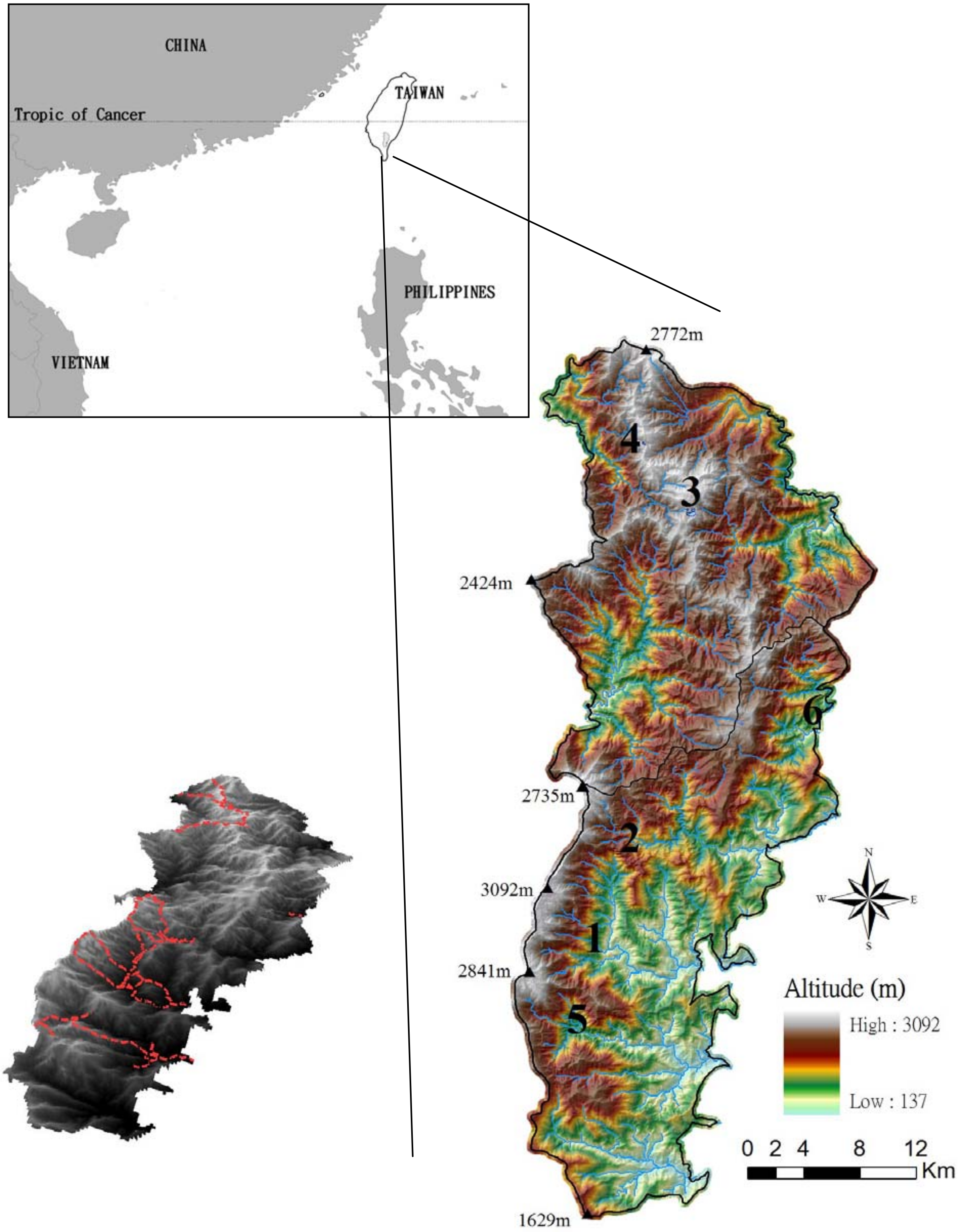

Figure 1.2. Location of the study area: Tawu Nature Reserve (lower part) and Twin-Ghost Lake Important Wildlife Area (upper part) in southern Taiwan showing 6 numbered survey zones. There is hunting pressure in zones 5 and 6. The bottom left small figure demonstrates 3D terrain of the study area with red lines indicating survey trails.

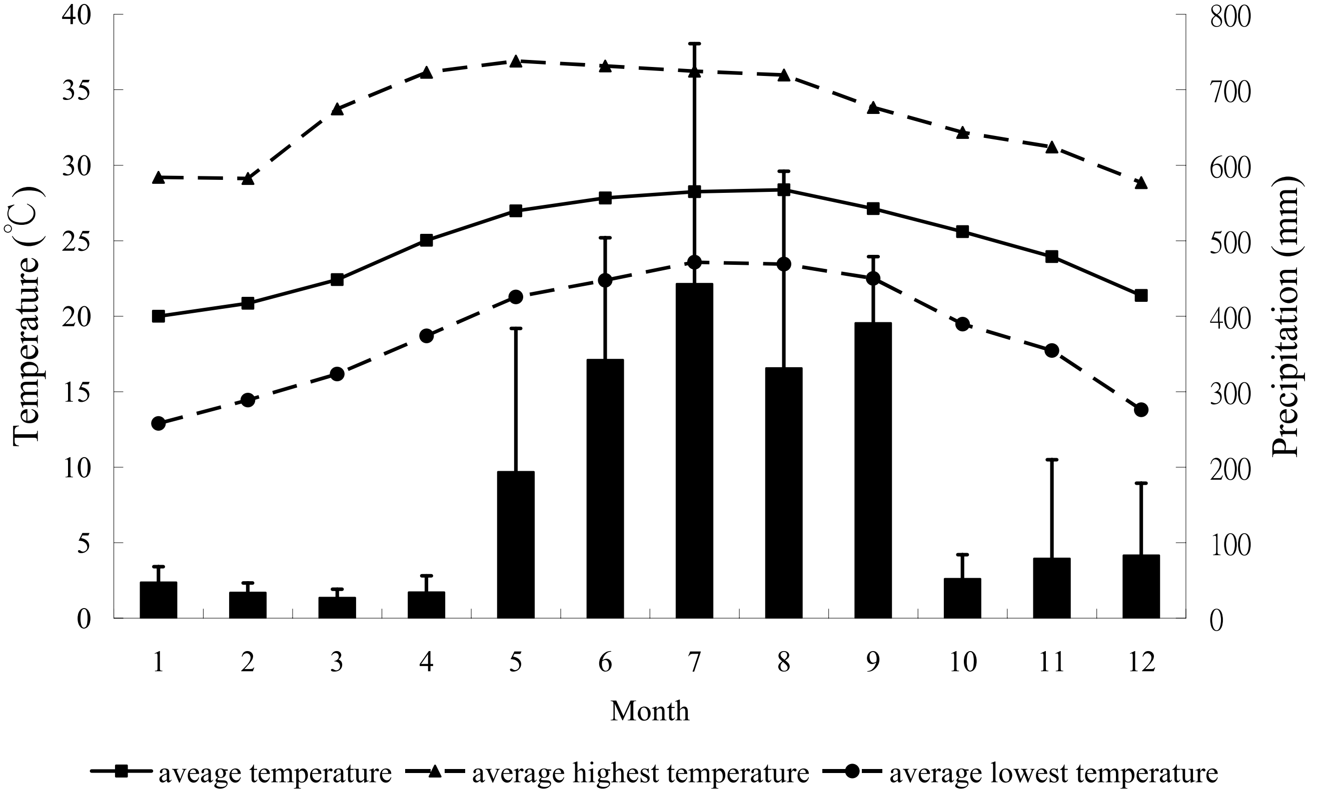

Figure 1.3. Monthly average temperature (solid line) with average highest and lowest temperature (dotted lines) and average rainfall (bar) with one standard deviation (error bar) across 4 years near Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan. Data were collected at the weather station nearest Tawu at seashore (altitude 8m) approximate 30 km south-southeast of the study area during the study period from 2001 to 2004.

Figure 1.4. Camera set up for camera trapping in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. Cameras (circled in red) were attached to a tree trunk facing downward to the trail or the intersection of trails at around 40-60 degree.

Chapter 2: Where have all the Formosan clouded leopards gone? Current status and conservation implications of Formosan clouded leopard

Introduction

No direct affirmative occurrence records of live clouded leopards, e.g. photographs or captures, have been reported by biologists for decades in Taiwan. Although suspected pugmarks were found in the 1990s near Yushan National Park in central Taiwan (Lue et al. 1992, Wang et al. 1996), the tracks were not clear and some biologists disagreed on the identification. Excluding unsubstantiated rumors of sightings and trapping by hunters, the latest two records are a fresh pelt of a young clouded leopard in 1989-1990 in eastern Taiwan (Wang et al. 1995) and a dead young clouded leopard in a snare in 1983 in southern Taiwan (Rabinowitz 1988). They are possibly the most persuasive and most recent records so far. However, these two records are still disputable. That is, no reliable Formosan clouded leopard occurrences have been documented for at least 17 years and more likely for decades.

Wayre (1969) and McCullough (1974) described the status of Formosan clouded leopards to be critically endangered. Rabinowitz (1988) focused on Formosan clouded leopards and interviewed 70 local people, mostly aboriginal hunters. Only 7 of 33 reported sightings were within 5 years of 1986 and most (23) occurred before 1976. All of the above were based on indirect information from local people. Lee and Lin (1992) reviewed past general faunal survey efforts in Taiwan and suggested that the clouded leopards were nearly or already extinct in Taiwan as almost no recent records had been reported. If there are any clouded leopards left in Taiwan, they must be surviving in remote areas in very small numbers, not likely a viable population. Thus, it is urgent to investigate the current status of Formosan clouded leopards and conduct conservation efforts accordingly before it is too late.

Karanth and Stith (1999) maintained that prey depletion is an influential factor in tiger population viability. With rapid development and commercial hunting in Taiwan during past decades, the prey base of Formosan clouded leopards is likely to be severely reduced. Furthermore, human encroachment in the lowlands, and clear-cutting of the forest also diminish suitable habitats of clouded leopards. Some larger mammals living in lowlands have become extinct or extremely rare. For example, Formosan sika deer are extinct and Eurasian otters have not been found for over 20 years, similar to the situation of Formosan clouded leopards (Wang and Lin 1986, Lin 2000). Leopard cats are also very rare and critically endangered (Pei and Chen 2006). This is largely due to the reduction of lowland habitats, which were converted to towns or agriculture lands. Thus, we hypothesize that prey depletion and habitat loss and fragmentation may be two critical determinants of the disappearance of clouded leopards in Taiwan.

With the exception of Rabinowitz's (1988) interviews, no field surveys dedicated to Formosan clouded leopards have been conducted prior to this study. Understanding the population and ecology of the prey species and the reasons for their disappearance is important for the conservation of clouded leopards. In addition, no quantitative studies have been conducted to understand the ecology of the clouded leopard's prey base and to assess the influence of human activities on the prey. The objectives of this study are three-fold: (1) search for affirmative evidence of clouded leopards in southern Taiwan and assess its population status, (2) study and assess the prey base and suitable habitats of Formosan clouded leopards and make recommendations for future conservation, (3) examine the historical pelt trades and occurrences of Formosan clouded leopards and discuss the hypothesis that clouded leopards were never in Taiwan.

Methods

Formosan clouded leopard field survey

I used hair snares and camera traps to search for evidence of clouded leopards in the study area. Details of placement and checking protocols of hair snares and camera traps were described in chapter 1. I also searched for tracks, claw marks, scats, and other signs. Camera traps were thereafter placed near suspected or hard to identify clouded leopard sign. Photographic rates from camera trapping have been shown to be highly correlated to densities of tigers (Carbone et al. 2001, O'Brien et al. 2003) and ocelots (Dillon 2005). Therefore, I compared the average number of camera trap days to get one clouded leopard photograph in other countries with the camera trapping effort in Taiwan to assess the population status of Formosan clouded leopards.

Prey assessment

Intuitively, camera trapping is similar to the hunting style of clouded leopards, i.e. leopards sit and wait on tree branches for passing prey (Lekagul et al. 1977, Davies 1990, Nowell and Jackson 1996). A photographic event of prey from camera trapping could thus be considered as one prey encounter. If, on the other hand, clouded leopards hunt by traveling and searching, prey encounters would be similar to animals flushed in line transects. Given 1) the high correlation between photographic rates from camera trapping and population densities (Carbone et al. 2001, O'Brien et al. 2003, Dillon 2005, Liang 2005), 2) the high correlation between photographic rates and animal encounter rates per km of line transects (Rao et al. 2005), and 3) the similarity of camera trapping and clouded leopard's hunting strategy, I used photographic rates from camera trapping as prey encounter rates and thus as a measure of prey availability.

The criteria to determine a photographic event (a species occurrence) were 1) consecutive photographs of the same species within 1 hour were counted as 1 species occurrence, 2) the stamped time of the first photograph of these consecutive photographs was taken as the species-occurrence time. After 1 hour, additional photographs were considered to be another occurrence event even if they were the same species, 3) different identifiable individuals were treated as a separate occurrence even though they appeared in the same photograph or the photographs were taken within 1 hour of the species-occurrence time. Following Pei (2002a), the photographic rate from camera trapping (Species Occurrence Index, SOI) was calculated for each camera trap site for each species as number of species occurrences per 1,000 camera trap hours. Since some animals are social (e.g., Formosan macaques), or some may appear as groups (e.g. male and female or female with young), consecutive photographs may be triggered by different individuals of the same species and group. As these are likely dependent events, I further defined these consecutive photographs, no matter that they were from the same or identifiably different individual, as 1 "group occurrence" event (a group occurrence event could consist of 1 or more species occurrence events). That is, the third criterion of species occurrence was relaxed. The Group Occurrence Index (GOI) was thus calculated as the number of "group occurrence" events per 1,000 hours. GOI was used as the prey encounter rate instead of SOI since a clouded leopard could prey on only one animal at a time even if it encountered a group of animals.

Emmons (1987) summarized data (captive and wild) from 6 felid species and determined that the daily meat(g) consumption rate per kg felid ($DMC_{g/kg}$) of big cats was

34-43 g/day/kg while ocelot-sized cats (~10kg) was 60-90 g/day/kg. However, most recent field data (Tables 2.1 and 2.2, and see appendix in Carbone et al. 2007) report generally higher daily consumption rates. For predators weighing over 21.5-25kg, there is a striking transition from feeding on small prey to large prey (Carbone et al. 1999). I calculated bootstrap means and bias-corrected 95% confidence intervals (CI) for the 12 felids in 2 groups demarcated by 25kg body weight. $DMC_{g/kg}$ for smaller cats had a mean of 79.2 g/day/kg (95% CI = 64.6-92.4), while the $DMC_{g/kg}$ of larger cats had a lower mean of 64.2 g/day/kg (95% CI = 49.9-75.0). A clouded leopard averaging 17kg (the mid point of weight range 11-23kg, Nowell and Jackson 1996) would require 1.1kg (95%CI = 0.9-1.3kg) of fresh meat per day per clouded leopard based on the estimation for big cats or 1.4kg (95%CI = 1.1-1.6kg) of fresh meat per day based on the estimation for smaller cats. Female Eurasian lynx are similar in weight to the average weight of clouded leopards and their daily consumption rates (97.6g/day/kg; Table 2.2) may be more similar to clouded leopards. That is, clouded leopards would correspondingly consume 1.7kg (97.6g/day/kg X 17kg) of meat per day. Captive clouded leopards (28.5kg male and 13.1kg female) have been fed, on average, 600g of fresh meat a day (Y. Chen and C. Yang, Taipei Zoo, Taiwan, personal communication). But, captive individuals do not need to travel and hunt, and wild female cats would require even more meat to raise cubs (Stander et al. 1997). This concurs with the fact that daily consumption rates of captive felids (K. Pei, Pingtung Rescue center for Endangered Animals, National Pingtung University of Science and Technology, Taiwan, personal communication, and also see Emmons 1987) were generally lower than my bootstrap estimations. Wild clouded leopards weigh less than 25kg and have body characteristics of both small cats to big cats (see review in chapter 1), I used 1.1kg/day/clouded-leopard as a conservative and possibly the minimum requirement of daily meat consumption, which is the lower bound of the 95%CI from small cat criterion and is the average daily meat consumption from big cat criterion.

I transformed the GOI to daily rates (multiplied by 24/1000) to represent the daily encounter rates of prey (DERP). To estimate available prey by weight per day, I multiplied the DERP by average adult body weights(g) of prey as "daily encounter rates of prey weight" (DERPg, in terms of grams) to see if the prey base met the daily food consumption requirements of clouded leopards. I adjusted the DERPg by the edible percentages of prey (Emmons 1987, Pedersen et al. 1999, Mills et al. 2004), i.e. 65% for large prey over 25kg, 80% for medium prey over 4kg, and 90% for small prey < 4kg (Table 2.5). Since, it is unlikely that a clouded leopard could completely consume a very large prey (e.g. sambar deer) before it decomposed under the tropical environments or was scavenged by Asiatic black bears and other carnivores. I restricted the amount of meat a clouded leopard could obtain from large prey to 50kg (assumes maximum daily consumption of 6kg or 1/3 body weight and 8 days of feeding on 1 carcass). I based this restriction on the daily meat consumption and kill rates of other wild felids (Table 2.1). The DERPg for each prey species was calculated as:

1. large prey > 25kg

   DERPg = DERP x {minimum of [average adult weight(g) x 65% or 50,000g]}

2. medium prey 4-25kg

   DERPg = DERP x (average adult weight(g) x 80%)

3. small prey < 4kg

   DERPg = DERP x (average adult weight(g) x 90%)

No data are available on hunting success and kill rates for clouded leopards, I used a 20%

hunting success rate (approximately the median value from Table 2.1) as a general guidance for clouded leopards. I then multiplied the total DERP and DERPg of all prey by 20% to approximately reflect the daily kill rates of prey (DKRP) and daily consumption rates of prey in grams (DCRPg). These 2 indices of prey base for Formosan clouded leopards in the study area were compared between different altitude zones and between areas hunted and not hunted. Moreover, I also calculated percentage of camera trap sites with detection for each prey species.

Altitude was categorized into 4 altitude zones, 150m-1,200m, 1,200m-2,000m, 2,000m-2,500m, and 2,500m-3,100m. These 4 altitude zones reflect major vegetation types graduating from broad-leave to coniferous forests. I calculated DERP for each camera trap site and an average DERP for each altitude zone. To avoid bias from camera trap sites with very low trapping effort, only sites operating camera traps more than 10 days were used. I then derived DERPg from the corresponding DERP for each species in each altitude zone. I applied Kruskal-Wallis test to examine DERP and DERPg differences among the 4 altitude zones. Jonkheere-Terpstra tests also were performed to test for altitudinal trends, i.e. increasing or decreasing occurrence frequencies along altitudinal gradients. I used Wilcoxon rank-sum test (one-sided) to examine whether DERP and DERPg differed between hunted and not hunted areas at altitudes lower than 2,000m. In addition to 13 potential prey species documented by camera traps, these tests also were conducted for 5 other sympatric carnivores. SAS 9.1.3 was used to conduct the statistical tests on DERP and DERPg. Since large prey (macaques and ungulates) comprised almost all of the DCRPg (see result), I calculated 95% bootstrap (1,000 replications) bias-corrected confidence intervals for DCRPg for altitudes above 2,000m (no human hunting) and below 2,000m (with and without human hunting, see chapter 1 for human hunting descriptions) using STATA 9.2.

Clouded leopards are unlikely to wait for a passing prey as long as a camera trap, although DERP is a good indicator of the average probability of a potential prey to be encountered. There are similarities between a clouded leopard searching for a good hunting spot to wait for prey to ambush and a researcher going to a camera trap site to set up the camera trap or to replace film and batteries. So, waiting time for a clouded leopard to ambush a prey was expressed as the time to first detection (TFD) of a potential prey by camera traps. This was calculated for each prey species. Survival analysis approach was used to analyze such time-to-event data to accommodate the “right-censor” situation when a particular prey was not detected at all at a camera trap site because either it was absent or the camera trapping effort was not long enough to document the less common species. I used Cox proportional hazard regression with TFD of each film roll being the dependent variable, altitude and hunting (0 for no hunting, 1 for with hunting) being the independent variables, and each roll of film being the sampling unit. Since a camera trap site may have more than 1 roll of film, a gamma-distribution frailty term (random-effect term) was added to model the dependency (or cluster) among different rolls of the same camera trap site. That is, those rolls of film of the same camera trap site shared the same frailty. SPLUS 7 was used to conduct the Cox proportional hazard regression with shared frailty model (Therneau and Grambsch 2000).

Among the 80 mammal species in Taiwan, bats, insectivores, and mice are not considered major potential prey of clouded leopards because of their light weight or aerial ability. However, spinous country rats (*Niviventer coxingi*) and Formosan white-bellied rats (*Niviventer culturatus*), the two largest forest rats in the Muridae of Rodentia weighing an average 68g, were considered as possible prey because Muridae remains have been found in the feces of clouded leopards (Grassman et al. 2005b). Among the 25 larger mammals (Table 1.1), I excluded 10 sympatric carnivores since no carnivores were found in scats of clouded leopards or were observed to be killed (Griffiths 1993, Nowell and Jackson 1996, Grassman et al. 2005b). Hares occur mostly in open habitat and sika deer are extinct. Birds, except pheasants, were not included in the potential prey list because of their light weight and flying agility. Although some birds were photographed by camera traps, their smaller size and rarity makes it unlikely they would be significant or meaningful in the diet of clouded leopards. The list of major potential prey of clouded leopards in Taiwan therefore includes 14 mammalian species and 4 avian Phasianidae species (Table 2.3).

In addition to the comparisons within the study area, I conducted a meta-analysis of DCRPg from all camera trapping studies (21 different areas) in Taiwan (Liu 2003, Pei et al. 2003, Hwang and Chian 2004, Hwang and Pei 2004, Pei 2004b;a, Wang 2004, Wu et al. 2004, Lai 2005, Wang and Hsu 2005, Wang and Huang 2005, Pei and Chen 2006) including 4 different altitude zones and the area with hunting activity in this study to understand factors influencing prey biomass for all of Taiwan. Since large prey (macaques and ungulates) comprised almost all of DCRPg (see results), DCRPg in this meta-analysis also was based on only the 5 largest herbivore prey. However, DCRPg of the 5 zones within the study area are based on SOI instead of previously used GOI to match other camera trapping studies in Taiwan. I hypothesized that human activity, distance to central Taiwan, and altitude could affect the prey biomass. Human activity (HA) was based on 3 values, i.e. accessibility from roads and villages (ARV), levels of human hunting pressure (HP), and history of forest practices (e.g. clear cut) or agricultural uses (HFP). When the area was generally within 5km of major roads or well-maintained logging roads or within 3km of aboriginal villages, ARV was assigned 1. Within these distances, the area was easily accessible within a day and human hunting and encroachment were common (personal observation). HP and HFP are rated from 0-3 (0: no hunting, 1: occasional hunting, 2: persistent seasonal hunting, 3: persistent hunting all year round) and 0-5 (0: primary forest, 1-5: estimated levels or percentages of disturbance with 1 being minor and 5 being complete removal of original primary forests), respectively, based on associated literature and actual personal field observations. ARV, HP and HFP were then scaled to 10 equally and summed to form an overall score of human activities, i.e. HA from 0 to 30. DCT was the distance from the center of the area to central Taiwan. ALT was average altitude of all the camera trap sites or midpoint of the altitude ranges of the study area if individual altitudes of camera trap sites were not reported. I used multiple linear regression and the information-theoretic approach (AIC_c) to select the best model. STATA 9.2 was used to conduct the analysis and calculate the 95% bootstrap bias-corrected confidence interval for the 5-herbivore DCRPg (sampling unit: area).

Habitat assessment

Procedures to identify current suitable habitat for clouded leopards in Taiwan (Fig. 2.1) were derived from the ecology and habitat requirements of clouded leopards reported in the literature (reviewed in Chapter 1):

1. I used GIS coverage of vegetation types derived from the latest Third National Forest Resources Survey conducted from 1990 to 1993 (Taiwan Forestry Bureau 1995) to identify forest types in Taiwan. Natural broadleaf forest at lowland, either primary or secondary, was considered the most suitable vegetation type since clouded leopards

occur mostly in tropical or subtropical lowland forests. Natural mixed broadleaf-conifer forest and cypress old growth forest, which occur at higher altitudes (usually > 1,600m), also were classified as suitable vegetation types although they may not be as favored as broadleaf. However, Taiwan white fir (*Abbies kawakamii*) forest, which generally occurs higher than 3,000m, was considered unsuitable because of the tree structures, which do not have extended branches for clouded leopards to use as hunting sites or to rest upon (Rabinowitz et al. 1987, Nowell and Jackson 1996), and insufficient prey. In addition, clouded leopard occurrences rarely have been documented above 3,000m throughout the world even in tropical areas. Non-forests, agriculture lands, bamboo forests, and plantation forests (mostly conifers) after clear-cut were also excluded as they do not have sufficient prey and/or are close to human development.

2. Since male clouded leopards have larger home ranges than females (Austin 2002, Grassman et al. 2005b), we used the average male clouded leopard home range size (40km^2) as a threshold to distinguish between primary and fragmented habitat. Suitable vegetation patches greater than 40km^2 were designated as primary habitat.
3. Based on clouded leopards' core area sizes (around 3km^2) and mean daily movement distance (1-2km), patches smaller than 4km^2 were considered too small for clouded leopards to utilize and were excluded.
4. I assumed clouded leopards could move between patches within 1km in one day based on their mean daily movement distances. Fragmented patches between 4km^2 and 40km^2 that were within 1km of primary habitat were considered suitable habitat. This step was recursively conducted once again to include those fragmented patches that were within 1km of the patches included previously to allow clouded leopards to

move between fragmented patches.

5. I created a 500m buffer along the boundary of the above suitable vegetation types and included the buffer as potential habitat. Clouded leopards moved 1 to 2 km on average (Austin 2002, Grassman et al. 2005b) and 500m was chosen as half of the shorter 1km average daily movement distance under a more strict consideration. That is, it is assumed that clouded leopards venture out of forests and need to return to the original forest during a single day. Furthermore, clouded leopards may hunt near edges (Grassman et al. 2005b). In the mean time, this buffering helps to eliminate the digitizing errors of cover maps and "nibbles away" some of the fragmented small patches within suitable vegetations to make it more contiguous.
6. Human encroachment and hunting is common and ongoing near villages and along roads. These human activities alter the forests for agriculture and decrease the prey base of clouded leopards. In addition, the vegetation map is 10 years old. The agriculture encroachment and hunting is likely to have expanded and increased during these 10 years. Based on field observations of development and agricultural uses near villages and roads and meta-analysis of camera trapping studies across Taiwan, this study subjectively assumed that suitable habitat must be at least 5km from villages and at least 3km away from major roads (but see discussion for justification). These distances are reasonable because if there are any Formosan clouded leopards living within these distances to villages and major roads, they likely would have been discovered.
7. Formosan macaques and Reeve's muntjacs are the most important prey of clouded leopards in Taiwan (see discussion). Most camera trapping studies in Taiwan had more pictures of Formosan macaques and Reeve's muntjacs than other species and

their photographic rates were higher at lower altitudes (this study). Lee and Lin (1990) showed that group size of Formosan macaques gets smaller with altitude increasing. Therefore, lower altitudes are likely better habitat for Formosan clouded leopards with respect to the abundance of prey (this study). Based on the altitudinal trends of the prey base (this study), I designated areas below 2,000m as suitable habitat for Formosan clouded leopards. The best habitats were below 1,500m. However, areas below 300m were mostly developed and were excluded as suitable habitat.

Maps of current suitable habitat for clouded leopards in Taiwan were produced for altitudes below 2,000m and altitude below 1,500m respectively.

Results

Formosan clouded leopard field survey

Only 4 hair snare stations got hairs. But, none were clouded leopard hairs. I placed 129, 53, 24 and 26 of 232 hair snare stations in survey zones 1 to 4 (see chapter 1), respectively (Fig. 2.2). Most hair snares were checked and reconditioned several times to work as continuously as possible. The total number of hair snare trap days could not be determined as it is unknown how long the lures lasted and when the Velcro was destroyed by animals.

Two hundred and sixty-three of 377 different camera trap sites (excluding camera failures and theft, Fig. 2.3) were straight trail sets and 129 sites were non-trail sets (Trailmaster active-infrared types, bait/lure sets, hair snare sets, call box sets, tree sets and cavity sets). Total trail sets and non-trail sets (263+129) exceeds 377 because some camera trap sites were set up as trail sets in the beginning and converted to non-trail sets;

612 rolls of film were retrieved. About 13,000 of 16,000 pictures developed were triggered by animals. Total camera trap days were at least 13,354 trap-days as some cameras failed to imprint time and dates onto the film. Camera trapping did not capture any clouded leopard pictures despite the extensive effort of camera trapping.

Average number of camera trap days to get one clouded leopard picture in other Southeast Asian countries ranged from 113 to 879 camera trap days (Table 2.4). In some places, clouded leopards were successfully photographed with as few as 8 to 24 camera trap sites.

Prey assessment

Camera trapping recorded all of the 6 large prey species (>4kg), 8 species of smaller prey (60g-1.6kg) and 5 sympatric smaller carnivores (Table 2.5). Except for very small animals (<50g), which are unlikely to be prey of clouded leopards or are too small to be significant, the list (Table 2.5) of major potential mammalian and avian prey of clouded leopards in Taiwan's major habitat is quite complete. That is, all the major mammalian prey except 2 flying squirrel species and 2 of the 4 major avian prey species were well documented by camera trapping in this study. We believe that the estimates of DERP based on the extensive camera trapping effort are also adequate (Chiang et al. 2007).

Reeve's muntjacs had the highest DERP (Table 2.5) and percentage of detection sites (Table 2.6) at altitudes < 2,500m and contributed over half of DCRPg at altitudes < 1,200m. Over 65% (0.6006/0.9204, Table 2.5) and 33% (0.1962/0.5879, Table 2.5) of prey encounters at the 2 lower altitude zones were Reeve's muntjacs. Formosan macaques were the second in terms of DERP and percentage of detection sites at altitudes < 2,500m.

But, Formosan macaques are not as heavy as Formosan serow and sambar deer making the DERPg of Formosan macaques less than Formosan serow and sambar deer at altitudes < 2,500m. Among the 4 species, Formosan serows dominated at altitude > 2,500m. Although wild boars are the second largest prey, the low DERP makes their DERPg lower than the other 4 large prey species at altitude < 2,500m. In total, macaques and the 4 ungulates (i.e., 5 herbivores) contributed over 99% of DCRPg and over 82% of the total prey encounters. Regarding the other prey, only Chinese pangolin and white-faced flying squirrel could satisfy a clouded leopard's one day energy need (i.e. the edible meat exceeded 1.1kg/day). For Swinhoe's pheasant, its edible meat was close to 1kg (Table 2.5). However, these three species constituted only 4.6% of the total prey encounters.

I detected significant decreasing trends in DERP and DERPg as altitude increased for the 3 larger prey: Formosan macaques, Reeve's muntjacs, Chinese pangolins, and 3 smaller prey: red-bellied tree squirrel, spinous country rat, and Swinhoe's pheasant (*Lophura swinhoii*) (Jonkheere-Terpstra test, all p-values <0.003, Table 2.5). There were significant differences between altitude zones, but no monotonic linear trends were observed for Formosan serows, sambar deer and yellow-throated martens. Among the 4 altitude zones, Formosan serows had the lowest DERP and DERPg at altitude 2,000m-2,500m while sambar deer and yellow-throated martens had the lowest DERP and DERPg at altitude 2,500m-3,100m. For other carnivores, gem-faced civet and crab-eating mongooses had the same decreasing trend (Jonkheere-Terpstra test, both p-values ≤0.002, Table 2.5). Conversely, only white-faced flying squirrels (p=0.0004), Formosan white-bellied rats (p<0.0001), Taiwan partridges (*Arborophila crudigularis*) (p=0.0132), and Siberian weasels' (p<0.0001) increased DERP and DERPg along the altitude gradient. The DERP and DERPg of white-faced flying squirrels were very low and the other 3 species are neither major prey species nor heavier than 0.5kg. Only wild boars, long-nosed tree squirrel, striped tree squirrels, and Formosan ferret-badgers did not have altitudinal differences.

Without human hunting activity, the DCRPg at altitudes higher than 2,000m did not exceed the 1.1kg/day/clouded leopard threshold, while altitudes below 2,000m had DCRPg higher than 1.1kg (see bottom of Table 2.5). Altitudes between 1,200m and 2,000m were almost equivalent to 1.1kg. DKRP and DCRPg increased as altitude decreased. Prey were encountered almost every day at altitudes <1,200m and more than 1 prey was encountered every 2 days for altitudes between 1,200m and 2,000m. Higher altitudes required > 3 days to encounter potential prey and the highest altitude zone took nearly 1 week. With a hunting success of 20% for clouded leopards, the expected kill rates would be 5.4, 8.5, 17.2, and 29.5 days per kill for the 4 altitude zones from low to high, respectively (see bottom of Table 2.5).

DERP and DERPg of Formosan macaques ($p=0.038$), Reeve's muntjacs ($p<0.0001$), sambar deer ($p<0.0001$), and Formosan serows ($p=0.0084$) (Table 2.7) was significantly lower in hunted areas than not hunted areas within the study area. Although DERP and DERPg of Chinese pangolins did not differ between hunted areas and not hunted areas within the study area ($p=0.0852$) based on $\alpha=0.05$ criteria, camera traps did not document any Chinese pangolin in areas with human hunting. The DERP, DERPg and percentage of detection sites of all major prey species (> 4kg) except wild boars were decreased in hunted areas (Table 2.7). Nevertheless, none of the 8 smaller prey species differed between hunted areas and not hunted areas within the study area. The DCRPg at altitudes below 2,000m with hunting, i.e. 573g/day, was reduced to much below the

1.1kg/day level; while in areas without human hunting DCRPg remained at a level higher than 1.1kg/day (see bottom of Table 2.7). The total prey encounter rate and DCRPg was reduced 43% (0.7857 to 0.4479) and 61% (1474.89 to 573.44) in hunted areas, respectively. DCRPg at altitudes $<2,000$m without hunting was greater ($p<0.05$) than 1.1kg/day/CL ($\overline{X} = 1,474$ g/day with 95%CI = 1,323-1,647 g/day), while altitudes above 2,000m without hunting was lower ($p<0.05$) than 1.1 kg/day/CL ($\overline{X} = 663$ g/day with 95%CI = 553-798 g/day). In hunted areas below 2,000m the DCRPg was lower ($p<0.05$) than 1.1 kg/day/CL ($\overline{X} = 574$ g/day with 95%CI = 390-826 g/day).

Time to first detection (TFD) of the larger prey species for sambar deer ($p=0.0078$), Formosan serows ($p=0.038$) and Reeve's muntjacs ($p<0.0001$) was significantly longer in hunted areas than not hunted areas within the study area. Except for striped tree squirrels, TFD of the other species did not differ between hunted and not hunted areas (Table 2.8). TFD of 9 prey species was also associated with altitude (Table 2.8). Except wild boar ($p=0.11$) and Formosan serow ($p=0.12$), TFD of the other 4 large prey >4kg, sambar deer ($p=0.0043$), Reeve's muntjac ($p<0.0001$), Formosan macaque ($p=0.15$), and Chinese pangolin ($p=0.0018$), increased as altitudes increased. For prey $<$ 2kg, TFD of Swinhoe's pheasant ($p=0.0032$), red-bellied tree-squirrel ($p=0.006$), and spinous country rat ($p<0.0001$) also increased as altitudes increased. In contrast, only TFD of white-faced flying squirrels ($p=0.0029$) and Formosan white-bellied rats ($p<0.0001$) decreased as altitudes increased (Table 2.8). With the exception of the 3 mustelids, the other 2 heavier carnivores, gem-faced palm civets and crab-eating mongooses, were detected quicker ($p=0.0076$ and $p<0.0001$, respectively) at lower altitudes.

For the 10 areas which were easily accessible (within 5km of major roads or well-maintained logging roads or within 3km of aboriginal villages, i.e. ARV=1), none of the 5-herbivore DCRPg exceeded 1.1kg/day (points at the right part of Fig. 2.4a). The average was 304g/day (95%CI = 188-417g/day). In contrast, many of the other 11 areas away from major roads and villages had higher DCRPg than 1.1kg/day ($\overline{X}$=1,371 g/day with 95%CI=953-1,922 g/day). The DCRPg for the 5 herbivore decreased as human activity increased ($F_{1,19}$=20.85, p=0.0002, Fig. 2.4a). When distance to central Taiwan (DCT) and average altitude (ALT) was added to the model (HA), the full model (HA+DCT+ALT) was the best model to explain the 5-herbivore DCRPg variations across Taiwan (R-square 0.76, Akaike weight 84.3%, ΔAIC_c of the second best model (HA+DCT) was 4.0, Table 2.9). No significant correlations ($\rho_{HA,DCT}$ = 0.167, $\rho_{HA,ALT}$ = -0.281, $\rho_{DCT,ALT}$ = -0.274, all p-value>0.2, n=21) were found among these 3 variables.

Habitat assessment

The total area of vegetation types suitable for clouded leopards for all of Taiwan (i.e. natural broadleaf, mixed broadleaf-conifer, and cypress old-growth forests before considering fragmentation and human disturbance) encompassed approximately 9,410 km^2 (step 1, Fig. 2.5a), which was nearly 1/4 of the area of Taiwan. After removing isolated blocks smaller than 4 km^2 and those between 4 km^2 and 40 km^2, which were too far away from primary habitats greater than 40 km^2, the total area of these "potential habitats" reduced to 8,523 km^2 (steps 2-4, Fig. 2.5b). The largest contiguous block, 4,781 km^2, which constitutes over half of the potential habitat, was in southern and eastern Taiwan (dark green in Fig. 2.5b) mostly on the eastern side of the Central Mountain Range and was separated from the remaining blocks by the high mountains (> 3,000m) of the Central Mountain Range. The second largest block (1,598 km^2) was in the Snow

Mountain Range (yellow in Fig. 2.5b); while the third largest block (695 km^2) was on the western side of the Central Mountain Range. These fragmented blocks were connected after applying the 500m buffer (see step 5, Fig. 2.6a). This buffering increased the area of potential habitat from 8,523 km^2 to 12,507 km^2. Removing areas around roads and villages, which are unlikely to be utilized by clouded leopards, halved the potential habitat to 6,734 km^2 (step 6, Fig. 2.6b). With this manipulation the largest contiguous block was now 2,555 km^2 in central/eastern Taiwan while the second largest was 2,022 km^2 in southern Taiwan encompassing the study area (Fig. 2.6b).

As noted earlier, prey base differed by altitude and sufficient prey could be found only below 2,000m (this study). Therefore, remaining areas with a sufficient prey base from the suitable clouded leopard habitat left only 4,688 km^2 below 2,000m and 2,830 km^2 below 1,500m (step 7, Fig. 2.7). The largest contiguous block below 2,000m was 1,329 km^2 and included the study area. In summary, most suitable habitats today are concentrated in southern and eastern Taiwan, which agrees with Kano's report over 70 years ago (Kano 1929) that clouded leopards were more common in southern and eastern Taiwan. The latest clouded leopard records also were located near these areas (Rabinowitz 1988, Wang et al. 1995). But, the current suitable habitat is fragmented to many smaller patches isolated by roads, agriculture lands and coniferous plantation forests, especially below 1,500m where the most abundant prey are found.

Discussion

Formosan clouded leopard field survey

No hair snare surveys on clouded leopards in the world had ever been published or conducted prior to this study. Although I had successfully tested hair snares for captive clouded leopards, it is unknown whether hair snares are effective for wild clouded leopards and how much effort is needed to detect their presence. Although success was reported for ocelots, bobcats (*Lynx rufus*), pumas (*Puma concolor*) and Canada lynx (McDaniel et al. 2000, Weaver et al. 2005, Harrison 2006, Zielinski et al. 2006), these were mostly conducted in temperate areas. Low detection rates have been reported in some lynx hair snare surveys conducted where population densities are low (Murphy et al. 2005). Our experiences in tropical forests suggested that hair snares may not work well in hot, humid areas with frequent rain. In this study, Velcro pads were gnawed or chewed off by spinous country rats, Formosan serows, sambar deer or other unknown animals, which would also pollute hair DNA. Lures did not last long, either. Typhoons and torrential rains often washed away the catnip and hot temperature evaporated catnip oil quickly. Ants also were observed moving away the dried catnip within 1 to 2 days after set up. Wind always blew away the visual lure aluminum pan. In addition, remoteness made frequent checking impossible and thus the long interval of exposure to sun and rain before retrieving the hairs may make the hair DNA unusable. A lot more effort may be required to detect clouded leopards in tropical areas by hair snares.

The 13,354 camera trap days were well above the average camera trap days required to obtain one clouded leopard picture in other countries (Table 2.4). The total number of camera trap sites in this study (377) were also high compared to some places which successfully document clouded leopard occurrences with as few as 8-24 camera trap sites (Table 2.4). If non-trail sets are excluded because of uncertain effects of lures or other factors, and only trail sets below 2,000m (i.e. areas with sufficient prey) are included, the 5,084+ camera trap days recorded is still very high compared to the 879 camera trap days per clouded leopard required in Peninsular Malaysia (Table 2.4).

However, the set up style and location selection of the camera traps in this study differs from others in many aspects. First, this study is the only one to set up cameras 2m high, tilting cameras (with the sensor detecting the same as the camera's view) downward 40-60 degree and detecting animals in a "bird's eye" view. Cameras in other studies were all set up around 0.5m high and detected passing animals in a "parallel to the ground" view. This makes the detection area different between this study and other studies. The detection range in this study was generally smaller and narrower than others as camera traps in other studies were set up at optimum locations for tigers and other large carnivores, mostly along logging roads, dry stream beds or wide open trails. The detection range of the "roads or wide open trails" is thus much wider than the width of our sampled trails within forests (<1m and mostly around 0.5m in the aspect of "bird's eye detection"). Detection rates have been found to differ between roads and forest trails. In a Brazilian rainforest, 96% of carnivore pictures were obtained on dirt roads, and ocelots' and pumas' photographic rates on roads were 14 times and 8.4 times higher than on forest trails, respectively (Trolle and Kery 2005). Similarly, Di Bitetti et al. (2006) and Dillon and Kelly (2007) found much higher ocelot photographic rates on roads than on newly cut trails in forests. For jaguars, Maffei et al. (2004) also reported 4-6 times higher photographic rates on roads than on trails in 2 of the 3 sampled areas while the third area had similar photographic rates between pipeline/dirt roads and old/clean trails. Larger cats are likely to prefer to travel on more open roads or clean trails than travel through dense vegetation in forests (Emmons 1988). Clouded leopards were observed to travel on logging roads (Rabinowitz et al. 1987) and the camera trapping studies having higher clouded leopard photographic rates tend to place camera traps along roads or more open tiger trails or tiger occurrence locations (Table 2.4). Although our camera traps were set up to aim at wildlife trails within forests, the trails were mostly about 0.5m in width and surrounded by dense vegetation. Furthermore, trail sets in this study sampled not only “good” locations, but also “bad” locations where little animal sign was observed. The purpose of the “downward” detection and the “not-all-optimal” location selection strategy was to make the detection ranges more consistent between different camera trap sites and to sample various habitat types so that habitat use could be studied. Based on differences of the sampling strategies and the comparison of photographic rates between roads and trails, the effort to get one clouded leopard picture for this study, if the clouded leopard was present, would be higher and may be up to several to 10 times more than other studies. Nevertheless, 5,084+ camera trap days from trail sets below 2,000m is still more than 5.8 times the maximum effort needed in Peninsular Malaysia (879 camera trap days/clouded leopard, Table 2.4); and the total 13,354 camera trap days is 15 times more. Carbone et al. (2001) used computer simulation based on a random walk model and showed that 1,000 camera trap days are sufficient to document tiger presence at low density of 0.4-0.7 tiger/100km^2. Thus, our effort was 13 times more than the random walk model prediction and may imply that the study area (930km^2) may have at most 1 clouded leopard. Given the hair snare and camera trapping effort conducted, the chance of clouded leopard existence in the study area is very slim. Even if they do exist, they are likely surviving in very low numbers and may not be able to sustain a viable population.

The study area is the largest and the most contiguous block of suitable habitat for clouded leopards left in Taiwan, yet no clouded leopards were found suggesting that the Formosan clouded leopard may be extinct, or on the brink of extinction, not only in the study area, but also in all of Taiwan. Many camera trapping studies have been conducted all over Taiwan by other researchers (Fig. 2.8) in the past 10 years for various purposes.

The camera trapping effort around the 8,523 km^2 of “potential habitat” in Taiwan totaled well over 40,000 camera trap days, including the 13,354 camera trap days in this study, yet no clouded leopard occurrence has ever been documented. The extensive camera trapping effort in Taiwan suggests that clouded leopards are very likely to be extinct in Taiwan. It is possible that there still may be some clouded leopards left in Taiwan, but I believe that the chance is very slim.

The use of photographic rates from camera trapping for prey base

Although density is usually used as an index of availability, such information is difficult and costly to obtain. For example, line transects to estimate prey densities were not feasible in the study area as it is difficult to sight animals in dense evergreen forests. Rarity of animal sightings, limited visibility and terrain ruggedness will violate assumptions and make estimates from line transects unreliable. In addition, density may not be representative of availability or encounter rates of prey (page 475 in Braun 2005). The use of camera trap photographic rates may provide a better way than densities to estimate prey availability. First, camera trapping is independent of prey species and is standardized and unbiased between different observers, weather conditions, and habitat types. It is much cheaper than density estimates and could be used on multi-species simultaneously. Second, the “downward detection” of camera traps utilized in this study is more similar to the hunting strategy of clouded leopards, i.e. waiting on tree branches. Even if clouded leopards switch to hunt by searching, which is similar to line transects, the encounter rates of animals on line transects also has been shown to be highly correlated to photographic rates from camera trapping (Rao et al. 2005). More importantly, photographic rates from camera trapping could be expressed as daily encounter rates of prey for comparison studies of daily requirements of meat, which could not be achieved by density estimates. Furthermore, even though densities were preferred as indices of availability or encounters, photographic rates from camera trapping were shown to be highly correlated to density estimates of ungulates (O'Brien et al. 2003) in Sumatra and sambar deer in Taiwan (Liang 2005), which are major prey species of big cats including clouded leopards.

However, clouded leopards would be better than researchers in selecting “camera trap locations” or “transects” for their own hunting purposes. Clouded leopards may use other clues and their own senses to pick the best spots to wait or hunt for passing prey. In addition, a clouded leopard may be able to ambush and chase in a greater distance than a camera trap’s detection range. Therefore, camera trap photographic rates based on a more general sampling may make our estimates of DERP and DERPg lower than actual encounter rates if animals are similarly unaware between a hiding clouded leopard and a camouflaged camera trap on a tree. Albeit clouded leopards may hunt at a greater distance than a camera trap could detect, the farther an animal is from a clouded leopard, the lower the hunting success tends to be (leopards in Stander et al. 1997). Dense vegetation also may limit the prey detection distance of clouded leopards, while the detection range of a camera trap may be larger than perceived, as a traveling animal within a certain distance of a camera trap is likely to travel along the trail and pass the camera trap sooner or later. Thus, under-estimation of DERP and DERPg may lead to conservative encounter rates in this study.

In contrast, we believed that our DKRP and DCRPg based on DERP and DERPg are likely to be overestimated. First, DERP estimates daily encounter rates of prey if clouded leopards wait and hunt all day for passing prey, which is unlikely. In terms of time spent in “waiting for passing prey”, camera traps may have higher encounter rates than clouded leopards albeit clouded leopards track the activities of their prey (Grassman et al. 2005b) and hunt when their prey are the most active. Secondly, for large prey in areas without human hunting, top carnivore predation is likely to be absent since no clouded leopards were found. The population densities of large prey lacking top-down regulation may thus be higher (Terborgh et al. 1999, Terborgh et al. 2001). In other words, DERP and DERPg may be higher than they were when clouded leopards existed. This would make the comparisons of DCRPg to the minimum daily meat requirement, i.e. 1.1kg/day/clouded leopard, more conservative. Third, DERPg assumes that a clouded leopard makes a hunting attempt per prey encounter and this is unlikely to be the real scenario. Cheetah attempted to hunt in 57.5% (average of male coalitions and female family groups) of prey encounters and in 20% or even lower under unfavorable conditions (Mills et al. 2004). Furthermore, hunting successes were maximum estimates because successful kills were easier and more obvious to register than unsuccessful hunts (Pedersen et al. 1999). When the rate of hunting attempts/prey encounter (e.g. using Cheetah’s 57.5% or 20%) and lower hunting success enters into the calculations, DKRP and DCRPg become even lower. Finally, the maximum meat consumption from large prey (50kg) used in this study is very likely too high for a clouded leopard based on the feeding ecology of female Eurasian lynx (Pedersen et al. 1999), which weigh similar to clouded leopards. Thus, DCRPg is likely to be biased high by sambar deer.

Even though DKRP and DCRPg were not precise or absolute measures of daily prey kill rates and consumption rates, conclusions from our DCRPg and 1.1kg/clouded leopard requirement comparisons should be reasonable and legitimate because DCRPg were likely overestimated and the minimum 1.1kg/clouded leopard threshold was a lower and conservative measure (see method). Furthermore, DERP and DERPg was unlikely affected by the above issues when DERP and DERPg were compared between different altitude zones and between hunted and not hunted areas for each prey species. This would certainly help understand the patterns and relative importance of various prey species and the altitudinal trends and human hunting influences.

Major potential mammalian and avian prey of clouded leopards in Taiwan

Camera trapping has been used in many studies of tigers and their prey (O'Brien et al. 2003, Karanth et al. 2004, Kawanishi and Sunquist 2004, Johnson et al. 2006) and has been proved as a successful tool in documenting clouded leopards’ prey in Taiwan from this study. Almost all major potential mammalian and avian prey species of Formosan clouded leopards were photographed.

The clouded leopard is renowned for its arboreal capability (Gonyea 1976;1978, Nowell and Jackson 1996). However, all the confirmed prey except primates are generally terrestrial. Clouded leopards may hunt primates in trees (Davies 1990) or on the ground (Gibson-Hill 1950). Since Formosan macaques frequently travel on the ground (Pei 1998), we conjecture that clouded leopards could ambush macaques either from trees or on the ground. Since most prey in trees could escape by flying, gliding or jumping to thinner or higher branches inaccessible to clouded leopards, Formosan macaques should be the most important and probably the only principal species of all the arboreal prey preyed upon in terms of encounter frequency and percentage of detection sites (Table 2.10), and most important of all, the meat weight contribution. This agrees with Kano’s report (Kano 1930) that clouded leopards prefer to prey on macaques based on his extensive interviews with aborigines in the 1920s when clouded leopards likely still survived in Taiwan. Other arboreal mammalian species and birds may be caught opportunistically either on trees or on the ground and would be insignificant in meeting clouded leopards' energetic requirements.

Grassman et al. (2005b) speculated that clouded leopards hunt more small prey (≤2.5kg) than large prey based on their radio telemetry data showing a high proportion of large daily movements. They assumed that clouded leopards would move less if they killed large prey. Two of the 6 confirmed prey species for clouded leopards (Grassman et al. 2005b) were over 24 kg, 1 was around 6kg and the other 3 were ≤2.5kg. Small mammals (≤2.5kg) constituted 78% frequency of occurrence (39% Muridae) in the 21 "medium-sized cat" scats they found for clouded leopards, Asiatic golden cats (*Catopuma temminckii*) and other medium cats in Thailand (Grassman et al. 2005b). No birds were found in the "medium-sized cats" scats. However, the possibility of the scats belonging to the smaller Asiatic golden cats might obscure the food habits of clouded leopards. Only 2 of the 7 clouded leopard scats found by Griffiths (1993) in Sumatra consisted of prey less than 2kg. It is unknown whether this was due to the difference of prey availability, competition with other sympatric big cats such as leopards and tigers, or clouded leopard behavior. However, the above percentages were only frequency data. Clouded leopards are capable of killing large prey (Pocock 1939, Lekagul et al. 1977, Therrien 2005b) including orangutans (Nowell and Jackson 1996, S. Wong, personal communication). Larger prey (>2.5kg) could be more important in terms of meat consumed based on either the confirmed prey or the un-differentiated "medium-sized cats" scat analysis. In Taiwan, over 80% of the encounters of major potential prey were macaques and ungulates greater than 9kg (DERP in Table 2.5). When larger prey are more frequently encountered and clouded leopards are capable of killing them, there would be little necessity to spend more energy to actively travel more distance in search of smaller prey in Taiwan. Clouded leopards in Taiwan used trees more often (54%, Rabinowitz 1988) than in Malaysian Borneo (18%, Rabinowitz et al. 1987), thus clouded leopards in Taiwan might actually spend more time in trees either waiting for passing prey or resting as they do not need to travel in search of smaller prey. Although clouded leopards in Taiwan would also hunt smaller prey (<5kg), the DERP would be less than 1/4 that of macaques and ungulates and total DERPg of the smaller prey would average less than 0.8% of the 5 largest prey for all altitudes! Thus, in Taiwan, spending a lot of time traveling to forage for smaller prey would not be optimal for energy maximization (Griffiths 1975, Pyke et al. 1977, Griffiths 1980).

The average prey weights of tigers and leopards in India are 91.5kg and 35.6kg, respectively (Karanth and Sunquist 1995), which is generally less than the cats' own body weights. By means of a meta-analysis of over 30 studies across 13 Asian and African countries, Hayward et al. (2006) similarly found that the ratio of leopard body weight to the preferred prey is 1:0.79, i.e. leopards preferred prey weighing less than their own body weight. Carbone et al. (1999) also summarized pertinent literature and predicted that carnivores weighing less than 21.5kg feed mostly on prey that is 45% or less of their own weight. Formosan macaques and Reeve's muntjacs average 9.5kg, which is around 55% of the clouded leopard's average body weight. Furthermore, they are approximately equal to the average weight of confirmed prey from scat analysis and field observations (Griffiths 1993, Grassman et al. 2005b). Although DERP and DERPg of macaques was not as high as muntjacs at altitudes < 2,500m, available biomass of Formosan macaques was likely underestimated since DERP and DERPg is based on groups. Formosan macaques usually travel in group of 20-30 individuals and make loud sounds when foraging making them easy to detect. Formosan macaques should be as important as Reeve's muntjac since clouded leopards are said to prefer primates in Taiwan (Kano 1930), though a Reeve's muntjac is likely to be more vulnerable and easier prey than one or a group of macaques.

In addition to Formosan macaques and Reeve's muntjacs, there are 4 other large and medium prey (>4kg, Table 2.5) in Taiwan (sambar deer, wild boar, Formosan serow, and Chinese pangolin). Although a clouded leopard has been observed feeding on a Malayan pangolin (*Manis javanica*, average weight 6kg) (Grassman et al. 2005b), DERP of Chinese pangolins was extremely low in my study area. Formosan serows, together with macaques and muntjacs, had a higher DERP and percentage of detection sites than sambar deer at all altitudes. These 3 species constituted over 90% of the total encounters of large and medium prey across all altitudes. But, sambar deer stand out as the more important prey in some altitude zones in terms of DERPg (i.e. more meat). Although clouded leopards would be capable of killing sambar deer weighing 165kg (Swinhoe 1862, Kano 1930, Nowell and Jackson 1996), skull analysis suggested that large prey need to be partially restrained for clouded leopards to deliver a powerful bite at the back nape (Therrien 2005b). This also suggests that sambar deer would not be easy prey like macaques or muntjacs, i.e. hunting attempts may be lower than other prey and hunting success could be much lower than the 20%. Eurasian lynx regularly prey on reindeer up to 4 to 8 times of their body weight. But, the reindeer killed were generally in poor body conditions (Pedersen et al. 1999). We speculate that clouded leopards would prey mostly on smaller, weaker or younger sambar deer, as large and healthy sambar deer are not only more difficult, but also not completely consumable before being scavenged, or decomposing. Therefore, the encounter rates of suitable-sized sambar deer as prey likely would be low. Even if 50kg is used as the maximum consumable meat in the DERPg calculation, 50kg is still conservative and likely too high for clouded leopards to consume in a short period before making the next kill. Thus, the importance of sambar deer may be inflated and the contribution of sambar deer is unlikely to be as large as its original DERPg implies. The last large prey, wild boars, may be similar to sambar deer, but the DERP was very low and the DERPg was even lower than for the other large prey. Moreover, wild boars often cause human injuries in Taiwan and may be too aggressive to be prey even for larger cats like leopards (Eisenberg and Melvyn 1972, Ramakrishnan et al. 1999, Hayward et al. 2006).

When the rarely encountered Chinese pangolin (average weight 4.5kg) and the unlikely prey flying squirrels and small carnivores (average weight < 3kg, Table 2.5) are excluded, the prey for clouded leopards in Taiwan sharply divides into two size categories (Table 2.5): ≥9kg (macaques and ungulates) and ≤1kg (birds and rodents). Although clouded leopards might also prey on smaller carnivores in Taiwan, there is no confirmed record of carnivores being prey of clouded leopards (Griffiths 1993, Nowell and Jackson 1996, Grassman et al. 2005b). For prey in the ≤1kg category, only pheasants are around 1kg and all the others are less than 0.4kg. Given their weight ranges and highest encounter rates and occupancies, we maintain that Formosan macaques, Reeve's muntjacs and Formosan serows should be the 3 most important prey species of clouded leopards in Taiwan. Sambar deer and wild boars may be taken occasionally. The other smaller prey (≤1kg) are likely to be killed incidentally and clouded leopards are unlikely to spend much time traveling in search of such small prey that is usually less than 0.4kg.

Altitudinal trends

Altitudes lower than 2,000m, which provide significantly more prey than 1.1kg/day/CL, are possibly the only suitable altitude range for clouded leopards in Taiwan. Of the three most important prey species of clouded leopards in Taiwan, Formosan macaques and Reeve's muntjacs decrease significantly as altitude increases, and Formosan serows occur the least frequently at altitudes between 2,000m and 2,500m (Table 2.5). Nearly half of the DCRPg (44%) of altitude zone 2,000m-2,500m came from sambar deer and wild boars. Thus, the DCRPg may be biased high by sambar deer and wild boars due to their larger size, potential danger, and likely lower hunting attempts and successes mentioned earlier. If sambar deer are excluded, the all-prey DCRPg drops almost 300g to 460g/day, which is similar to the DCRPg of altitude zone 2,500-3,100m and far below the expected daily requirement (1.1kg/day) for a clouded leopard.

Expected kill rates (days/kill) at the 4 altitude zones (from low to high) were 5.4, 8.5, 17.2 and 29.5 days, respectively (Table 2.5). At altitudes below 1,200m clouded leopards would have almost the same average kill rates as the similar-sized female Eurasian lynx and other larger cats (average 1 kill per 5 days in: Breitenmoser and Haller 1993, Okarma et al. 1997, Stander et al. 1997, Pedersen et al. 1999, Power 2002). In contrast, it would take almost a month to make a kill if clouded leopards lived at altitudes above 2,500m. As altitudes get higher, prey >25kg (i.e., heavier than a clouded leopard) constituted a higher percentage of total prey available (DERP:12%, 21%, 26%, 53%; DERPg:35%, 59%, 64%, 85%, for the 4 low-to-high altitude zones, respectively; calculated from Table 2.5), which may not be good for clouded leopards (Griffiths 1980, Carbone et al. 1999). That is, clouded leopards would tend to hunt either large prey more (e.g. sambar deer, wild boars and serows), or spend more energy searching for smaller prey, which likely would result in more travel and an increase in home range size. As a result, the energetic requirement would increase making the daily meat requirement higher than 1.1kg/day at higher altitudes, which had less sufficient prey than 1.1kg/day.

Although smaller carnivores (<3kg) are not included in the potential prey of clouded leopards, the total DERPg of the 5 smaller carnivores decreases at higher altitudes (Table 2.5). Even if the smaller carnivores were included in DCRPg, they would not contribute enough to reach the required 1.1kg/day for altitudes higher than 2,000m. Thus, we believe areas above 2,000m in Taiwan are unsuitable to sustain a population of clouded leopards. Although no data of prey base is available for altitudes above 3,000m, I expect the prey base to be less than at lower altitudes based on the altitudinal distribution patterns of prey (Table 2.5) and personal observations.

If setting up or revisiting a camera trap site is analogous to a clouded leopard traveling to hide in a hunting spot, TFD is less at lower altitudes for most prey species (Table 2.8). From the perspective of prey availability, lower altitudes should be the best habitat for clouded leopards in Taiwan. The results of altitudinal trends based on TFD (Table 2.8) and DERP (Table 2.5) were similar except that the altitudinal trend was not significant for the Taiwan partridges in TFD. This indicates that TFD is a good indicator of photographic rates. But, there were 2 major differences between TFD and DERP (photographic rates). TFD treats no detection as right-censored and is included in the analysis while DERP ignores false absence and treats no detection as 0 encounter no matter how long the camera trapping effort is. Second, TFD analyzes only the first occurrence event for each roll of film while DERP includes all events.

Influences of hunting and other human activities

DERP and DERPg of all large and medium prey (>4kg) except wild boars and Chinese pangolins were significant lower in areas with human hunting (Table 2.7), making the DCRPg in areas with human hunting lower than 1.1kg/day minimum requirement. Similarly, TFD was also significantly longer in areas with hunting activity except for wild boars, macaques, and Chinese pangolins. That is, clouded leopards would have to wait longer or spend more energy searching for prey in areas with uncontrolled hunting, and the prey base may not sustain a population. Although DERP and DERPg of Chinese pangolins did not differ between hunted and not hunted areas, the p-value (0.085) was close to 0.05 (Table 2.7). The absence of Chinese pangolins from camera trapping surveys in hunted areas may signify the population was also likely lower in hunted areas as Chinese pangolins are valuable for their medicinal uses. In contrast, none of the smaller prey (<2kg) and carnivores, except yellow-throated martens, differed between areas with human hunting and without human hunting. This is largely because hunters target larger species for their meat or commercial value, and smaller animals are less likely to be captured by the use of larger leg-hold traps, snares and night spotlight shooting (many smaller prey are diurnal). Flying squirrels are heavily hunted, but camera traps seldom photographed flying squirrels on the ground and the hunting influence is unlikely to be revealed by camera trapping. Macaques are also arboreal, but spend quite some time traveling on the ground (second highest overall GOI and SOI of all camera trapped species). They are not a major hunted species, but hunters sometimes still shoot macaques and hunters' traps may still impose an influence on the population.

Rao et al. (2005) also found lower encounter rates and photographic rates from camera trapping of many species closer to villages where bush meat was hunted. This inverse relationship between abundance of targeted wildlife and accessibility or proximity to human settlements has been documented elsewhere (Clayton et al. 1997, Peres and Lake 2003). With the substantial hunting pressure, forest alterations, and disturbances close to major roads and villages (i.e., human activity, HA), the prey base is unlikely to fulfill clouded leopards' needs in these easily accessible areas (Fig. 2.4a) unless the area is protected from hunting and maintained as primary forests. However, such areas could barely be found in Taiwan. In addition to hunting, clear cutting for timber and agricultural encroachment were also extensive for the past hundreds of years especially during the 20th century. Plantation forests and agricultural lands are found to be absent of the large herbivores or to have much less herbivores when they are a mosaic or close to primary or secondary forests (Spearman's rank correlation -0.82 between the 5-herbivore DCRPg and history of forest practices and agricultural uses used in HA, $p<0.001$).

Larger variations of the 5-herbivore DCRPg in less disturbed areas (Fig. 2.4a) probably come from sambar deer and altitudinal differences. When sambar deer are excluded from the 5 large herbivore prey species (Fig. 2.4b), the standard deviation was reduced from 877 to 425 g/day and the CV dropped from 65.8% to 46.4% considering only the 11 less-easily-accessible areas with higher and more variable DCRPg. Sambar deer were not found in 8 of the 10 easily accessible areas and were extremely rare in the other 2. The other 11 areas, away from human encroachment, also tended to have less sambar deer at the southernmost or northernmost areas than areas in central Taiwan. Lee and Lin (2006) pointed out that sambar deer are more abundant around mosaics of Taiwan fir forests and Yushan cane grasslands occurring at altitudes higher than 3,000m. Such vegetation is abundant in central Taiwan as many high mountains (>3,000m) are present. However, the Taiwan fir forests and Yushan cane grasslands is completely absent in the study area and other areas in northern or southern Taiwan where the mountains are lower. Cross-island roads have made the areas around northern and southern Taiwan more or less fragmented from central Taiwan, which acts like a “source” for sambar deer and other larger prey due to larger areas and remoteness. Based on the current literature, the study area seems to be the southernmost limit of sambar deer distribution in Taiwan. Thus, population density of sambar deer in the study area may not be as high as other areas around central Taiwan. Some of these areas around central Taiwan have more or less hunting activity reported, but they still have a sufficient number of large prey for clouded leopards, contrasting to the hunted areas in southern and northern Taiwan. It is possible that these areas are close to the “source populations” in central Taiwan where larger and contiguous primary forests, including large areas at altitudes > 3,000m preferable by sambar deer, are still found. In addition to sambar deer, “source areas”, which are generally very remote and too far for hunters to be willing to hunt, may also provide refuge for other herbivore species. This is shown in the best model based on human activities (HA), distance to central Taiwan (DCT), and average altitude to explain the 5-herbivore DCRPg variations across Taiwan (Akaike weight 84.3%, Table 2.9). That is, a higher herbivore biomass could be sustained in areas with less human activity, at lower altitudes and closer to central Taiwan.

The study area (see Fig. 2.7) is basically the southernmost primary forests remaining in Taiwan, and surrounding areas were encroached upon from the east and west sides making the study area an elongated shape. The elongated narrow shape makes the study area more accessible from both sides. Thus, the study area has little remote areas which are free from human hunting. Being far away from central Taiwan plus the long history of heavy hunting may make the study area unable to provide sufficient prey for a long time before the hunting ban in 1973. In contrast to the study area, lower altitudes closer to central Taiwan but away from major roads and aboriginal villages seem to be able to tolerate certain levels of human activity while providing sufficient prey for clouded leopards at the same time. However, the contribution to DCRPg would come more and more from sambar deer for places near central Taiwan. Since sambar deer are large and may not be the most important prey, human activity needs to be much less or even none to maintain sufficient prey for clouded leopards when sambar deer are excluded (Fig. 2.4b).

Historically, many larger mammals in Taiwan were threatened or critically endangered due to commercial hunting, poaching, and human encroachment (Lee and Lin 1992). Sika deer, with more than 120,000 deer pelts exported annually in 1630's (Chiang 1985), are now extinct due to commercial hunting and loss of lowland habitat (McCullough 1974). Before the Wildlife Conservation Law was enacted in 1989, at least 26,000 muntjacs, 7,300 serows, 6,700 wild boars, 3,500 macaques, 200 sambar deer and tens of thousands of other smaller wildlife were poached for meat and pelts annually (Wang and Lin 1986). The illegal hunting likely imposed much heavier cropping pressure on the larger prey of clouded leopards since the statistics of poaching did not include animals not sold to game meat shops, utilized by hunters/aboriginal villages themselves, and those rotten and wasted animals that died in traps due to infrequent checking in remote areas. Hunting pressure documented in this study is likely far weaker than the illegal hunting before 1989. But, prey base in hunted areas was lower than the needs of clouded leopards even though the forest is still primary or minimally disturbed in my study area. Previous commercial hunting and poaching may have pushed the prey base (DCRPg) lower than we documented in the hunted areas of this study. Although sufficient prey was found in areas without hunting, very few places at altitudes < 2,000m were free from hunting before 1989. It is likely that clouded leopards' prey were severely diminished all over Taiwan for tens of years before 1989. We believe that the historical uncontrolled hunting, which has been much greater than the hunting pressure documented in this study, in combination with the loss of habitat due to human encroachment and timber harvest, which was maximal during the 20th century, caused prey depletion, which could not sustain a healthy clouded leopard population in almost all of Taiwan. Even if remote areas around central Taiwan retain some prey for clouded leopards, the generally higher altitude may not have been able to support a clouded leopard population in the past even though 5 of the 7 most recent clouded leopard records (except the latest record around eastern Taiwan in 1989-1990) between 1981-1983 were found in Yushan National Park (Rabinowitz 1988), which is close to central Taiwan (Fig. 2.7).

Comparison to other countries

Compared with the prey base of clouded leopards from camera trapping studies conducted in other countries (Table 2.11) with populations of clouded leopards, the DCRPg in other countries (N=6, $\overline{X}$=455g/day with 95% CI=(301, 605) g/day) is significantly lower than in Taiwan. This may be due largely to the differences of camera trapping locations mentioned previously. Trolle and Kery (2005) found that tapir (*Tapirus indicus*) and some non-carnivore mammals were photographed more often on forest trails than dirt roads, while carnivores were the reverse. Many big cats and other carnivores use dirt roads/open trails for travel and it is possible that their prey may use the open roads without cover less to avoid predation. In addition, the mammalian prey of clouded leopards camera trapped in Taiwan is quite complete while some mammals like primates were known to exist, but not recorded at all in other Southeast Asian countries, e.g. some prey may avoid open roads. This may be why DKRP/DCRPg in this study was higher, as trail sets within forests were utilized exclusively in this study while other Southeast Asian camera trapping studies put cameras mostly along roads or in more open habitats focusing on tigers. If camera traps in the other studies had been put on forest trails where clouded leopards actually hunt instead of travel paths along roads, the final DCRPg likely would have been higher as higher photographic rates may have documented more potential prey species. Furthermore, it is unknown whether lower height of camera traps in other countries (0.5m) would be detected more easily by passing prey species than high camera traps in Taiwan (2m). Horizontal detection of low camera traps may fail to detect some smaller animals, which could also be prey of clouded leopards, while high camera traps may be more similar to clouded leopards hunting perspective on the trees. Protocols of camera trapping studies in Taiwan are pretty much the same, thus comparable. However, the camera trapping protocol used in this study differed from those in other countries not only in the camera trap locations, but also in the height of camera traps. Caution should be used when comparing camera trapping rates between Taiwan and other Southeast Asian countries with different protocols, especially when camera trap locations in relations to roads differed (Trolle and Kery 2005). On the other hand, there were tigers, leopards and other large carnivores competing with clouded leopards for prey in these Southeast Asian countries except Borneo. These large carnivores may be regulating or limiting their prey. This may possibly make the DKRP/DCRPg lower in other Southeast Asian countries because of lower prey densities. In contrast, there was no clouded leopard predation and human hunting in my study area, i.e. free of top-down regulation. Nevertheless, clouded leopards in Thailand spent a large portion of time moving

(Grassman et al. 2005b), and clouded leopards (*Neofelis diardi*) in Borneo were observed traveling more on the ground (82%, Rabinowitz et al. 1987) than clouded leopards (*N. nebulosa*) in Taiwan (46%, Rabinowitz 1988), which may imply less abundant prey in Thailand and Borneo forcing clouded leopards to travel more in search of prey.

Current suitable habitat

The 500m buffers created around potential habitat (see methods) increased potential habitat nearly 4,000 km^2, close to half of the original area, raising two possible issues. First, the potential habitat is likely to be seriously fragmented, not compact, and with a lot of edges (Fig. 2.5b). This may not be good for an interior species like clouded leopards (Grassman et al. 2005b). Second, the extra buffer zones are mostly unsuitable habitat such as higher altitudes (>2,000m), agricultural lands, plantation forests and even landslides and cliffs. Clouded leopards may just travel through and may not hunt near the edges at all as these buffer zones do not have sufficient prey due to the vegetation types.

The meta-analysis of camera trapping studies in Taiwan showed that the prey base close to major roads and villages is on average less than 1/3 of the 1.1kg/day required by clouded leopards. Therefore, after removing potential habitats (buffer) within 3km of major roads or within 5km of villages, which would not provide sufficient prey, Fig. 2.6b is likely the maximum available potential habitat (buffered) left for clouded leopards in Taiwan. Although the southern block encompassing the study area is 532 km^2 (21%) smaller than the central block, the southern block is more compact with fewer edges. But, the interior excluded regions of the central block, which are mostly primary Taiwan fir forests and Yushan cane grassland above 3,000m, may be utilized by clouded leopards. That would make the central block even larger and more compact if clouded leopards used the habitats at higher altitudes. Being located in central Taiwan, the central block may be able to provide marginally sufficient prey at higher altitudes. However, to survive in higher altitudes (>2,000m) with less prey, the prey biomass would largely come from sambar deer, which may not be favorable as discussed previously. We maintain that suitable habitats for clouded leopards are largely at altitudes lower than 2,000m and the best habitats are at altitudes lower than 1,500m with even more abundant prey. Clouded leopards may extend part of their home ranges to higher altitudes, but the habitat there is marginal.

Although sufficient prey was documented in parts of the study area, the total area with sufficient prey may not be large enough to support a viable population of clouded leopards since the suitable habitat with sufficient prey (Fig. 2.7) is assumed to be completely undisturbed and abundance of prey unaffected by hunting or other human activities. Over 50% of the study area is exposed to persistent hunting (personal field observations) and is still included in the suitable habitat below 2,000m (Fig. 2.7). Given that human activities could lower the prey base below requirement, the area of suitable habitat in Taiwan with sufficient prey below 2,000m (4,688 km^2, Fig. 2.7) may actually be 50% less than it is implied assuming that 50% of the suitable habitat in all Taiwan is exposed to hunting similar to my study area. Even though the total area of suitable habitat below 2,000m without hunting could be 2,344 km^2 (50% of the total area 4,688 km^2 of suitable habitat at altitudes < 2,000m in all of Taiwan), habitat fragmentation (Fig. 2.7) could impose further problems. That is, the largest block located in southern Taiwan (1,329 km^2), which encompasses the study area, may provide less than 670 km^2 (50% of 1,329 km^2) of habitats with sufficient prey; the other fragmented blocks provide even less area. Populations in these smaller patches might be very small and prone to local extinction.

In summary, habitat loss and fragmentation, and prey depletion, are likely to act together and drive the disappearance of clouded leopards in Taiwan. Habitat loss and fragmentation not only diminished habitat and fragmented the population into smaller subpopulations, but also reduced prey base simultaneously. Prey depletion was caused by hunting, which further worsened the habitat loss situation and made the several isolated smaller populations even more prone to extinction due to lack of prey.

Historical pelt trade, occurrences or nonexistence of clouded leopards in Taiwan

Formosan clouded leopards were first scientifically revealed to the world in 1862 by Swinhoe who acquired a flat skin from aborigines (Swinhoe 1862). Since then, others have reported the status and distribution of clouded leopards in Taiwan (Kano 1929, Wayre 1969, McCullough 1974, Rabinowitz 1988, Lee and Lin 1992, Wang et al. 1995). However, none of these were based on records of live clouded leopards. Rather, most were based on interviews with aborigines and those records were difficult to substantiate. Some have questioned whether clouded leopards ever existed in Taiwan since almost all hard evidence, excluding sighting or captures by aborigines, of Formosan clouded leopard records were pelts, which could be easily traded into Taiwan from other countries in Southeastern Asia. In contrast, export of clouded leopard pelts were actually documented in some reports. Swinhoe (1862) noted that aborigines from the remote interior of Taiwan mountains brought skins of clouded leopards to towns to barter with the Chinese. He also got a few more clouded leopard skins near the ports in northeastern and southern Taiwan (Swinhoe 1864). Records of exporting furs or meat of clouded leopards could even be traced back earlier to the 13th century (Kuo 1973) when traders in

Penghu islands, isles between Taiwan and Mainland Asia, traded in dried leopard meat from the aborigines of Taiwan and sold to China (Chau 1225, Hirth and Rockhill 1966). The earliest record of “leopard skin” in Taiwan was in the 7th century when Taiwan aborigines wore bear or leopard skins as substitutes of armor (histories from an ancient book “Sueisu A.D. 636” summarized in Chiang 1985). Even if the authors of the previous two ancient history books in A.D. 636 and 1225 had not been to Taiwan and their descriptions inaccurate, Wang (1349), who actually visited Taiwan, still reported that leopards, sika deer, and muntjacs were harvested by Taiwan aborigines for pelt trade to the Chinese. Chiang (1985) suggested that the pelt trade mentioned by Wang (1349) must have been ongoing for a long time based on the notion that traders separated pelts of sika deer from muntjacs. Since the 14th century the clouded leopard pelt trade has been continuously documented in the historic literature regarding Taiwan, although many of these were simply citing one another. Wearing clouded leopard pelts by Taiwan aborigines also were noted in the last three hundred years during the China Ching Empire (Huang 1722) and the Japanese Rule Period between 1895 and 1945 (Kano 1929, Yang 2000). The clouded leopard pelt trade was emphasized not only during the 19th century (Swinhoe 1862, Tang 1891), but also during the Japanese Rule Period when clouded leopards were hunted by aborigines and pelts were sold to Japanese solders (Rabinowitz 1988). Tang (1891) mentioned that the price of leopard pelts were tens of times the price of deer pelts. Hence, trade of clouded leopard pelts might have begun since the 13th century or even earlier and lasted till the 20th century. In other words, clouded leopards in Taiwan had been under harvest for pelts for centuries. Some documents mentioned that tigers, which may refer to clouded leopards, existed in Taiwan during the Dutch Rule Period in the 1600s (Campbell 1987). Since leopards and tigers were usually used interchangeably for big cats, it might imply that clouded leopards were a replacement for tigers, which were used by the Chinese for medicinal or luxurious purposes. Since tigers may be harder or more expensive to get in China, this could induce heavy demand on clouded leopards in Taiwan. In contrast to Kano's (Kano 1929) descriptions that clouded leopards were more common in southern and eastern Taiwan, Dong (1753) noted that Taiwan leopards (large and broad leaf spot pattern) were distributed in northern Taiwan, and were hard to acquire and more expensive than the pelts of the different mainland leopards (coin spot pattern). Also, leopard pelts were high value and sought after by government officials in northern Taiwan (Chen 1715). The differences might indicate that clouded leopards in northern Taiwan were already vanishing during the 18th and 19th centuries when human activities were more concentrated in northern Taiwan. Many local history books on northern Taiwan in the 18th and 19th centuries also mentioned the leopard pelt trade. Chou (1839, pages 207 and 211) described the custom tax for leopard pelts in Hsia-Men, an important port in southeastern China for Taiwan to import goods into China. Thus, it is possible that the leopard pelt trade from Taiwan had been ongoing commercially for a long time. By the 20th century, clouded leopards may have been surviving only in southern and eastern Taiwan. Hunting clouded leopards for pelt and meat trade might have imposed additional pressure on the Formosan clouded leopard population and could be another reason for their disappearance besides the lowland habitat loss and prey depletion, which happened rapidly during the past centuries.

Although many of the historic documents hundreds of years ago were not as accurate as today or were simply citing older literature, some of the literature may be reliable in descriptions of the life styles and economics of Taiwan aborigines. Nevertheless, it is still arguable that the clouded leopard pelts traded from Taiwan to other places did not originate in Taiwan, but were imported from somewhere else. However, Taiwan aborigine inhabitants of the mountains did not have the ability of sea trade (Wang 1349, Chiang 1985). Furthermore, it is unreasonable that clouded leopard pelts came from Mainland Asia and were exported back to Mainland Asia from Taiwan unless the pelts came from southern Asia islands such as Borneo or Sumatra. However, clouded leopards from Borneo and Sumatra had darker coloration (Kitchener et al. 2006) while traded pelts from Taiwan were tawny and yellow (Swinhoe 1862;1870) and belonged to the same clouded leopard group from Mainland Asia in appearance (Kitchener et al. 2006). Even though official government trade records of clouded leopard pelts could not be found in Taiwan, it is unlikely that aborigines obtained clouded leopard pelts from Mainland Asia and then traded with the Chinese to export to the Mainland Asia again. It is also unreasonable that only pelts of clouded leopards, but no other big cats were seen in Taiwan if importing leopard pelts into Taiwan had been popular at that time. Although sources of clouded leopard pelts were difficult to substantiate, a live young clouded leopard captured and raised by aborigines was actually observed in 1900 in an aboriginal village adjacent to the study area by a Japanese anthropologist (Yang 2000). This is the only record of a live clouded leopard observed in Taiwan by non-natives.

In addition to the pelt trade records and the sighting of a live young clouded leopard captured from the wild, genetic analysis further showed that Taiwan clouded leopards slightly diverged from the other mainland subspecies in haplotypes (Buckley-Beason et al. 2006). The genetic analysis used 7 samples (only one was successful in extracting DNA) from National Taiwan Museum. Although the origins were unmarked, the samples were inherited from the Japanese museum in Taiwan. Since the collections include very small clouded leopard kittens and the number of adult pelts coincided with that reported in the Taiwan mammal guide written in Japanese (Horikawa 1932), those samples were likely to be collected locally, which genetic analysis supports.

Conclusion and conservation implications

It is very probable that clouded leopards are extinct in Taiwan due to the historical pelt trade of clouded leopards, loss of lowland habitat, prey depletion, and hunting. If there are still some individuals left, it is urgent to find out whether they still survive in those areas lacking surveys (Fig. 2.8) and conduct conservation efforts accordingly as these remaining clouded leopards will be facing issues of isolated small populations, inbreeding depression and lack of suitable habitat and prey. Given sufficient funds and public agreement, it is necessary to consider reintroduction as the population size may be too small to be viable. Although genetic research recommends mainland Asia subspecies for reintroduction to Taiwan (Buckley-Beason et al. 2006), they have only 1 genetic sample from Taiwan. It is necessary to acquire more samples to assure the genetic differences. This genetic information could be used to identify any possible Formosan clouded leopards kept privately. Since these privately kept clouded leopards are aging and some people claimed their clouded leopards to be generations of Formosan clouded leopards, further genetic work needs to be done as soon as possible. It being the topmost carnivore in Taiwan, reintroduction of clouded leopards may also play its ecological role concerning the pest problem of Formosan macaques causing damage to farmers' crops and the forthcoming issue of ungulate overabundance in remote mountains where large carnivore predation and anthropogenic hunting is lacking.

A sufficient prey base and enough areas of suitable habitat also need to be assured. The special prey structure in Taiwan (2 extreme size categories) would make clouded leopards more sensitive to the population fluctuations of the 5 large herbivores, especially muntjacs, macaques and serows. Since hunting is also an issue in Taiwan, further detailed studies to quantify hunting effects on these herbivores need to be done so that reopened hunting in the future could be well managed and controlled to make sure that clouded leopards could obtain sufficient prey, especially in the lower altitudes, which are the best habitat for clouded leopards, but the most accessible by hunters. With proper management of larger prey species, populations of smaller prey would not be a problem. Conservation and management efforts should be focused on the larger prey species. Furthermore, establishing corridors between fragmented patches could maintain a larger connected area for clouded leopards. Corridors between the two largest blocks, the southern block and the central/eastern block, should be the first priority.

Clouded leopards, leopard cats, Eurasian otters and sika deer, which are restricted to much lower altitudes in Taiwan, have become extinct or critically endangered. Current surviving larger mammals have much wider altitudinal distributions. Nevertheless, many of these species are still confined to lower altitudes. Rugged and steep terrain actually worsens the fragmentation of lowlands, which are blocked by high mountains. The corridors between southern Taiwan and other parts of protected areas will be important for these lowland species. Current protected areas in lowlands are not well established. In addition, a new law being revised, which restricts development at high altitudes, may make the development pressure of lowlands even worse and more demanding. To make reintroduction plans of sika deer, Eurasian otters, and clouded leopards successful, and to guarantee survival of current populations of leopard cats, Chinese pangolins and other low-altitude species, lowland conservation in a landscape perspective will be an important and critical issue in the future wildlife conservation of Taiwan.

Table 2.1 Daily meat consumption (g) per kg felid (DMC$_{g/kg}$), daily meat consumption (kg) per individual (DMC$_{ind}$), kill rates (days/kill), and hunting success of 6 felid species.

Species	Geographic region	Sex/cub /season	weight (kg)*	DMC$_{g/kg}$	DMC$_{ind}$	Kill rates (days/kill)	Hunting success	Source
Cheetah (*Acinonyx jubatus*)	South Africa	male	43	32.6	1.4		19.3%	(Mills et al. 2004)
Puma (*Puma concolor*)	North America	male	53.1	36.4	1.9			(Laundre 2005)
		female	40.6		1.5			
		male			4-4.3			
		female			2.2			(Ackerman et al. 1986)
Lion (*Panthera leo*)	South Africa	dry season(♀)		69	8.7	3.9-5.6	17%	(Stander 1992)
		wet season(♀)	126	111	14			
						4.4	21%	(Power 2002)
Leopard (Panthera pardus)	Namibia South Africa	male	44.6	68-73	3.1-3.3			
		female (wo/cub)	25	41-57	1.6±0.5		38%	(Stander et al. 1997)
		female(w/cub)	25	85-90	2.5±0.5			
Eurasian lynx (*Lynx lynx*)	Europe	female	18.1	88.4-121.6	1.6-2.2	5-5.4		(Okarma et al. 1997)
				82.9-193.4	2.5±1	5	53%, 83%	(Pedersen et al. 1999)
						5-5.4		(Breitenmoser and Haller 1993)
Canada lynx (*Lynx canadensis*)	Canada		9.8			2.4	8.5, 21.5%	(Nellis and Keith 1968)
							30±5%	(Murray et al. 1995)

* average adult weight are based on data from (Nowell and Jackson 1996) if not reported in original literature

Table 2.2 Daily meat consumption (g) per kg felid ($DMC_{g/kg}$) of 12 felid species based on field data from 26 studies cited in Table 2.1 and appendix 1 in Carbone et al. (2007).

Common name	**Scientific name**	**Average Body weight (kg)***	**$DMC_{g/kg}$**
Jungle cat	*Felis chaus*	7	50.3
Canadian lynx	*Felis canadensis*	9	98.1
Serval	*Leptailurus serval*	11	80.3
Caracal	*Felis caracal*	11	90.1
Ocelot	*Felis pardalis*	12	58.8
Eurasian lynx	*Lynx lynx*	18	97.6
Leopard	*Panthera pardus*	37	82.8
Cheetah	*Acinonyx jubatus*	45	73.9
Puma	*Puma concolor*	48	61.6
Jaguar	*Panthera onca*	65	52.3
Lion	*Panthera leo*	136	74.3
Tiger	*Panthera tigris*	177	40.2

[*] average body weight is obtained from the original literature, from Carbone et al. (2007) or from Nowell and Jackson (1996) if not reported in the original literature

Table 2.3 Major potential prey of clouded leopards in Taiwan

Order	Family	English name	Scientific name
Rodentia	Muridae	Spinous country rat	*Niviventer coxingi*
		Formosan white-bellied rat	*Niviventer culturatus*
	Sciuridae	Red-bellied tree squirrel	*Callosciurus erythraeus*
		Long-nosed tree squirrel	*Dremomys pernyi owstoni*
		Striped tree squirrel	*Tamiops marutimus*
		White-faced flying squirrel	*Petaurista alborufus lena*
		Indian giant flying squirrel	*Petaurista philippensis*
		Hairy-footed flying squirrel	*Belomys pearsonii kaleensis*
Primates	Cercopithecidae	Formosan macaque	*Macaca cyclopis*
Pholidota	Manidae	Chinese pangolin	*Manis pentadactyla pentadactyla*
Artiodactyla	Cervidae	Reeve's muntjac	*Muntiacus reevesi micrurus*
		Sambar deer	*Cervus unicolor swinhoii*
	Bovidae	Formosan serow	*Nemorhaedus swinhoei*
	Suidae	Wild boar	*Sus scrofa taivanus*
Passeriformes	Phasianidae	Taiwan Partridge	*Arborophila crudigularis*
		Bamboo Partridge	*Bambusicola thoracica*
		Swinhoe's Pheasant	*Lophura swinhoii*
		Mikado Pheasant	*Syrmaticus mikado*

Table 2.4 Clouded leopard (CL) camera trapping effort in different regions of Southeast Asia.

regions	Southern Taiwan (this study)		Myanmar	Thailand	Sarawak	Peninsular Malaysia	Lao	Peninsular Malaysia	Peninsular Malaysia	Sumatra
Style	2m high, 40-60 degree detection		0.5m high, horizontal detection (detection area would be higher than the way we used in Taiwan)							
Camera trap locations	Cover various habitat types, including those with fewer animals. Both trail sets and lure sets.		near a salt lick or fruiting tree	trails, roads, dry stream beds with tiger signs	wildlife trails, paths or tracks	old logging roads	near active animal trails within 500m of random coordinate	animal trails	trails and roads	logging roads
Altitude range	150 - 3,092m	<1,500m	409-1,874m	540-1,310m mostly 700-800m	uk	20-538m	400-2,257m (not actual sampled)	<2,150m (highest of peninsula)	70-898m	uk
Number of sites	377	218	64	71	8	24	247	164	135	20
Camera trap days	13,354+*	6,800+*	1,238	1,886	1,127	5,972	3,588	6,787	14,054	uk
Camera trap days/CL	N/A	N/A	113	189	376	460	≤718	849	879	uk
# of CL pictures	0	0	11#	10	3	13	≥5	8	16	6
Source	This study		(Rao et al. 2005)	(Lynam et al. 2001)	(Azlan and Lading 2006)	(Azlan and Sharma 2006)	(Johnson et al. 2006)	R. Laidlaw, unpublished data	(Kawanishi and Sunquist 2004)	(Martyr 1997)

* "+" indicates higher camera trap days due to a few working cameras failing to imprint date/time.

Corrected by dividing reported number 77 by 7 in original reference as all numbers of pictures are multiplier of 7 and 77 clouded leopard pictures are way too high compared to other studies.

Table 2.5 Daily encounter rate of prey (DERP), and prey consumable weight (DERPg), and test statistics of 14 prey and 5 carnivore species for 4 altitude zones in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. Kruskal-Wallis (K-W) tested altitudinal differences and Jonkheere-Terpstra (J-T) tested altitudinal trends for DERP and DERPg.

	Species descending order by prey weight	max edible weight (g)[1]	average adult weight (kg)[2]	150-1,200m (N=72)		1,200-2,000m (N=49)		2,000-2,500m (N=43)		2,500-3,100m (N=22)		K-W p-value	J-T test p-value
				DERP	**DERPg**	DERP	**DERPg**	DERP	**DERPg**	DERP	**DERPg**		
Prey > 4 kg	Sambar deer	50,000	165[a]	0.0251	**1,255.3**	0.0342	**1,709.4**	0.0291	**1,454.4**	0.0016	**79.0**	0.0032	0.1594
	Wild boar	28,470	43.8[b]	0.0093	**263.5**	0.0040	**114.4**	0.0074	**211.2**	0.0089	**252.4**	0.1644	0.4988
	Formosan serow	18,200	28[c]	0.0792	**1,440.6**	0.0862	**1,568.5**	0.0403	**734.2**	0.0858	**1,561.3**	0.0048	0.5537
	Reeve's muntjac	8,000	10[d]	0.6006	**4,804.6**	0.1962	**1,569.5**	0.1198	**958.0**	0.0069	**54.9**	<0.0001	<0.0001
	Formosan macaque	7,200	9[e]	0.0931	**670.6**	0.0984	**708.5**	0.0532	**382.9**	0.0374	**269.4**	0.0087	0.0023
	Chinese pangolin	3,600	4.5[f]	0.0056	**20.0**	0.0046	**16.6**	0.0000	**0.0**	0.0000	**0.0**	0.0025	0.0003
Prey < 2 kg	White-faced flying squirrel	1,370	1.522[g]	0.0002	**0.2**	0.0000	**0.0**	0.0016	**2.2**	0.0105	**14.4**	<0.0001	0.0004
	Swinhoe's pheasant	990	1.1[h]	0.0244	**24.2**	0.0363	**36.0**	0.0069	**6.8**	0.0027	**2.7**	0.0007	0.0007
	Red-bellied tree squirrel	324	0.36[i]	0.0107	**3.5**	0.0157	**5.1**	0.0000	**0.0**	0.0000	**0.0**	0.0007	0.0002
	Long-nosed tree squirrel	324	0.36[j]	0.0024	**0.8**	0.0028	**0.9**	0.0010	**0.3**	0.0044	**1.4**	0.5639	0.8893
	Taiwan partridge	281	0.312[k]	0.0048	**1.4**	0.0083	**2.3**	0.0134	**3.8**	0.0115	**3.2**	0.0694	0.0132
	Striped tree squirrel	63	0.07[i]	0.0000	**0.0**	0.0000	**0.0**	0.0013	**0.1**	0.0017	**0.1**	0.2222	0.0697
	Formosan white-bellied rat	61	0.068[l]	0.0000	**0.0**	0.0062	**0.4**	0.0182	**1.1**	0.0088	**0.5**	<0.0001	<0.0001
	Spinous country rat	61	0.068[i]	0.0650	**4.0**	0.0949	**5.8**	0.0004	**0.0**	0.0000	**0.0**	<0.0001	<0.0001
Carnivore	Yellow-throated marten	1,197	1.33[e]	0.0053	**6.4**	0.0190	**22.8**	0.0127	**15.2**	0.0027	**3.2**	0.0100	0.2849
	Siberian weasel	431	0.479[e]	0.0007	**0.3**	0.0108	**4.7**	0.0144	**6.2**	0.0236	**10.2**	<0.0001	<0.0001
	Formosan ferret-badger	788	0.876[e]	0.0339	**26.7**	0.0296	**23.3**	0.0173	**13.7**	0.0372	**29.3**	0.4792	0.2904
	Gem–faced civet	2,028	2.253[e]	0.0285	**57.8**	0.0259	**52.5**	0.0075	**15.2**	0.0024	**4.8**	0.0097	0.0020
	Crab-eating mongoose	1,260	1.4	0.0350	**44.1**	0.0255	**32.1**	0.0074	**9.4**	0.0000	**0.0**	<0.0001	<0.0001
	Prey total			0.9204	8,488.6	0.5879	5,737.3	0.2926	3,755.0	0.1801	2,239.3		
	Prey total after 20% hunting success			0.1841 (DKRP)	**1,697.7 (DCRPg)**	0.1176 (DKRP)	**1,147.5 (DCRPg)**	0.0585 (DKRP)	**751.0 (DCRPg)**	0.0360 (DKRP)	**447.9 (DCRPg)**		
	Expected kill rates (days/kill)			**5.4**		**8.5**		**17.2**		**29.5**			

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

[2] References: [a] (Lee and Lin 2003). [b] K. Pei unpublished data. [c] (Tsai 2005). [d] (McCullough et al. 2000). [e] C. Chen personal communication and unpublished data, Rescue Center at National Pingtung University of Science and Technology, Taiwan. [f] (Chao 1989). [g] (Lee 1998). [h] (Dunning 1993). [i] (Silva and Downing 1995). [j] similar size to red-bellied tree squirrel. [k] (Sun 2001). [l] similar size to Formosan white-bellied rat.

Table 2.6 Percentage of detection sites of 14 prey and 5 carnivore species for 4 altitude zones in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. Percentage of detection sites greater than 50% is marked in bold.

	Species descending order by prey weight	150-1,200m (N=72)	1,200-2,000m (N=49)	2,000-2,500m (N=43)	2,500-3,100m (N=22)
Prey > 4kg	Sambar deer	41.7%	49.0%	46.5%	4.5%
	Wild boar	23.6%	12.2%	27.9%	36.4%
	Formosan serow	**77.8%**	**71.4%**	**58.1%**	**100%**
	Reeve’s muntjac	**97.2%**	**91.8%**	**74.4%**	9.1%
	Formosan macaque	**79.2%**	**73.5%**	**74.4%**	**54.5%**
	Chinese pangolin	16.7%	4.1%	0%	0%
Prey < 2kg	White-faced flying squirrel	1.4%	0%	4.7%	27.3%
	Swinhoe’s pheasant	43.1%	44.9%	20.9%	9.1%
	Red-bellied tree squirrel	23.6%	20.4%	0%	0%
	Long-nosed tree squirrel	4.2%	10.2%	4.7%	4.5%
	Taiwan Partridge	12.5%	18.4%	32.6%	27.3%
	Striped tree squirrel	0%	0%	2.3%	4.5%
	Formosan white-bellied rat	0%	6.1%	32.6%	27.3%
	Spinous country rat	**62.5%**	**65.3%**	2.3%	0%
Carnivore	Yellow-throated marten	16.7%	38.8%	34.9%	18.2%
	Siberian weasel	2.8%	30.6%	46.5%	63.6%
	Formosan ferret-badger	45.8%	34.7%	34.9%	40.9%
	Gem–faced civet	40.3%	36.7%	25.6%	9.1%
	Crab-eating mongoose	48.6%	34.7%	18.6%	0%

Table 2.7 Comparison of daily encounter rate of prey (DERP), and prey consumable weight (DERPg), and percentage of detection sites of 14 prey species and 5 carnivores in altitude <2,000m between areas hunted and not hunted in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

	Species descending order by prey weight	max edible weight (g)	average adult weight (kg)	**No hunting (N=121)**			**With hunting (N=22)**			Wilcoxon rank-sum 1-sided p-value[*]
				DERP	**DERPg**	Detection percentage	DERP	**DERPg**	Detection percentage	
Prey > 4 kg	Sambar deer	50,000	165	0.0288	**1,439.2**	44.6%	0.0011	**56.4**	9.1%	<0.0001
	Wild boar	28,470	43.8	0.0071	**203.1**	19.0%	0.0151	**429.1**	27.3%	0.1639
	Formosan serow	18,200	28	0.0820	**1,492.4**	75.2%	0.0374	**679.8**	50.0%	0.0084
	Reeve's muntjac	8,000	10	0.4368	**3,494.5**	95.0%	0.1452	**1,161.9**	68.2%	<0.0001
	Formosan macaque	7,200	9	0.0953	**685.9**	76.9%	0.0703	**505.8**	63.6%	0.0380
	Chinese pangolin	3,600	4.5	0.0052	**18.6**	11.6%	0.0000	**0.0**	0.0%	0.0852
Prey < 2 kg	White-faced flying squirrel	1,370	1.522	0.0001	**0.1**	0.8%	0.0000	**0.0**	0.0%	0.8642
	Swinhoe's pheasant	990	1.1	0.0292	**28.9**	43.8%	0.0196	**19.4**	45.5%	0.3325
	Red-bellied tree squirrel	324	0.36	0.0128	**4.1**	22.3%	0.0088	**2.9**	22.7%	0.4837
	Long-nosed tree squirrel	324	0.36	0.0026	**0.8**	6.6%	0.0000	**0.0**	0.0%	0.2532
	Taiwan Partridge	281	0.312	0.0062	**1.8**	14.9%	0.0125	**3.5**	27.3%	0.0952
	Striped tree squirrel	63	0.07	0.0000	**0.0**	0.0%	0.0011	**0.1**	4.5%	0.1538
	Formosan white-bellied rat	61.2	0.068	0.0025	**0.2**	2.5%	0.0024	**0.2**	4.5%	0.3965
	Spinous country rat	61.2	0.068	0.0771	**4.7**	63.6%	0.1344	**8.2**	63.6%	0.4278
Carnivore	Yellow-throated marten	1,197	1.33	0.0109	**13.0**	25.6%	0.0008	**1.0**	4.5%	0.0044
	Siberian weasel	431	0.479	0.0048	**2.1**	14.0%	0.0119	**5.1**	13.6%	0.4317
	Formosan ferret-badger	788	0.876	0.0322	**25.4**	41.3%	0.1031	**81.3**	77.3%	<0.0001
	Gem–faced civet	2,028	2.253	0.0274	**55.6**	38.8%	0.0196	**39.7**	31.8%	0.2562
	Crab-eating mongoose	1,260	1.4	0.0311	**39.2**	43.0%	0.0376	**47.3**	50.0%	0.3744
	Prey total			0.7857	**7,374.5**		0.4479	**2,867.2**		
	Prey total after hunting success (20%)			0.1571	**1,474.9** **(DCRPg)**		0.0896	**573.4** **(DCRPg)**		

[*] SAS exact test of differences of DERP and DERPg between hunted and not hunted areas. P-values are the same for DERP and DERPg because DERPg is DERP multiplied by a constant (edible weight).

Table 2.8 Hazard ratios of altitude (per 100m) and hunting (0: no hunting, 1: with hunting) influences on time to first detection (TFD) of a species using Cox proportional hazard regression with gamma shared frailty to model dependency between different rolls of film of the same camera trap site. Hazard ratios that are N/A are due to no detection or only one detection in areas with hunting. Data are from all trail-set camera traps in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. When there is no detection in one particular roll of film, the TFD is right censored and the total camera trap days of the roll are used as censored TFD. P-values < 0.05 are marked in bold and asterisked to indicate significance.

	Species (descending order by prey weight)	Altitude (per 100m) Hazard ratio	Hunting Hazard ratio
Prey > 4 kg	Sambar deer	**0.945 ****	**0.145 ****
	Wild boar	0.967	1.342
	Formosan serow	0.980	**0.503 ***
	Reeve's muntjac	**0.852 *****	**0.129 *****
	Formosan macaque	**0.971 ***	0.856
	Chinese pangolin	**0.813 ****	N/A
Prey < 2 kg	White-faced flying squirrel	**0.191 ****	N/A
	Swinhoe's pheasant	**0.950 ****	1.120
	Red-bellied tree squirrel	**0.920 ****	0.893
	Long-nosed tree squirrel	1.030	N/A
	Taiwan partridge	1.020	1.880
	Striped tree squirrel	1.370	N/A
	Formosan white-bellied rat	**1.330 *****	3.360
	Spinous country rat	**0.897 *****	0.726
Carnivore	Yellow-throated marten	1.032	0.229
	Siberian weasel	**1.14 *****	1.400
	Formosan ferret-badger	0.97	2.040
	Gem–faced civet	**0.949 *****	0.687
	Crab-eating mongoose	**0.910 *****	0.784

* p<0.05, ** p<0.01, *** p<0.001

Table 2.9 Linear regression model comparisons of daily consumption rate of prey meat in grams (DCRPg) for macaques, sambar deer, Reeve's muntjacs, Formosan serows and wild boars from camera trapping studies conducted in 21 (N) areas across Taiwan during 2001-2006. HA[*]: index of human activity; DCT: distance (km) to central Taiwan where higher mountains and larger contiguous primary forests are present; ALT: average altitude of camera trap sites.

Model	**ΔAIC_c**	**Akaike weight**	**R-square**
HA + DCT + ALT	0.0	0.845	0.76
HA + DCT	4.0	0.117	0.65
HA	7.3	0.022	0.52
HA+ALT	8.0	0.016	0.58
DCT	17.7	0.000	0.22
ALT	22.9	0.000	0.00

[*] HA was based on 3 values, i.e. within 5km from roads or 3km from villages (0 or 1), levels of human hunting pressure (0-3), and levels of forest disturbances (e.g. clear cut or agricultural uses, 0-5). These 3 values were then scaled to 10 equally and summed to form an overall score of human activities, i.e. from 0 to 30.

Table 2.10 Species photographed by tree camera trap sets in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. Ten tree sets were aimed at tree trunk/branch at different heights. Some trees were angled and leaning somewhat to the side. Total camera trap days was at least 272, but based on the average trap days per roll, may be close to 296. Independent pictures were defined as pictures of the same species separated over 1 hour and were based on group of animals instead of individuals.

Species	Number of independent pictures	Percentage	Percentage of detection sites
Spinous country rat	32	25.6%	40%
Formosan macaque	27	21.6%	50%
Formosan white-bellied rat	19	15.2%	10%
Gem-faced palm civet	14	11.2%	20%
Formosan ferret badger	12	9.6%	30%
Red-bellied tree squirrel	8	6.4%	50%
Striped tree squirrel	4	3.2%	10%
Formosan serow	3	2.4%	10%
Yellow-throated marten	2	1.6%	20%
Taiwan whistling thrush (*Myiophoneus insularis*)	2	1.6%	20%
Siberian weasel	1	0.8%	10%
Crested serpent eagle (*Spilornis cheela*)	1	0.8%	10%
Unknown bat	1		10%
Total (excluding bat)	**125**		

Table 2.11 Comparisons of daily kill rate of prey (DKRP) and daily consumption rate of prey meat in grams ($DCRP_g$) between Taiwan and other Southeast Asian countries. Gaur (*Bos frontalis*), Tapir (*Tapirus indicus*), elephants (*Elephas maximus*) and rhinoceros (*Dicerorhinus sumatrensis*), which are too large and very unlikely to be prey of clouded leopards, were excluded from this analysis.

Region/country	Camera trap days	DKRP	$DCRP_g$	Source
Southern Taiwan[1] altitude < 2,000m	4,233+	0.130	1,463	This study
Sarawak, Borneo	1,127	0.033	209	(Azlan and Lading 2006)
Myanmar[2]	1,238	0.019	378	(Rao et al. 2005)
Thailand	1,886	0.032	623	(Lynam et al. 2001)
Lao[3]	3,588	0.020	275	(Johnson et al. 2006)
Peninsular Malaysia	14,054	0.025	567	(Kawanishi and Sunquist 2004)
Sumatra[3]	6,973	0.042	678	(O'Brien et al. 2003)

[1] Based on trail sets having greater than 10 camera trap days.

[2] Photographic rates were divided by 7 to correct for possible errors as all reported camera trapping photographic rates were multipliers of 7 and way too high compared to nearby countries.

[3] Only larger prey for tigers were reported and used for the DKRP/DCRPg calculation

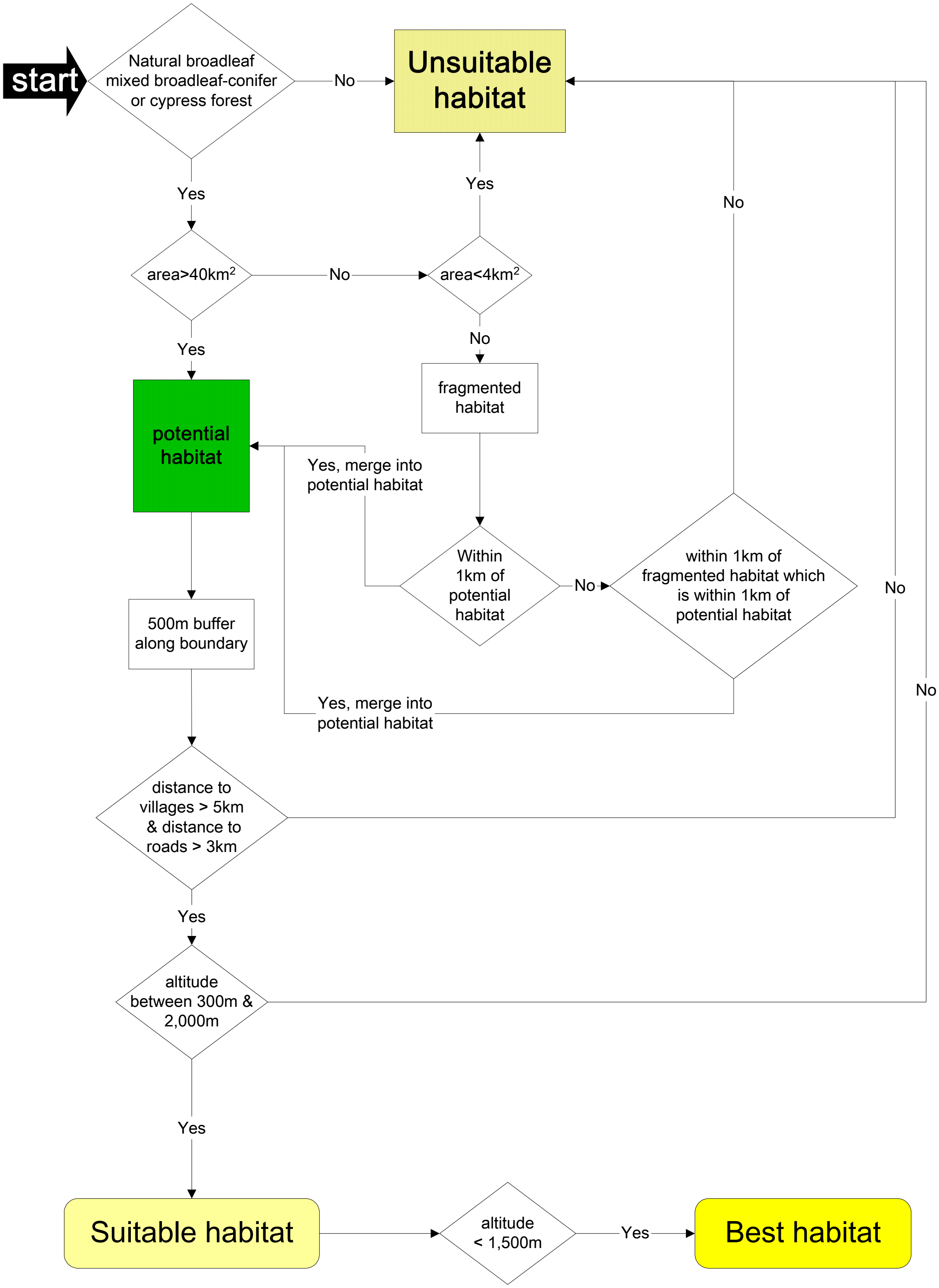


Figure 2.1. A flow chart to identify the suitable (<2,000m) and the best (<1,500m) habitat for clouded leopards in Taiwan.

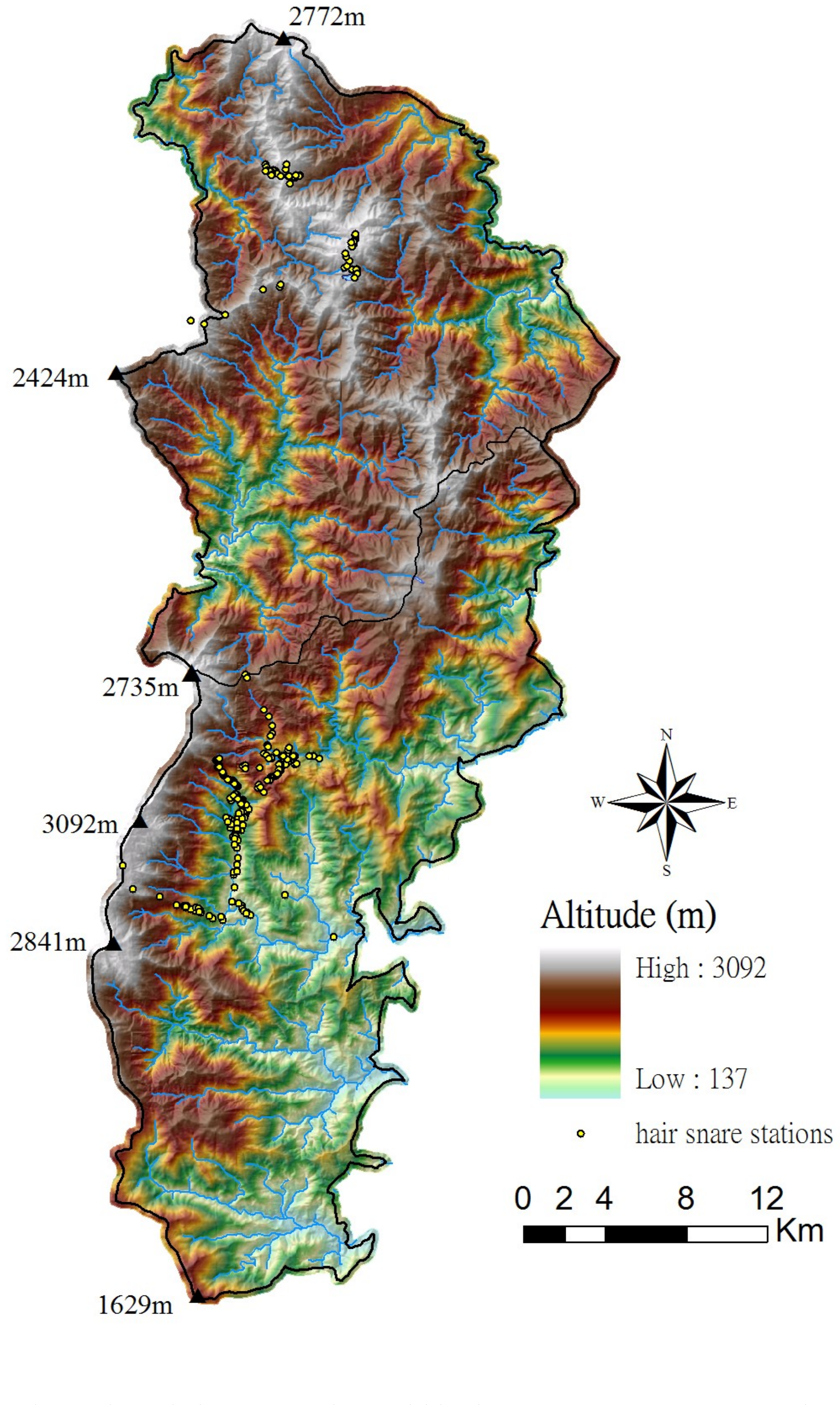


Figure 2.2. Locations of 232 hair snare stations within the Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area in southern Taiwan, 2001-2004.

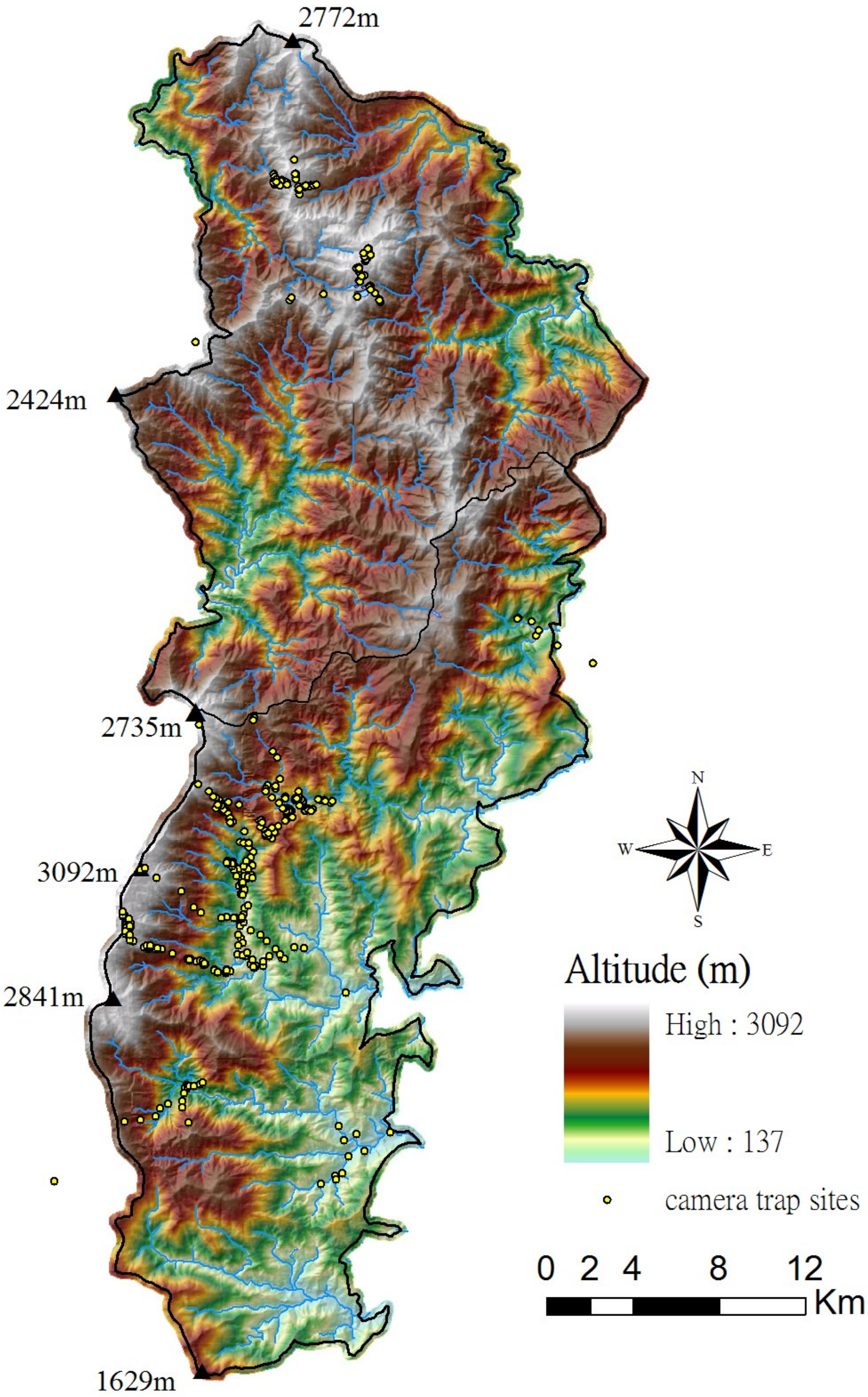
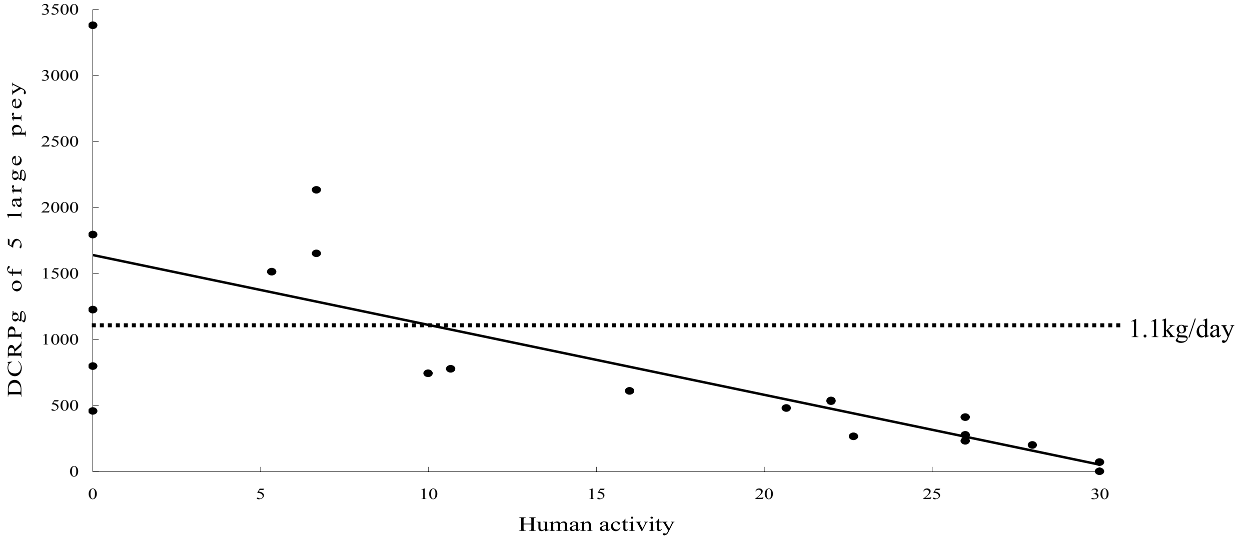


Figure 2.3. Locations of all 377 camera trap sites within the Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area in southern Taiwan, 2001-2004.

(a) Macaques and 4 ungulates



(b) Macaques and 3 ungulates (excluding sambar deer)

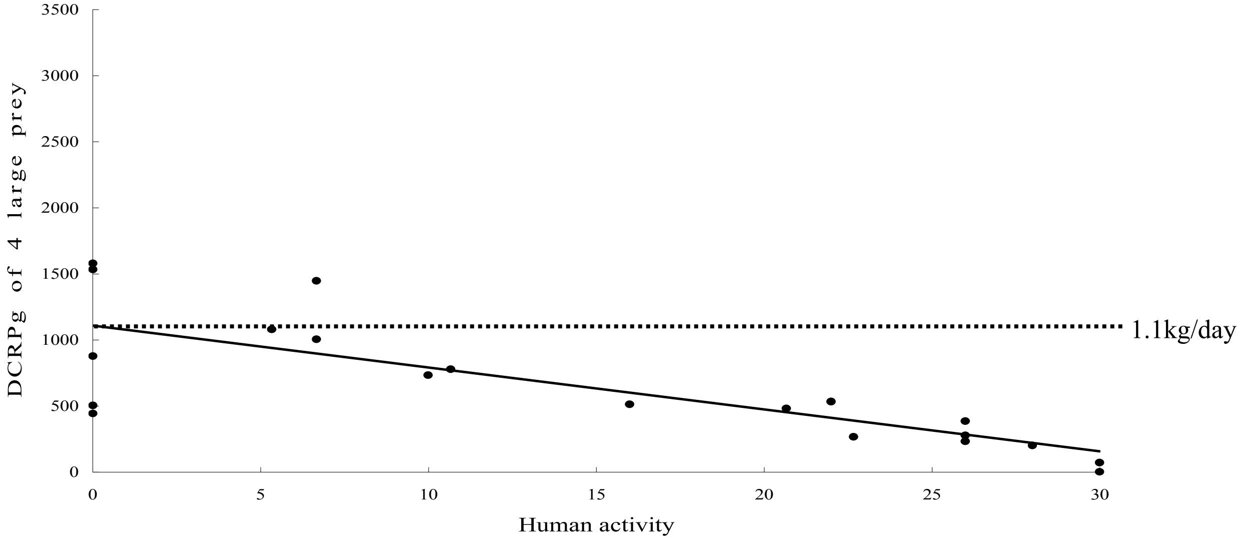
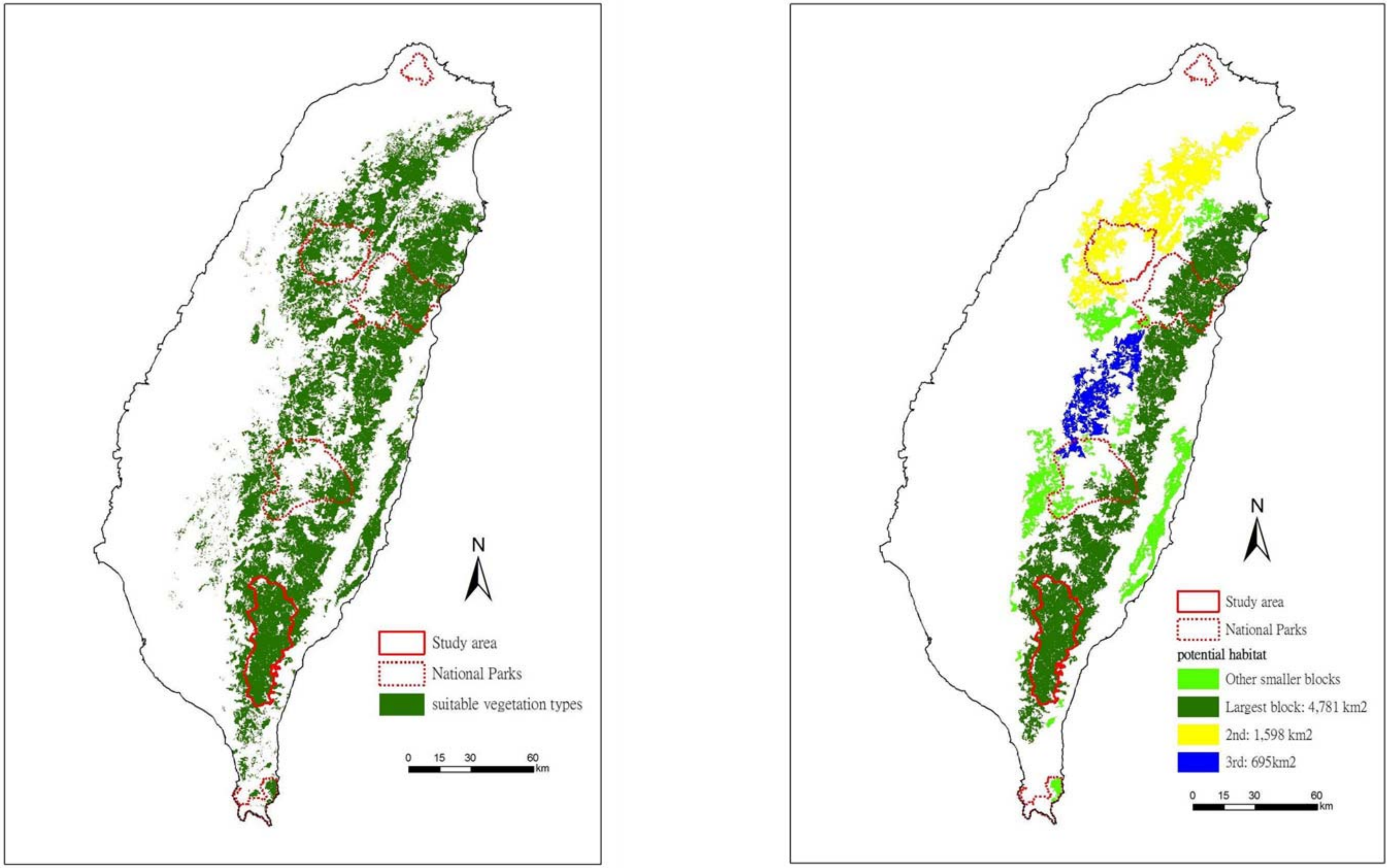


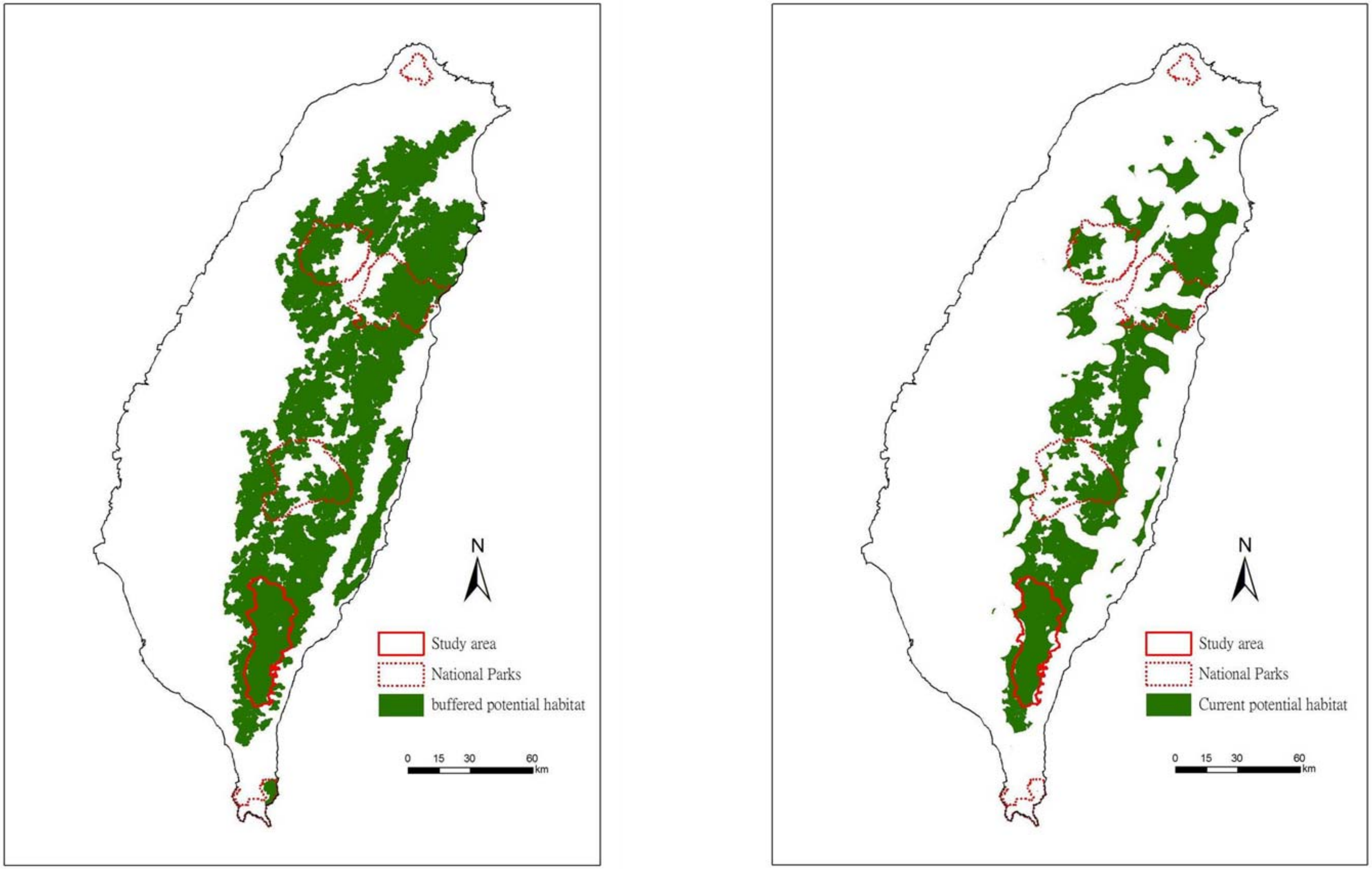
Fig 2.4 Daily consumption rate of prey meat in grams (DCRPg) of (a) macaques and ungulates and (b) macaques and ungulates excluding sambar deer versus different levels of human activity (HA). Data (N=21 areas) were extracted from this study (N=5) and other camera trapping studies (N=16) across Taiwan (Liu 2003, Pei et al. 2003, Hwang and Chian 2004, Hwang and Pei 2004, Pei 2004b;a, Wang 2004, Wu et al. 2004, Lai 2005, Wang and Hsu 2005, Wang and Huang 2005, Pei and Chen 2006) during 2000-2006. HA was based on 3 values, i.e. within 5km from roads or 3km from villages (0 or 1), levels of human hunting pressure (0-3), and levels of forest disturbances (e.g. clear cut or agricultural uses, 0-5). These 3 values were then scaled to 10 equally and summed to form an overall score of human activities, i.e. from 0 to 30.



(a) Suitable vegetation types: natural broadleaf forests (primary or secondary) and mixed broadleaf-conifer forests.

(b) Potential habitats: remove isolated small patches from (a). Different colors denote different contiguous blocks except light green for isolated smaller patches

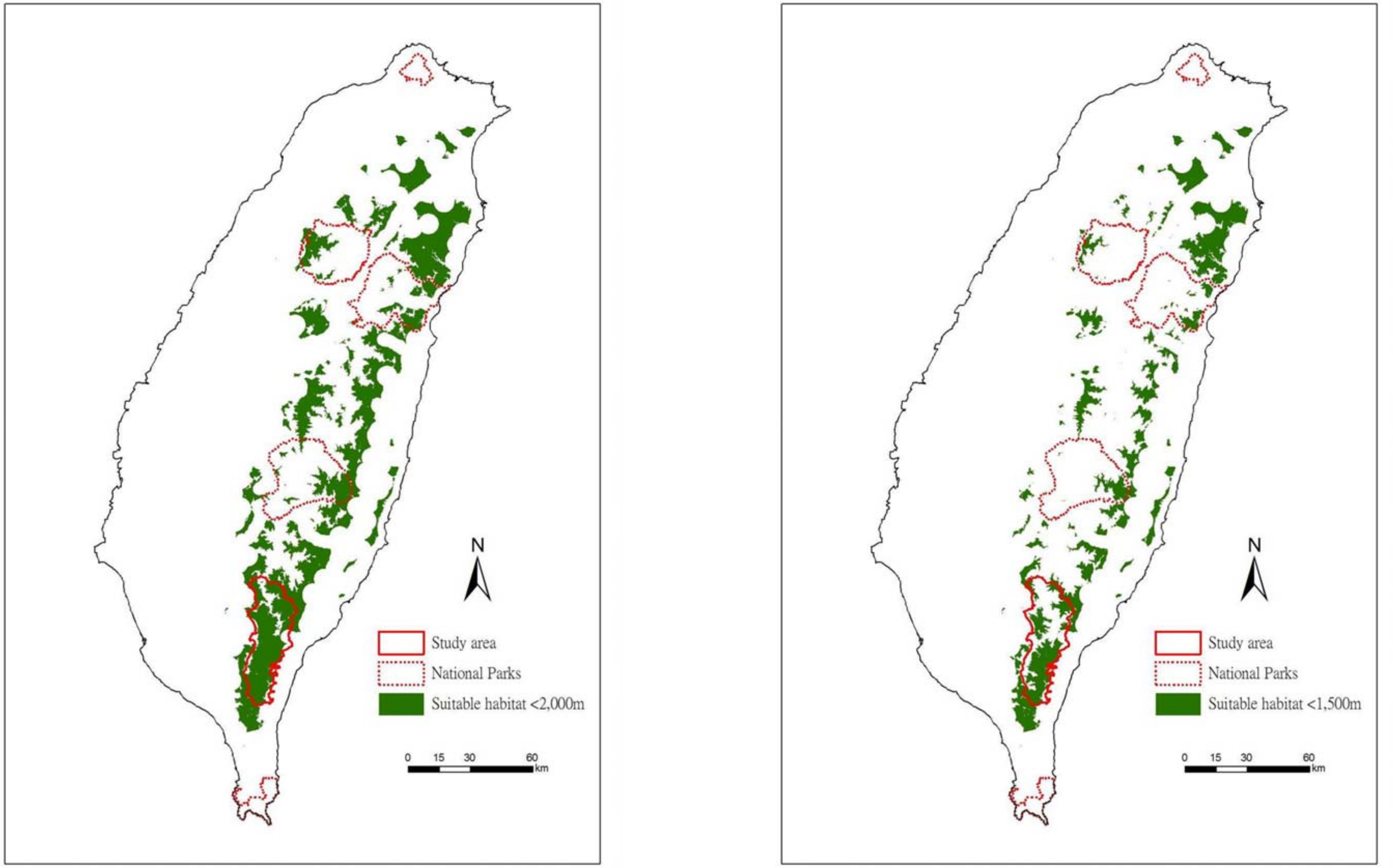
Figure 2.5 Suitable habitat analysis for clouded leopards in Taiwan based on a vegetation map produced by Taiwan Forestry Bureau in 1995.



(a) Buffered potential habitat: applied 500m (half of mean daily movement distance of clouded leopards) buffer to the potential habitat in Fig. 2.5b.

(b) Current potential habitat: remove areas within 5km from roads or 3km from villages to reflect most recent encroachment and prey depletion by human activity.

Figure 2.6 Suitable habitat analysis (continued from Fig. 2.5) for clouded leopards in Taiwan based on a vegetation map produced by Taiwan forestry Bureau in 1995.



(a) altitude < 2,000m

(b) altitude < 1,500m

Figure 2.7. Current range of suitable habitats for clouded leopards in Taiwan based on a vegetation map produced by Taiwan forestry Bureau in 1995. These maps take prey base into consideration, i.e. altitudes < 2,000m provide sufficient prey, while altitudes < 1,500m is best for abundant prey.

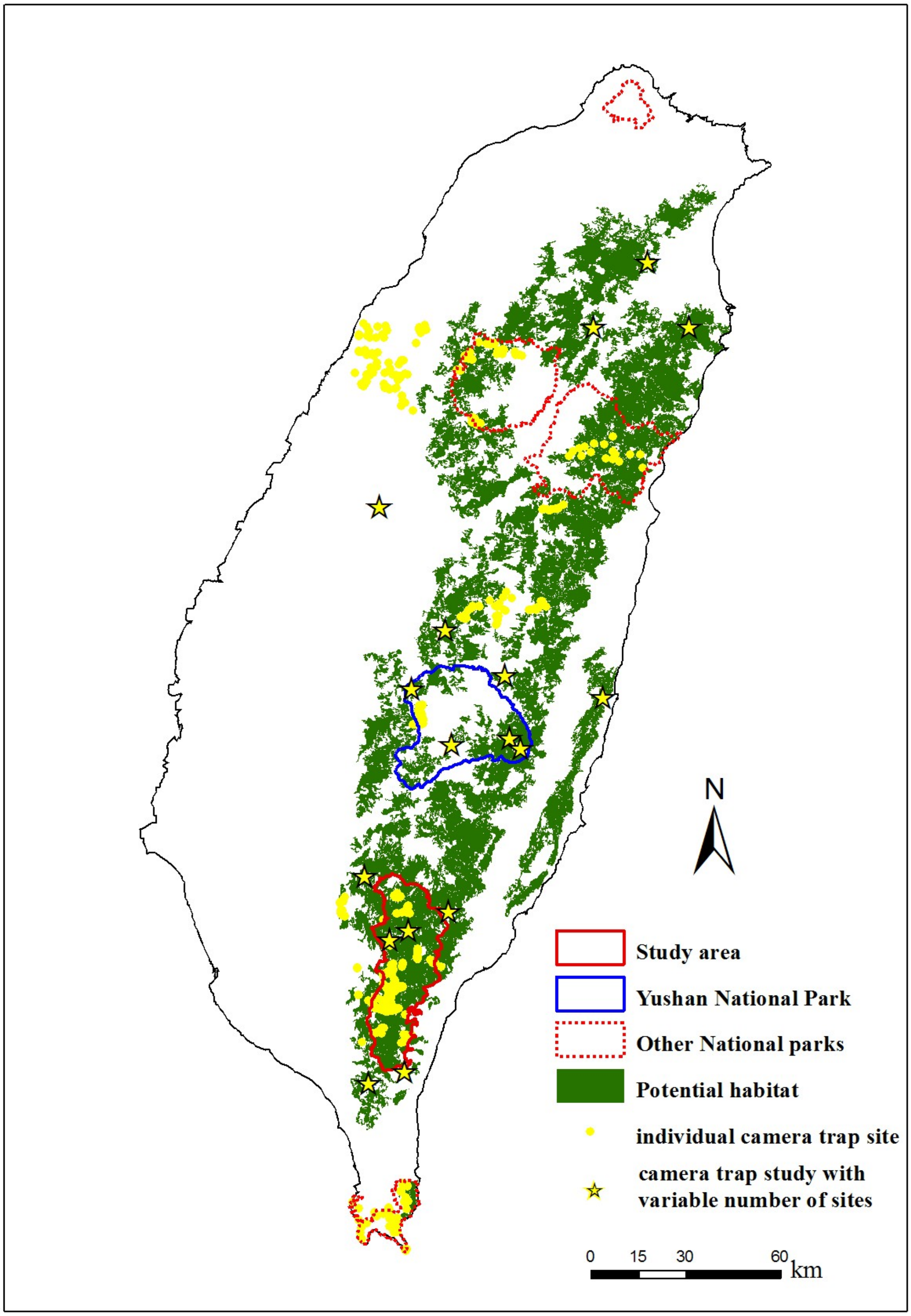


Figure 2.8. Camera trapping studies (yellow dots and stars) conducted around the potential habitat of clouded leopards in Taiwan during 2000-2006.

Chapter 3: Distribution, occurrences patterns, and habitat segregation of major prey of Formosan clouded leopards in southern Taiwan: A comparative study of Formosan macaques and 4 ungulates

Introduction

Prey abundance is crucial to the survival of big cats (Karanth and Stith 1999) and is positively correlated to the density of big cats (Karanth et al. 2004, Kawanishi and Sunquist 2004). Thus, understanding where major prey occurs more frequently would be beneficial to the conservation of clouded leopards. Previous results suggest that areas with less human activity and at lower altitudes could provide more prey for clouded leopards in Taiwan (see chapter 2). However, to identify more specific sites as hot spots for habitat preservation or for reintroduction of clouded leopards in the future, it would be necessary to understand prey habitat use and be able to predict their distributions. Ability to predict prey distribution is important, but it is demanding and costly, and almost impossible to survey all mountainous forests of Taiwan because of the ruggedness and remoteness.

In Taiwan, many of the major prey species of clouded leopards (e.g. ungulates) are also important game species of the aborigines (native tribesman in Taiwan). Although hunting is currently banned in Taiwan, illegal hunting is still present in many places and ungulate populations may be kept low in these hunted areas. This seems to contradict the goal of a clouded leopard reintroduction plan in the future (i.e. maintaining abundant prey). However, legal hunting is a rising issue and may be considered in the foreseeable future, at least legal for the aborigines to respect their traditional culture. Thus, baseline information on habitat use by these species becomes important so that habitat could be managed to increase biomass of these species to meet both hunters' and clouded leopards' needs in the future. In contrast, ungulates in remote areas without human hunting are freed from predation as the major, and possibly the only, large predator, the clouded leopard, has disappeared. Herbivore populations lacking regulation by top predators may become overabundant (Terborgh et al. 1999, Terborgh et al. 2001) and over browse or over graze their habitat. Although it is unknown whether these herbivores in Taiwan could be "top-down" regulated by clouded leopards, it would be helpful to understand how interspecific competition regulates the ungulate community or which environmental factors limit their distribution and abundance in a "bottom-up" manner, as clouded leopards are unlikely to be reintroduced in the near future. Understanding their habitat use and segregation may shed some light on the management and conservation of these species. However, while some research has been conducted on individual species, no detailed study on the community of the 5 large herbivores (e.g. Formosan macaque and 4 ungulates) has ever been conducted in Taiwan.

Many metrics have previously been used as indices of habitat use or quality, including but not limited to, time spent in habitat, distance traveled in habitat, counts of uses or occurrences in habitat types, population densities, and predation risks in different habitats (see review in Buskirk and Millspaugh 2006). Photographic rates from camera trapping combined properties of several of the above metrics. The higher the photographic rate, the more frequently a species, either the same or different individuals, occurs at and is utilizing that particular habitat. In other words, photographic rates from camera trapping could be regarded as activity levels at that particular habitat. It may imply more food so that animals spend more time foraging nearby. This could be seen from the camera trapping pictures of many ungulates that were browsing or grazing.

Predation risk may also be low where an animal occurs more often as photographic rates from camera trapping have been shown to be inversely related to predation risk (Hernandez et al. 2005). Furthermore, photographic rates were highly correlated to population densities of some herbivores (O'Brien et al. 2003) and wild cats (Carbone et al. 2001, Dillon 2005) and similar correlations were demonstrated by computer simulations as well (Carbone et al. 2001). In Taiwan, photographic rates of sambar deer were found to be correlated to fecal pellet counts (Liang 2005), which were often used to calculate ungulate densities (Neff 1968, Fuller 1991, Campbell et al. 2004, Brodie 2006). That is, photographic rates from camera trapping could be regarded as indices of population abundance (Carbone et al. 2001, Carbone et al. 2002, but see Anderson 2001, Jennelle et al. 2002) and habitat use.

Detection and nondetection based on camera trapping data has been used as presence and absence in logistic regression to study habitat use (Chen 2002, Wang et al. 2006) and distribution modeling (Hilty et al. 2006). However, nondetection does not necessarily imply absence, and false absence (e.g. presence but not detected) could bias the final result (MacKenzie 2006). When camera trapping effort is sufficient, probabilities of false absence may be very low (Chen 2002, Hilty et al. 2006). But, even low rates of false absence could still bias the statistical results (Tyre et al. 2003). It would be even worse if camera trapping effort between different sites varied a lot, making the detection probabilities of species presence different across sites. Moreover, different occurring rates among all presence sites is not utilized at all in presence/absence analysis. To utilize such information, Lai et al. (2003) and Lai (2005) used species photographic rates (i.e. SOI, see chapter 1) in multiple linear regressions to model species abundances in southern Taiwan. Nevertheless, camera trap sites with SOI=0 are still possible false absence because of either insufficient camera trapping effort or random errors. In addition, photographic rates are either 0 or positive and multiple linear regression may predict negative photographic rates. This could be an issue for rare species with excessive false absences.

Using presence and absence information reveals environmental factors limiting distribution, while models based on abundance focus on those factors affecting abundance. Mechanisms influencing distribution and abundance may differ (Nielsen et al. 2005) and a two-stage conditional model may be able to answer such questions (Cunningham and Lindenmayer 2005, Nielsen et al. 2005). That is, the first stage is to analyze presence and absence while the second stage is to analyze abundance conditional on presence. The zero-inflated count model (Lambert 1992) is a mixture model for count data and utilizes two-process analysis to address the possible false absences and excessive zero counts from absent sites (zero-inflated). It recently has been used to study habitat attributes influencing occurrence to model species distribution and abundance (Welsh et al. 1996, Pearce and Ferrier 2001, Cunningham and Lindenmayer 2005, Nielsen et al. 2005, Lemckert et al. 2006). However, many of these studies simply adopted counts from field surveys to reflect abundance and the efforts were hard to quantify and were assumed equal for all sites or ignored. Varying effort was seldom addressed in analysis. Other factors, e.g. different investigators, habitat types, and weather etc., may also result in potential bias in abundance counts. Camera trapping provides a standardized tool to document frequencies of species occurrence, which is basically bias-free from the afore-mentioned factors. Using zero-inflated count models for rates, the exposure time (i.e. camera trap days) is incorporated into the model so that effort, false absence, and excessive zeros (absent sites) are all addressed. Thus, environmental factors affecting distribution and abundance could be identified.

Since Formosan macaques and the 4 ungulates comprise almost the whole prey biomass for clouded leopards (>99% of DCRPg, see chapter 2), my analyses will be focused on Formosan macaques, Reeve's muntjacs, sambar deer, Formosan serows and wild boars. Regarding the other smaller prey species, information on altitudinal distribution patterns is likely to suffice for clouded leopard prey conservation and detailed analysis could also be conducted whenever it is needed.

Methods

Photographic rate from camera trapping (SOI or GOI, see chapter 1) is actually one type of count data standardized by camera trapping effort (i.e. camera trap days, or exposure time). Baseline models for count data is the standard Poisson model (variance = mean) or the negative binomial model allowing for overdispersion (i.e. variance > mean), which is often observed in ecological data. The standard Poisson model for rate is

$$r_i t_i = \{\exp(\gamma \mathbf{x}_i)\} t_i$$

where r_i is the photographic rate for site i, t_i is the camera trap time for site i, $\mathbf{x}_i$ is the covariate vector for site i, and γ is the regression model covariate coefficient vector. Exponentiation forces the count outcome to be 0 or positive. Rewrite using $t_i = \exp(\ln t_i)$, the equation becomes

$$r_i t_i = \{\exp(\gamma \mathbf{x}_i + \ln t_i)\}$$

This is simply a standard Poisson regression model with a regression coefficient of the camera trap time (ln) constrained to 1 (i.e., adjusted to different exposure time) while $r_i t_i$ is the expected photographic events (i.e., number of pictures) for the ith camera trap site having t_i camera trap time.

However, the Poisson model assumes that there is a positive probability of detecting an animal and 0 indicates failure to detect or false absence (random zeros from Poisson distributions). Except for omnipresent species, this assumption is not reasonable for areas where animals never occur (i.e. true absence). For non-omnipresent species, nondetection (i.e. 0 pictures) consists of false absence (zero counts conditional on presence) and true absence (excessive zeros). Zero-inflated Poisson regression (ZIP) (Lambert 1992) models counts of species occurrences (c_i) with excessive zeros by

$c_i = 0$, with probability p = logit ($\alpha \mathbf{x}_i$) in the always-0 group

$c_i = \{\exp(\beta \mathbf{y}_i + \ln t_i)\}$, with probability 1-p in the not-always-0 group

c_i is the expected outcome given camera trap time t_i, $\mathbf{x}_i$ and $\mathbf{y}_i$ are the covariates incorporated in the two-part models and their corresponding regression coefficient vectors α and β. In other words, this mixture zero-inflated Poisson model allows zeros to be generated by two distinct processes. The first logit model could be regarded as distribution mechanism, which limits species presence (probability of absence is p while probability of presence or occupancy is 1-p). The second Poisson process determines counts of species occurrences, which is also possible to produce zero counts due to sampling (i.e. false absence is modeled). That is,

Probability ($c_i = 0 \mid \mathbf{x}_i, \mathbf{y}_i$) = p + (1-p) x Probability ($c_i = 0 \mid \mathbf{y}_i$, species present)

Probability ($c_i > 0 \mid \mathbf{x}_i, \mathbf{y}_i$) = (1-p) x Probability ($c_i > 0 \mid \mathbf{y}_i$, species present)

Zeros consist of two types, one is structural zeros, which is inevitable (i.e. true absence), while the other is random zeros due to sampling conditional on species presence (i.e. false absence). Although the Poisson part actually models frequencies of occurrence events (I refer to it as occurrences hereafter), the modeled occurrences patterns were likely related to abundance patterns as photographic rates were correlated to population abundance. However, the Poisson model assumes the mean is equal to the variance, but overdispersion (variance > mean) is often observed in ecological data. Thus, the Poisson model may not provide an adequate fit. Negative binomial (NB) regression is another count model similar to Poisson regression except that it incorporates one more variable (i.e., α) to model the overdispersion (i.e. variance=mean + αXmean^2 > mean). Zero-inflated negative binomial regression (ZINB) simply substitutes the Poisson model with the negative binomial model to accommodate overdispersion.

Details of placement and checking protocols of camera traps and measurements and calculations of environmental characteristics at camera trap sites were described in chapter 1. For habitat covariates derived from those environmental characteristics in table 1.3 and table 1.4, I conducted an initial screen to choose the variables of interest by scatter plots and correlation analysis to reduce the number of covariates. Highly correlated covariates (correlation coefficient > 0.6) were dropped or combined so that only a single variable was used unless it was thought to be meaningful. For example, tree densities, heights, and branch heights were calculated originally in 3 categories (i.e. DBH 1-5cm, 5-20cm, >20cm for small, medium, and large trees). However, habitat measures from small and medium trees were highly correlated. Therefore, these 2 size categories (small and medium) were combined and only 2 size categories were used (i.e. DBH 1-20cm and >20cm for smaller and larger trees). Post correlation analysis also showed that measures from DBH 1-20cm were highly correlated with those derived from DBH 1-5cm and 5-20cm. Density related covariates (e.g. basal area, shrub and tree densities) were log (natural) transformed to reduce skewness and variations and to pull extreme high values closer to the bulk to approach normal distribution so that influence of sampling errors is minimal.

ZINB for rates was used to analyze habitat use in terms of distribution (the logit part) and occurrences (the negative binomial part) mechanisms. The negative binomial part is the NB2 model with variance function $\mu+\alpha\mu^2$ (μ is the expected mean and α is the overdispersion parameter, see page 71 in Cameron and Trivedi 1998). When $\alpha=0$, the NB2 model reduced to a Poisson model (i.e. mean=variance). Since the logit part (analogous to logistic regression) models distribution (i.e. probability of occupancy or presence/absence), I used only those meso-habitat characteristics derived from Table 1.4 (e.g. derived from the 40mX40m DEM model) as covariates in the logit part to model distribution in a larger scale (Table 3.1). Another advantage is that species distribution maps based on probability of occupancy could be produced using GIS. For the occurrences part, I included some of the meso-habitat characteristics and all the micro-habitat variables (measured on site within 17.8m radius) as the covariates in the negative binomial or Poisson part (Table 3.2) to model occurrences conditional on presence.

I used backward selection to eliminate redundant covariates until p-values of all covariates were < 0.1. All the models during backward selection formed the base of candidate models. To add in some extra simpler models in the candidate models, I continued to do backward selection and remove a few more covariates until substantial increase of AIC_c (>2) were observed. These candidate models were selected using the information-theoretic criteria (AICc: Burnham and Anderson 2002). Models with $\Delta AIC_c < 2$ were considered as supported. I calculated Akaike model weights based on ΔAIC_c to improve precision of the covariate coefficients and the model predictions and to reduce model selection bias (Burnham and Anderson 2002). Final explanations for distribution, occurrences patterns, and habitat segregations were based on the overall model averaged coefficients of variables (i.e. odds ratios for the logit part and incidence rate ratios for the negative binomial part when one variable increases by 1 standard deviation of the variable within all camera trap sites holding the others constant). In addition to the ΔAIC_c, normalized maximum-likelihood R^2 (Nagelkerke 1991) of supported models was also reported.

To assess the performance of the supported models selected by ΔAIC_c, predicted probabilities of different numbers of occurrences (q_i, probabilities of observe i occurrences) were plotted against observed proportion (i.e. probability) of different numbers of occurrences to visually assess model fit. Predicted probabilities of different counts were calculated by model averaging all supported models' predictions based on Akaike weights. I conducted a Pearson goodness-of-fit test using observed frequencies (i.e. number of camera trap sites having i occurrences) and expected frequencies (i.e. total number of camera trap sites multiplied by q_i). To avoid cells with expected frequencies <5, cells with expected frequencies < 5 were pooled. Because it is unknown whether nondetection is true absence or false absence, the regular 2x2 classification table of logistic regression could not be generated for sensitivity and specificity tests for the logit part. Error predictions could be assured for known presence sites only. Thus, I calculated probability of error predictions of absence (PEPA), i.e. average of probabilities of absence, from known presence sites to assess the accuracy of the logit part. PEPA was calculated for the fitted data and for another separate camera trapping data set. This separate camera trapping data set consisted of those camera trap sites which were not included in this habitat analysis because they were lure sets, trail sets with <10 camera trap days, trail sets in hunted areas, or those sets failing to imprint date/time on the films. It is unknown how the lures affected the occurrences of herbivores. If the lures and hunting activity deterred or reduced herbivores, detection of the species could still be considered as presence. If herbivores were attracted by the lures and traveled to the lure sites from far away, such error rates could be regarded as an overestimate. This separate validation data set includes 146 camera trap sites in the study area. However, this separate validation data set was neither random nor stratified samples of the whole study area and may not be representative.

Because of possible false absences, observed occupancy (i.e. number of detection sites divided by total sites) was likely lower than true occupancy. Probability of occupancy was often used interchangeably as occupancy estimate (MacKenzie 2006) and probability of occupancy was synonymous to probability of occurrence or probability of presence. Since ZINB (or ZIP) estimated probabilities of absence (p_i) for all camera trap sites, it is possible to estimate occupancy. I calculated conditional estimate of true occupancy by Bayes' theorem (page 123-125 in MacKenzie et al. 2006) using probability of nondetection obtained from the negative binomial NB2 part in the ZINB model or from the Poisson part in the ZIP model for camera trap sites without detection (adjusted to camera trap days for each site). Percentage of false absence (PFA) was calculated as the conditional estimate of occupancy minus the naïve observed occupancy. Estimated occupancy was calculated for 4 altitude zones (350-1,200m, 1,200-2,000m, 2,000-2,500m, and 2,500-3,000m, see chapter 2), respectively. I calculated Pearson's correlations between estimated occupancies and 3 different abundance indices based on photographic rates (i.e. OI, 1/OI, and ln(OI)) to see the possible relationships between distribution and abundance.

ZINB analyses were conducted in STATA 9.2 (StataCorp LP, College Station, Texas, USA). STATA conducted likelihood-ratio test (Long and Freese 2006) to examine overdispersion (i.e. ZINB vs. ZIP model) and Vuong test (Vuong 1989) for comparing ZINB and negative binomial (or ZIP vs. Poisson). When overdispersion was not significant (i.e. α does not differ from 0), Poisson model would be used instead of negative binomial model. When the zero-inflated count model did not perform significantly better than the Poisson or Negative Binomial count model (i.e., Vuong test $p < 0.05$), negative binomial or Poisson regression would be fitted depending on whether overdispersion was observed. This may imply that the species is omnipresent and it is not necessary to fit a zero-inflated model. Pearson goodness-of-fit test was conducted using SAS 9.1.3.

For Formosan macaques, which are social and, wild boars, which sometimes occurred in a group of several individuals, “group occurrence” (see definition of GOI in chapter 1) was used as the number of events; while “species occurrence” (see definition of SOI in chapter 1) was used for Reeve’s muntjac, sambar deer, and Formosan serow, which are mostly solitary. Seasonality (dry vs. wet season, see chapter 1) was included in the regression as a dummy variable and number of occurrence events were calculated for dry and wet seasons, respectively. When season covariate was excluded during backward selection with p-value>0.1 (i.e. no significant seasonal effect), the number of occurrence events in different seasons were pooled regardless of the season even though the camera trap site ran through different seasons (i.e. total number of occurrence events for a single site regardless of the season). Only camera trap sites working at least 10 camera trap days (in a single season if season covariate was examined) were included in the analysis.

Species distribution maps (e.g. probability of occupancy, or 1 minus probability of absence) within the study area were produced using the logit part of the averaged model. To reduce the effects of prediction errors and to consider movement of animals, predicted probability of occupancy were averaged with 48 neighboring cells using a 7x7 window (i.e., prediction maps were based on a 40mX40m DEM model and a 7x7 window was equivalent to 280mX280m or 7.84ha). This area is generally close to the reciprocal of densities (i.e. area per individual or social group) of these herbivores (Wu and Lin 1993, Saunders and McLeod 1999, McCullough et al. 2000, Nowicki and Koganezawa 2001, Lee and Lin 2006). Although 7.84ha may be smaller or larger depending on variable densities within the study area, the mean value of total 49 neighboring cells with related environmental characteristics should provide a more precise expected value and less variable prediction.

Results

Formosan macaque

Three models were included as supported models (Table 3.3). Nagelkerke R^2 ranged from 0.31 to 0.33. Overdispersion parameter α was greater than 0 ($p<0.0001$) and ZINB was preferred over NB ($p<0.003$) for all supported models. Multi-model inference suggested that dry season, higher altitude, smaller standard deviation of slope within 1.44ha, and closer to cliff lowered the probability of occupancy (Table 3.4). In areas where Formosan macaques were present, they occurred more frequently in the wet season (almost doubled), higher NDVI (greenness), smaller slope, convex terrain, lower heterogeneity of terrain shapes, higher shrub cover and visual obscurity, drier aspect (south facing), and lower values of canopy cover (Table 3.4). Larger photographic area would increase the number of pictures. Predicted probabilities of different numbers of occurrences fitted the observed numbers of occurrences reasonably well (Fig 3.1, $\chi^2=6.87$, $df=7$, $p=0.44$, probabilities for numbers of occurrences >6 were pooled as a single category). Probabilities of error predictions of absence from known presence for dry and wet season were 0.070 and 0.031 for the fitted data and 0.069 and 0.007 for the separate validation data. Predicted maps of the probability of occupancy for Formosan macaques in dry and wet seasons (Fig. 3.2) showed that Formosan macaques had lower probability of occupancy at high altitude and in areas close to cliff during the dry season in contrast to the predictions of omni-presence during the wet season.

Reeve's muntjac

When seasonality was considered, SEASON in the negative binomial part and ALTSEASON in the logit part were removed during backward selection. Therefore, analysis was conducted without separating dry season and wet season. Seven models were included as supported models (Table 3.5). Nagelkerke R^2 ranged from 0.68 to 0.70. Overdispersion parameter α was greater than 0 ($p<0.0001$) and ZINB was preferred over NB ($p<0.0001$) for all supported models. Multi-model inference suggested that lower NDVI, smaller standard deviation of slopes, steeper slope, higher altitude, more cliff areas within 1 km^2, and farther from river lowered the probability of occupancy (Table 3.6). In areas where Reeve's muntjacs were present, they occurred more frequently in lower altitude, less cliff within $1km^2$, non-rhododendron forest, gentler slope, lower standard deviation of visual obscurity, lower heterogeneity of tree densities among 3 size tree classes, higher values of canopy cover, and lower canopy height (Table 3.6). Predicted probabilities of different numbers of occurrences fitted the observed numbers of occurrences reasonably well (Fig 3.3, $\chi^2=12.72$, $df=17$, $p=0.75$, probabilities for numbers of occurrences >10 were pooled into several groups). Probabilities of error predictions of absence from known presence were 0.019 for the fitted data and 0.006 for the separate validation data, respectively. Predicted maps of the probability of occupancy for Reeve's muntjacs (Fig. 3.4a) showed that Reeve's muntjacs had low probability of occupancy at high altitude, steep terrain, and barren cliff and coniferous forests (including plantation forests) with low NDVI.

Formosan serow

When seasonality was considered, SEASON was removed during backward selection. Therefore, analysis was conducted without separating dry season and wet season. Nine models were included as supported models (Table 3.7). Nagelkerke R^2 ranged from 0.30 to 0.37. Overdispersion parameter α was greater than 0 ($p<0.0001$) for all supported models and ZINB was preferred over NB ($p<0.05$ for 8 supported models and $p=0.051$ for one supported model). Multi-model inference suggested that lower NDVI and fewer cliff areas within $1km^2$ lowered the probability of occupancy (Table 3.8). In areas where Formosan serows were present, they occurred more frequently in lower altitude, closer to cliff, farther from river, convex terrain, lower heterogeneity of terrain shapes, lower shrub cover, higher rock cover and visual obscurity, lower density of large trees (DBH>20cm), lower heterogeneity of tree densities among 3 size tree classes, higher basal area, lower large tree (DBH>20cm) height, more tree stratum, and higher heterogeneity of canopy cover (Table 3.8). Predicted probabilities of different numbers of occurrences fitted the observed numbers of occurrences reasonably well (Fig 3.5, $\chi^2=8.97$, $df=9$, $p=0.44$, probabilities for numbers of occurrences >8 were pooled into 2 groups). Probabilities of error predictions of absence from known presence were 0.036 for the fitted data and 0.074 for the separate validation data, respectively. Predicted maps of the probability of occupancy for Formosan serows (Fig. 3.4b) showed that Formosan serows had relatively few areas of low probability of occupancy (red) except at large area of gentle terrain with low NDVI. When NDVI of the supported models was replaced by ALT, increase of AIC_c was generally within 0.3. Since NDVI is costly and altitude is easier to get, using ALT instead of NDVI should still provide an adequate model. Since NDVI could reveal forest changes, but ALT can not, using ALT may be applicable only to areas without histories of timber harvest.

Sambar deer

When seasonality was considered, SEASON was removed during backward selection. Therefore, analysis was conducted without separating dry season and wet season. Six models were included as supported models (Table 3.9). Nagelkerke R^2 ranged from 0.44 to 0.49. Overdispersion parameter α was greater than 0 ($p<0.05$) and ZINB was preferred over NB ($p<0.0003$) for 3 supported models. For the other 3 supported models (model 1, 2, 4 in Table 3.9), overdispersion parameter α was close to zero and ZINB was not preferred over NB (Vuong test $0.11<p<0.21$). But, when zero-inflated was removed and only negative binomial model was fitted, overdispersion parameter α was greater than 0 ($p<0.001$) and AIC_c increased substantially (>40) than the original ZINB models. Thus, these 3 models were still included as the supported ZINB models. Multi-model inference suggested that higher altitude and closeness to cliffs lowered the probability of occupancy (Table 3.10). In areas where sambar deer were present, they occurred more frequently in lower NDVI and annual solar radiation, higher altitude, closer to river, non-Rhododendron forest, convex terrain, lower heterogeneities of terrain shapes, lower shrub height, higher shrub density, lower rock cover, lower density of smaller trees (DBH<20cm), higher densities of large trees (DBH>20cm), higher heterogeneity of tree densities between 3 size tree classes, lower tree height of smaller trees, lower heterogeneity of tree heights between two size classes, fewer tree stratum, and dryer aspect (south facing) (Table 3.10). Larger photographic area slightly increased the number of pictures but its relative importance was low (0.32, Table 3.10). Predicted probabilities of different numbers of occurrences fitted the observed numbers of occurrences reasonably well (Fig 3.6, $\chi^2=3.26$, $df=5$, p=0.66, probabilities for numbers of occurrences >4 were pooled into a single category). Probabilities of error predictions of absence from known presence were 0.091 for the fitted data and 0.087 for the separate validation data, respectively.

Patterns of altitude differed between the distribution and the occurrences parts. But, when the constant term in the logit part was considered, probability of absence at altitudes higher than 2,050m right beside a cliff area (i.e. CLIFFDIST≤40m, 1 cell in the DEM) would start to exceed 0.5. In other words, sambar deer were unlikely to occur nearby cliff areas at high altitudes, which were generally at ridge tops and away from rivers, and could be seen from the predicted map of the probability of occupancy for sambar deer (Fig. 3.4c). But, sambar deer had a general trend of increasing occurrence rates when altitude increased conditional on presence.

Wild boar

ZINB regression had difficulties in convergence during maximum likelihood estimation of the full model even after rescaling down covariates to reduce the variations of covariates and to avoid rounding errors. Forward selection was used instead to select covariates for the logit part while retaining all covariates in the negative binomial part. Selection of covariates in the logit part based on AIC_c included 3 variables. Backward selection was conducted on the negative binomial part thereafter.

When seasonality was considered, SEASON was removed during backward selection. Therefore, analysis was conducted without separating dry season and wet season. Overdispersion parameter α was nearly zero and the zero-inflated Poisson model was fitted. Six models were included as supported models (Table 3.11). Nagelkerke R^2 ranged from 0.24 to 0.31. ZIP was preferred over Poisson ($p<0.03$) for 6 supported models. Multi-model inference suggested that lower NDVI, higher standard deviation of slopes, and closer to river lowered the probability of occupancy (Table 3.12). In areas where wild boars were present, they occurred more frequently in lower NDVI and annual solar radiation, higher shrub height, lower heterogeneity of shrub distances, higher rock cover, lower visual obscurity, lower tree height of smaller trees, lower canopy height, and dryer aspect (south facing) (Table 3.12). Predicted probabilities of different numbers of occurrences fitted the observed numbers of occurrences very well (Fig 3.7, $\chi^2=0.28$, $df=2$, $p=0.87$, probabilities for numbers of occurrences >1 were pooled into a single category for statistical test). Probabilities of error predictions of absence from known presence were 0 ($3.3\text{x}10^{-9}$) for the fitted data and 0.043 for the separate validation data, respectively.

Similar to the sambar deer, patterns of NDVI differed between the distribution and the occurrences parts. When the constant term in the logit part was considered, probability of absence at NDVI less than 0.47 assuming RIVERDIST≤40m and minimum SLOPESTD would start to exceed 0.5. But, only 1 site had NDVI <0.47. In other words, wild boar are unlikely to occur at areas with high standard deviation of slopes unless with higher NDVI and distance to nearest river. The predicted map of the probability of occupancy for wild boar (Fig. 3.4d) showed relatively fewer and sparser areas in low probability of occupancy with less obvious pattern than the other herbivore. Wild boar may be more widely distributed than predicted or even omni-present as the variances of the covariates in the logit part were extremely high (Table 3.12). But, the Vuong test showed a better fit of the zero-inflated model than a Poisson model implied that the inflated zeros may be not necessarily due to the mechanism of distribution.

Habitat segregation

Differences in the distribution and occurrences patterns could be observed between the 5 herbivores (Table 3.13). In distribution patterns (i.e. probability of occupancy, Fig. 3.2 and 3.4), all species generally had the same trend in altitude/vegetation type of habitat characteristics but differed more in terrain ruggedness. Probability of occupancy was higher at lower altitude or higher NDVI (correlation of altitude and NDVI=-0.6, $p<0.0001$). Formosan serows tended to occur at cliffy areas. But Formosan macaques, Reeve's muntjacs, and sambar deer were more likely to occur farther from cliffs or in less cliffy areas. Reeve's muntjacs were the most affected by terrain ruggedness. Cliffy areas and steeper terrain lowered their probabilities of occupancy. To be present at steep terrain close to cliffs, existence of gentler terrain nearby may be necessary for their occurrences (i.e. high standard deviation of slopes, positive relationships with SLOPESTD).

When these herbivores were present and co-occurred, they segregated habitat uses in the following aspects:

1. Altitude/vegetation:

    Reeve's muntjacs and Formosan serows occurred more frequently at lower altitudes and Formosan macaques used higher NDVI (i.e. higher leaf area and productivity or greener vegetation, generally at lower altitude) areas more frequently. But, sambar deer and wild boars had completely different occurrences patterns in terms of altitude or NDVI.

2. Terrain ruggedness:

   Similar to the distribution pattern, Formosan macaques and Reeve's muntjacs did not prefer steep terrain or cliffy areas in contrast to Formosan serows.

3. Moisture gradient and wetness:

   Conditional on presence, sambar deer occurred more at areas closer to rivers while Formosan serows occurred more frequently away from rivers. Although occurrence rates of Reeve's muntjacs and wild boars did not differ relative to rivers, their probabilities of occupancy also decreased at areas closer to rivers suggesting that Reeve's muntjacs and wild boars may also segregate habitat use from sambar deer, which occurred more frequently near rivers.

4. Forest understory:

   For the two larger ungulates, wild boars occurred more frequently in rocky areas and areas with higher shrub height contrasting to sambar deer. Although Formosan serows also used rocky areas more frequently similar to wild boars, Formosan serows responded differently to visual obscurity and avoided shrubby areas (negative relationships with SHRUBCO). When Formosan macaques foraged or traveled on the ground, they also preferred higher visual obscurity similar to Formosan serows. But, unlike Formosan serows, Formosan macaques used areas with higher shrub cover more than

Formosan serows. The smallest herbivores, Reeve's muntjacs, did not react particularly to any forest understory characteristics except VOSTD.

5. Forest structures:

   Formosan macaques' use of ground was not much affected by forest structures except that they used the ground more often under lower values of canopy cover. Reeve's muntjacs were opposite and occurred more in higher values of canopy cover. For the 4 ungulates, except wild boars, segregation was observed in tree densities and tree stratum, but not in forest characteristics at the higher layer of forest structure such as tree heights and canopy structure. Smaller ungulates, Reeve's muntjacs and Formosan serows, occurred more in forests with lower heterogeneity of tree densities while sambar deer just the reverse. Fewer large trees and more tree stratum increased the occurrence rates of Formosan serows, but decreased the occurrence rates of sambar deer. Wild boars were not observed to differ from the other species with regards to forest structures.

Estimated occupancy, false absence rates, and photographic rates (OI)

Significant correlations were found between estimated occupancies and all 3 expressions of abundance indices (i.e. OI, 1/OI, ln(OI)) for Formosan macaque in dry season and Formosan serow among 4 altitude zones (all $p<0.05$, Table 3.14). For Reeve's muntjac, estimated occupancies were correlated to 1/OI and ln(OI) (all $p<0.05$, Table 3.15). No significant correlations between estimated occupancies and 3 forms of photographic rates were found for Formosan macaque in wet season, sambar deer, and wild boar (all $p>0.5$). But, correlations for sambar deer were high (Table 3.14) albeit not significant (p-values 0.079 for 1/OI and 0.084 for ln(OI)), which was likely due to low sample size. In contrast, higher occupancy could have a lower OI between some altitude zones for Formosan macaque in the wet season, wild boar, and also sambar deer (Table 3.15). The reciprocal of OI or ln(OI) had the highest explanation power for Reeve's muntjac, Formosan serow, and sambar deer; while OI was better than 1/OI or ln(OI) for Formosan macaque in the dry season. Reciprocals and logarithms have the effect of reducing the variation at high OI to smaller values. Better explanation power of 1/OI and ln(OI) than OI suggested that occupancy was insensitive to variation at high OI or, in other words, high population abundance. That is, occupancies dropped faster at low OI than at high OI. Overall false absence rates (FAR) for the 5 species ranged from the lowest 3.0% for Reeve's muntjacs to the highest 68.2% for wild boars and varied among altitude zones (Table 3.15). Higher occurrence rates (OI) tended to have lower FARs, but not in a simple linear relationships.

Discussion

Seasonality, arboreality, and altitudinal pattern

Seasonal differences were found only for Formosan macaques, which were photographed more frequently on the ground in the wet season. This is likely related to the differences of foraging strategy between arboreal macaques and terrestrial ungulates. Macaques forage both on the ground and in trees (Poirier 1986), while the 4 terrestrial ungulates forage on the ground only. Thus, food of Formosan macaques (e.g. tree fruits and leaves) would be influenced by seasonal phenology more than food of other ungulates (e.g. browse and grass on the forest understory). Switching diet seasonally has been observed in Formosan macaques with fruits taken more in wet season, but more tree leaves in the dry season.(Wu and Lin 1993, Su and Lee 2001). Formosan macaques forage in trees for leaves more in the dry season, but could forage on the ground for dropped mature fruits or newly grown ground vegetation in the wet season. Furthermore, they were more inactive (i.e. traveled less and rested more) in winter in order to digest leaves (Wu and Lin 1993). Thus, photographic rates of Formosan macaques on the ground in the dry season should decrease. Other behavioral adaptations to weather conditions may also make the ground photographic rates of Formosan macaques in dry season lower. For example, Formosan macaques huddled together and slept for a longer time in trees in winter (Wu and Lin 1993). In contrast, they may seek shade on the ground or at lower parts of the forest for cooling instead of high in the canopy during hot hours in the summer wet season (Wu and Lin 1993).

Kuroda (1940) and Poirier (1986) stated that Formosan macaques at high altitudes would migrate to lower altitudes in winter. This agreed with the interaction term ALTSEASON in the distribution model (logit part in ZINB) that higher altitudes during the dry season had a higher probability of absence. However, when ALTSEASON in the logit part of the best ZINB model ranked by AIC_c was replaced by SEASON (i.e. no interaction), AIC_c decreased 0.14 suggesting that a model without interaction of season and altitude explained similarly well. Nevertheless, Formosan macaques at an altitude>2,500m were not photographed in winter at all, but were documented in other seasons. Our results were the first study that provided evidence, at least indirectly, for the seasonal altitudinal migration of Formosan macaques in Taiwan (Lee 1991).

In contrast to no seasonal differences of occurrence rates in our models for the other 4 terrestrial ungulates, other studies in Taiwan had found some seasonal differences of activity levels. McCullough et al. (2000) conducted a radio telemetry study of Reeve’s muntjacs at altitudes 2,000-2,200m in our study area and found that females showed lower percent activity in summer and in winter than in other seasons. Chen (1990) found less signs and feces of Formosan serows at altitudes>3,500m in December in central Taiwan and suggested that Formosan serows at higher altitudes may migrate to lower altitude in winter. Japanese serows (*Naemorhedus crispus*), previously regarded as conspecific to Formosan serows, also practiced similar altitudinal migration during winter (Okada and Kakuta. 1970, cited in Chen 1990). Daily sighting rates of sambar deer at altitudes 2,900m~3,300m on alpine Yushan-cane grassland in central-northern Taiwan were also lowest in winter (Guo 2004). In lower altitudes of central-eastern Taiwan, signs of wild boars were higher in summer at altitude 300-700m but higher in winter at higher altitude 900-1,100m (Wu 1993). Snow is extremely rare at the high altitudes in our study area and the lowest monthly average temperature is generally above 0℃ (see chapter 1). But, at altitudes>3,000m in central and northern Taiwan, snow regularly occurs and the lowest monthly average temperature drops below 0℃. Limitations of available food and harsh weather may force Formosan serows and sambar deer at altitudes>3,000m in central and northern Taiwan to lower their activity levels or to migrate to lower altitudes. Our study area covered a wider altitudinal range of 350m-3,100m than the other two studies on Reeve's muntjacs and wild boars. If there were seasonal differences, it might be masked by the wider altitude range. Unlike other studies, seasons in this study were divided only into dry and wet seasons instead of 4 seasons. In addition, lower percent activity was observed only for female Reeve's muntjacs (but not for males) both in the dry and wet seasons (McCullough et al. 2000). Seasonal differences were unlikely to be shown in our analysis. Home ranges of an introduced population of Reeve's muntjacs in England did not shift or change sizes seasonally (Forde 1989, Chapman et al. 1993).

Since Reeve's muntjacs in Taiwan were less likely to occur at higher altitude and were rare even if they did occur, influence of harsh condition at higher altitudes would be minimal. In central Taiwan, camera trapping did not show seasonal differences in photographic rates of Reeve's muntjacs at altitude 1,900m~2,600m (Liang 2005) leading to the conclusion that Reeve's muntjacs do not have seasonal changes in distribution or occurrences patterns in our study area. With regards to wild boars, our low detection rates may not have enough information to reveal the seasonal differences if they exist.

Since Formosan macaques are mostly arboreal, activities on the ground do not reflect their habitat use (e.g. arboreal behavior) completely. This is probably why most characteristics of forest structure did not affect occurrences of Formosan macaques on the ground because only terrestrial habitat uses were analyzed. However, our results in distribution and occurrences patterns along the altitude gradient concurred with other population surveys of Formosan macaques in Taiwan, which stated that Formosan macaques were more easily sighted, had larger group sizes (Lee and Lin 1990), and had smaller home ranges at lower altitudes (Wu and Lin 1993). This suggests that our use of ground photographic rates of Formosan macaques in groups were correlated to their altitudinal pattern of population abundance. Thus, ground OI could be used for population monitoring of the arboreal Formosan macaques even though camera trapping documented only terrestrial occurrences. However, care must be taken regarding seasonal variations.

Altitude and NDVI affected either the distribution or occurrences patterns of all species except wild boars which were affected by NDVI only. In addition to changes in temperature, vegetation also varied along the altitudinal gradient in Taiwan (Su 1984). NDVI offered a better explanation than altitude in the negative binomial part (i.e. occurrences) for Formosan macaques as NDVI is a greenness index and reflects the photosynthetic activity and productivity of plant matter (Box et al. 1989, Goward et al. 1991, Ustin et al. 1991, Hsieh and Cheng 1995), which is closely related to the food source of Formosan macaques. This has also been reported in other primates whose home ranges had higher NDVI than average values of the area surveyed (baboons, Papio hamadryas, in Zinner et al. 2001, grivet monkey, Chlorocebus aethiops aethiops, in Zinner et al. 2002). NDVI was correlated to altitude (correlation coefficient=-0.6, p<0.0001), but demonstrated a slight mid-domain phenomenon (higher at around altitude 1,000m). Lower NDVI at higher altitudes was due mostly to more coniferous trees. Therefore, lower altitudes are likely to provide a better habitat with more food for Formosan macaques. However, NDVI may not directly relate to the food source of other terrestrial ungulates as they forage on the ground and NDVI is largely determined by trees in the forested study area. Significance of NDVI, regarding the distribution or occurrences patterns of terrestrial ungulates, may be a combination of altitude, terrain physiognomy, forest structure, and plant species composition.

Forest structure and terrain

Reeve's muntjacs and Formosan serows occurred more frequently in forests with lower heterogeneity of tree density between different size (DBH) categories (i.e. lower TREEDENCV). TREEDENCV was positively correlated to STREEDEN (Pearson ρ=0.45, p<0.0001, n=189), but negatively correlated to LTREEDEN (Pearson ρ=-0.38, p<0.0001, n=189). In other words, higher TREEDENCV of forests tend to have a higher density of smaller trees (STREEDEN, DBH<20cm), lower density of larger trees (LTREEDEN, DBH>20cm), and a larger standard deviation between the densities of smaller and larger trees. Introduced populations of Reeve's muntjac in England had higher densities in older stands (Hemami et al. 2004), which may tend to have more larger trees and fewer smaller trees (i.e. lower TREEDENCV). Moreover, higher altitudes, further from rivers, and near ridges also have more small trees (Pearson $\rho=0.33-0.38$, $p<0.0001$, n=189). But, large trees were not as highly correlated (Pearson $-0.2<\rho<0.2$, p=0.04, 0.97, 0.05 for ALT, RIVERDIST, and SLOPEPOS_E, respectively, n=189), which may be due to adaptation of coniferous trees in harsh environment (e.g. higher altitude and windy ridge). In addition to forest age, higher TREEDENCV also may be associated with disturbance or stress to the vegetation due to some mechanisms such as altitude, terrain, soil, temperature, wind, or other factors. These harsh conditions may make NDVI lower (e.g. higher altitude and wind) so that Reeve's muntjacs and Formosan serows were less likely to be present in low NDVI areas.

In contrast to Reeve's muntjacs and Formosan serows, sambar deer occurred more frequently at lower NDVI and higher altitude, conditional on presence. Lee and Lin (2004;2006) used fecal pellet counts to estimate population densities of sambar deer at altitudes 1,200m~3,500m in central Taiwan and also found that higher altitudes tended to have higher population densities. But, they also suspected that historical and current hunting pressure on sambar deer at lower altitudes caused the population density there to be lower. Nevertheless, hunting pressure was unlikely to be a significant factor in our study area. Lee and Lin (2006) also found that sambar deer population density was highest at the edge of forests and in Yushan cane grasslands and preferred forests in early succession. Our results generally concurred with their findings as sambar deer occurred more in forests with fewer tree strata, lower tree heights of smaller trees (DBH>20cm) and lower heterogeneity of tree heights between size classes, and higher TREEDENCV (e.g. younger forests or forests in disturbed or harsh conditions). There is no Yushan cane grassland in our study area. Thus, edges were mostly distributed along rivers or close to barren cliff areas. Flooding caused by torrential rains and typhoons during the wet season also would introduce disturbances to riverine forests annually. Sambar deer occurred more near rivers (Table 3.10) where they may use the edges and those early succession forests. However, sambar deer were unlikely to occur in areas close to cliffs (Table 3.10) and probably would not use the edges near barren cliffs. Formosan macaques and Reeve's muntjacs also avoided steep and cliffy terrain or areas close to cliffs (Table 3.13). In contrast, Formosan serow, renowned for its ability of living in steep and rugged terrain (Dien 1964, McCullough 1974), was the only species that showed preference of steep terrain and cliffs (Table 3.13). Some of the reported feeding plants of Formosan serows grow on disturbed slopes of early succession stages (McCullough 1974, Lue 1987) and indeed, we observed Formosan serows feeding on shrubs in recent landslide not covered by forest. These plants are likely pioneer species and will also grow near forest gaps. This may be why Formosan serows occurred more in higher CANOPYGAP (Table 3.8). Japanese serows avoided sika deer to reduce competition (Koganezawa 1999, Nowicki and Koganezawa 2002). Similarly, Formosan serows also may avoid sambar deer by foraging on plants near cliffs unavailable to or difficult for sambar deer and Reeve's muntjacs. Formosan serows also occurred less frequently near rivers, which were preferred by sambar deer (Table 3.13). Moreover, sambar deer avoided rocky areas, but Formosan serows occurred more in rocky areas, which also agreed with field observations of Formosan serows (personal observations and McCullough 1974).

Forest understory and feeding strategy

In a coniferous forest in England, the introduced Reeve's muntjacs selected areas with more diverse ground vegetation and more mature nut producing broad-leaf trees (Chapman et al. 1985). Similarly, we observed a tendency of more diverse understory vegetation at lower altitudes where Reeve's muntjacs occurred more frequently. Reeve's muntjacs in our study area had a higher probability of presence at higher NDVI (Table 3.6), which may imply more broad-leaf trees and thus higher production of tree fruits. Nevertheless, Reeve's muntjacs did not exhibit particular preference in forest understory characteristics (Table 3.6). Reeve's muntjacs are selective browsers and spend more time searching for high quality plants (Hofmann 1985, Kay 1987, Putman 1989). Our simple measures of forest understory did not separate plant species and may include unfavorable herbs or shrubs. Thus, these understory characteristics may not directly correlate to the food quantity of Reeve's muntjacs.

In contrast, Formosan serows and sambar deer are intermediate feeders between selective browsers and roughage eater (Hofmann 1985). However, Formosan serows have tend to be selective browsers (Hofmann 1985, Ochiai 1999), while sambar deer tend to be roughage eaters based on their digestive physiology (Hofmann 1985). A diet study of sambar deer in our study area (Lee and Lin 2003) showed that sambar deer were intermediate feeders with a tendency to eat roughage at high altitudes (2,000m~2,500m), but a tendency toward selective browsing at low altitudes (350m~1,000m). This may suggest that the higher quality food for browsing at lower altitudes was more abundant than at higher altitudes and that the competition for browse at lower altitudes may be higher among Reeve's muntjacs, Formosan serows, and sambar deer where food resources are limited. Altitudinal differences in browse and grass availability may affect the distribution and occurrences patterns of these 3 herbivores. That is, sambar deer occurred more at higher altitudes because of their physiological tendency toward eating roughage, while lower altitudes may be preferable for selective browsers like Reeve's muntjacs and Formosan serows. Sambar deer's flexibility to consume different plants (Lee and Lin 2003) may explain why our measure of higher shrub density, without differentiating species, had some positive relationships with the occurrences of sambar deer. But, it is unclear why higher shrub cover lowered the occurrences of Formosan serows.

Since Formosan macaques forage mostly on trees and wild boars are more omnivorous and can utilize a different foraging strategy (e.g. rooting), competition for food with other terrestrial herbivores may not be substantial. Actually, camera trapping photographed several Formosan macaques and a Reeve's muntjac in the same picture. Formosan macaques also were observed to forage peacefully with Reeve's muntjacs and Reeve's muntjacs were feeding on foliage and fruits dropped from trees to the ground by Formosan macaques (T. Liao personal communication). This is maybe one reason why the distribution and occurrences patterns of Formosan macaques and Reeve's muntjacs were similar and dramatic segregation was not found. Canopy leaves and fruits are generally unavailable to Reeve's muntjacs, but they seem to take advantage of these high quality foods when they are available. In addition to Reeve's muntjacs, other terrestrial ungulates may also benefit from Formosan macaques foraging on the trees. For example, 77% of the foraging behavior of wild boars at low altitudes in central-eastern Taiwan was feeding on fallen fruits instead of rooting (Wu 1993). Sika deer also were reported to glean for dropped food under the trees on which Japanese macaques (*Macaca fuscata yakui*) were foraging and Japanese macaques were seldom aggressive toward the sika deer (Majolo and Ventura 2004). Thus, sambar deer may also have a feeding association with Formosan macaques. However, food quantity may affect this feeding association

(Majolo and Ventura 2004). That is, if food in the trees becomes less abundant for Formosan macaques (i.e. lower NDVI or less broad-leaf trees at higher altitudes), Formosan macaques may need to forage more on the ground. Competition for food between Formosan macaques and the larger ungulates like sambar deer and wild boars may then begin to occur. Thus, differences of occurrences patterns in NDVI observed in the present study (Table 3.13) may, therefore, reduce competition between Formosan macaques and the 2 largest ungulates, sambar deer and wild boars.

Predation pressure on habitat use

In addition to competition for food resources, predation also may play a role in habitat use and occurrence patterns (Jeffries and Lawton 1984, Sih et al. 1985, Lima and Dill 1990, Brown et al. 1999). Since clouded leopards were likely extirpated, the remaining potential large predators are Asiatic black bears, yellow-throated martens, and mountain hawk eagles (*Spizaetus nipalensis*). Yellow-throated martens occurred more frequently at higher altitudes (i.e. >1,200m, see chapter 2&4). Signs and photographs of Asiatic black bears were mostly at altitudes>1,900m in the study area and were very rare (see chapter 4). Mountain hawk eagles also were observed more often at altitudes>1,000m than at altitudes<1,000m in southern Taiwan (Lin et al. 2005, Sun 2005 and personal observations in the study area). Reeve's muntjacs are the most vulnerable prey species and are potential prey of all 3 predators (personal, H. Wu and hunters' observations, Y. Sun unpublished data, and Matyushkin 1987, Hwang et al. 2002) (Wu 2004, Koh 2007). Formosan macaques probably faced predation pressure from mountain hawk eagles (Y. Sun unpublished data and Iida 1999, Tsai 2007b), while Formosan serows could be preyed upon by yellow-throated martens (Sathyakumar 1999, Tsai 2007a) and Asiatic black bears (personal observations and Hwang et al. 2002). But, sambar deer and wild boar were unlikely to be their prey because of their large body sizes and their ability to inflict injury. The tendency of large predators to be more prevalent at higher altitudes may in part explain why Formosan macaques, Reeve's muntjacs, and Formosan serows occurred less at higher altitudes while sambar deer and wild boar did not have this altitudinal trend (Table. 3.13). Our camera trapping data showed that Formosan macaques and yellow-throated martens (see chapter 4) were completely diurnal while Reeve's muntjacs were much more active at crepuscular hours. In other words, Formosan macaques faced the two diurnal predators (e.g. yellow-throated martens and mountain hawk eagles) and used habitat with higher visual obscurity and shrub cover when they were on the ground, possibly to avoid predation. However, the more vulnerable Reeve's muntjacs did not seem to seek cover (Table 3.6). Reeve's muntjacs could reduce the probability of being preyed upon by diurnal predators with higher activity levels at crepuscular and night hours when the predators were less active. Higher occurrence rates at smaller VOSTD implied that Reeve's muntjacs utilized habitat with homogeneous higher visual obscurity or homogeneous lower visual obscurity. It is possible that Reeve's muntjacs had different usage of visual obscurity during daytime and at night because of different predation pressure. Nevertheless, Formosan macaques (3.3%) and Reeve's muntjacs (0.8%) may not be the major prey of mountain hawk eagles (120 nest-feeding records near the study area: Y. Sun unpublished data and Tsai 2007b) and yellow-throated martens (Tsai 2007a). Asiatic black bears rely a lot on vegetative foods (Hwang et al. 2002) and are very rare in the study area. Predation on Formosan serows, sambar deer, and wild boars by Asiatic black bears probably occurs only sporadically and is limited to smaller and weak individuals or young. Influences of large predators on distribution and occurrences patterns of macaques and 4 ungulates may not be substantial given that clouded leopards were extirpated and human hunting was absent. The effect of competition may be stronger when predation pressure is absent or very low (Gurevitch et al. 2000). We observed overbrowsing of the forest understory in part of the lower altitudes of the study area. This implied that competition for food among terrestrial herbivores may be high. This study recorded the highest Reeve's muntjac and Formosan serow photographic rates among all camera trapping studies across Taiwan, and it may be that Reeve's muntjacs and Formosan serows in the interior part of the study area, which has no hunting, have the highest population densities in Taiwan (using photographic rates as indices of ungulate population densities, O'Brien et al. 2003). After at least 10 years of population growth without regulation by large predators and human hunting, they may have reached or overshot carrying capacity. Populations of sambar deer also may be increasing. Sambar deer would compete for browse with Reeve's muntjacs and Formosan serows in high densities at the lower altitudes of the study area. Thus, habitat segregation of these 3 cervids and bovid may be more pronounced to reduce interspecific competition. Formosan macaques and wild boars were less segregated from the other 3 herbivores (Table 3.13) which may be because they could eat food resources in trees or underground by rooting unavailable to the other 3 species. Diet differences, competition for food, and physiological adaptation to the environment (e.g. Formosan serow in steep terrain and cliff, Formosan macaques on trees, and wild boar's use of underground resources by rooting behavior) are probably more important mechanisms in affecting habitat segregation of the 5 herbivores than predation by large predators in the study area.

Relationships of distribution (occupancy), abundance, and false absence rates

The relationships between distribution and population abundance have long been recognized as interrelated (Brown 1984, Hanski et al. 1993) and occupancy was advocated as a state variable in population and habitat studies (MacKenzie et al. 2006). O'Brien et al. (2003) found that densities of some ungulates estimated by distance-sampling could be modeled by camera trapping photographic rates (1/OI). Our results of correlations between occupancy and 1/OI for Formosan macaque in dry season and 3 ungulates supported the idea of using occupancy as a state variable for population studies. However, density was modeled by the exponent of 1/OI (linear model of 1/OI and ln(density)) in O' Brien et al. (2003). Since occupancy is insensitive to high OI, the relationships between occupancy and abundance may be more complex. For example, it is possible that significant changes in occupancy would not be detected until population density decreased substantially (e.g. species could be omni-present or high-occupancy, but with different high and low population densities). Thus, monitoring occupancy alone might not be sufficient to detect reductions in population abundance. In this study, there were instances where significantly different occupancies had contradictory patterns of abundance (e.g. Formosan macaque in wet season, sambar deer, and wild boar. Table 3.14, using photographic rates as indices of abundance), and this could lead to incorrect conclusions about population trends. Seasonal differences in Formosan macaque occurrence also suggested that cautions must be taken in occupancy estimates when animals may exhibit seasonal changes of distribution and abundance. Interpreting the relationships between occupancy and abundance may require more attention depending on species, scale or other factors (see review in Gaston and Lawton 1990, Lawton 1993).

A multi-species study, including marsupials, reptiles, birds, and plants in Australia, presented less desirable results of relationships between the probability of occupancy and population abundance (see Pearce and Ferrier 2001). Although some species did show strong correlations between probability of occupancy and abundance, species without correlations suggested there may be different mechanisms between distribution and abundance (Nielsen et al. 2005). Our results (Table 3.13) also showed that for all 5 species some environmental characteristics were in the logit part (i.e. distribution), but not in the negative binomial part (i.e. abundance indices or occurrences). Although this might be due to collinearity of covariates, it is also possible that animals may choose a place meeting some requirements to live, but these environmental characteristics would not affect their abundance. For example, areas close to cliffs would affect the probability of occupancy of Formosan macaque and sambar deer. However, distance to nearest cliff may not affect their abundance at all when the distance exceeded some threshold and the terrain was not related to the cliff at all. Formosan macaques, Reeve’s muntjacs, and Formosan serows had some common covariates with the same pattern both in the occupancy and occurrences parts (Table 3.13). Coincidentally, they also had positive correlations between probability of occupancy and OI (Table 3.15). However, seemingly conflicting patterns of altitude and NDVI in distribution and occurrences were found for sambar deer and wild boars (Table 3.15). Lower probability of sambar deer occupancy at high altitudes was likely because the logit model identified areas close to cliffs and ridge tops, which were most likely to occur at higher altitudes (Fig. 3.4c). Conditional on presence, sambar deer occurred more frequently when altitude increased, which concurred with the population estimates of sambar deer at altitudes from 1,200m to 3,500m in central-eastern Taiwan (Lee and Lin 2004;2006). Wild boars also had contradictory NDVI patterns in occupancy and occurrences (Table 3.12). The reason may be similar to sambar deer that the logit model identified some extreme habitat unsuitable for wild boars or even some outliers, which could not be explained by the Poisson model. However, the high variances and p-values (0.999) of the logit covariates may indicate a poor fit of the logit model or a low sample size. Actually, ZIP models for wild boars had lower Nagelkerke R^2 than ZINB models of the other 4 species. These may be due to the low detections of wild boars. Only 43 out of 185 camera trap sites photographed wild boars and just 34 of the 43 sites had only 1 occurrence event. Thus, information on differences of occurrence rates may be limited for wild boars. Nevertheless, the Poisson part revealed that wild boars occurred more frequently at lower NDVI, higher shrub height, and lower canopy height and tree heights of smaller trees, which concurred with local hunters' experiences and the findings in central-eastern Taiwan that wild boars preferred higher shrub/grassland and more open forest (Wu 1993). Therefore, even for data with few detections, trends of habitat use could still be revealed by zero-inflated count models.

Since the false absence rates (FAR) were relatively high, treating nondetection as absence in logistic regression would give biased results (Tyre et al. 2003, MacKenzie 2006). Correlations of FAR and OI implied that probability of detection is a function of population abundance (MacKenzie et al. 2006). In other words, influences of false absence are likely to be more pronounced in rare species. False presence could also incur bias (Royle and Link 2006). But, we believed that the probability of misidentifying large mammals in our camera trapping pictures was basically 0. The logit parts of our ZINB and ZIP models should provide more adequate explanations of presence and absence (e.g. distribution) than regular logistic regression because the negative binomial or Poisson parts modeled possible false absences. However, our uses of the regular ZINB and ZIP models (Lambert 1992) were different from the two-process ZIP (or ZINB) models used in some other literature (Welsh et al. 1996, Cunningham and Lindenmayer 2005). The two-process ZIP (or ZINB) (Welsh et al. 1996, Cunningham and Lindenmayer 2005) first conducted a logistic regression between count>0 and count=0 (i.e. detection vs. nondetection) and thereafter used a zero-truncated Poisson (or negative binomial) regression on data with count>0. This was actually a hurdle regression (Mullahy 1986). Although this was advocated as easier to interpret, cautions must be taken in the explanations of logistic regression because of possible false absences.

Model validation

Probabilities of error predictions of absence from known presence (PEPA) were all less than 8% for the fitted and separate data sets. This indicated that the probability of misclassifying a presence site as an absence site was quite low. However, it is difficult to evaluate probability of misclassifying an absence site as a presence site because a nondetection site could be either a presence site (i.e. false absence) or an absence site (i.e. true absence). Since this type of misclassification error is usually tolerable and less critical for the purpose of preservation, prediction maps of probability of occupancy would still be valuable. Furthermore, we presented the maps of probability of occupancy using neighborhood averaging so that predicted absence sites with lots of high probabilities of presence sites nearby are unlikely to be absent and vice versa. Averaging would correct such possible errors and increase the precision of probability of occupancy. Positive relationships of average probability of occupancy and abundance indices (e.g. photographic rates) among the 4 altitude zones for most species studied implied that the neighborhood averaged probability of occupancy would also relate to population abundance. But, differences in population abundance at high occupancy possibly could not be observed on prediction maps because of the insensitivity to abundance at high occupancy (e.g. lower altitudes in Fig. 3.2 and 3.4).

Conservation implications

Since clouded leopards are likely extinct in Taiwan, these 5 large herbivores generally bear little predation pressure from the natural large predators. Interspecific competition may become more relevant when they are released from predation (Gurevitch et al. 2000). But, environmental limitation as a bottom-up mechanism on these herbivores in Taiwan has never been explored before. This was the first study ever conducted on the whole large herbivore community in Taiwan instead of on individual species. In addition, it was basically under a condition without predators and human hunting in a natural and primary forest having minimum human disturbances on the vegetation.

Niche overlap between Reeve's muntjacs, Formosan serows, and sambar deer may be more obvious because of overlapping diets. But, interactions among these 3 sympatric ungulates had never been studied in Taiwan. Our study revealed the habitat segregation among these 3 species for the first time in Taiwan. Sambar deer segregated habitat use from Formosan serows and Reeve's muntjacs in many environmental characteristics, which serows and muntjacs preferred in common (Table 3.13). That sambar deer and Formosan serows further differed in cliff preference suggested that sambar deer and Formosan serows may be avoiding each other. Japanese serows tended to avoid sika deer (Nowicki and Koganezawa 2002) and it has been found that Japanese serows became rare when sika deer expanded distribution and increased population size

(Nowicki and Koganezawa 2001). We documented the highest photographic rates of Reeve's muntjacs and Formosan serows among all camera trapping studies in Taiwan, but not sambar deer. Our study area consisted of the largest remaining lowland primary forest, which is less favorable to sambar deer (see discussion). This may be why there were more Reeve's muntjacs and Formosan serows in the study area. However, historical timber harvest, agriculture and human encroachment created edges and forests in early succession preferred by sambar deer across Taiwan. In contrast, the lowland primary forest, where Reeve's muntjacs and Formosan serows occur more frequently, decreased in the past years across Taiwan. Sambar deer, the largest terrestrial mammal in Taiwan, barely have any predators and the population is increasing. Their diet is also very flexible (Lee and Lin 2003) and they may outcompete Reeve's muntjacs and Formosan serows. We strongly feel the importance to assess the potential influence of increasing number of sambar deer in fragmented habitats on Formosan serow and even Reeve's muntjacs, two of the three most important prey of clouded leopards in addition to Formosan macaques.

Even a small deer species like Reeve's muntjac could cause browsing impacts to forests (Cooke and Farrell 2001). Overbrowsing the forest understory has been observed in part of the study area where there was no human hunting. Based on our results and field observations, Reeve's muntjacs and Formosan serows are at high densities in the interior part of the study area because human hunting and large predators are absent. Browsing impacts to the forest need to be assessed and monitored and could be an issue in the near future. Browsing impacts may become more obvious when sambar deer populations increase and expand. In addition to the possible problem of overbrowsing by these 3 species, Formosan macaques and wild boars have been causing damage to croplands and orchards. The current management strategy of complete protection for these large herbivores (except wild boar) may need to be adjusted gradually depending on the population status in different areas. Human hunting could be one of the options to cull populations when necessary. These 5 herbivores, except Formosan macaques, are major game species for the aborigines in Taiwan. Our results on habitat use could provide information for habitat management to increase habitat quality and population abundance to meet satisfaction of hunters and other stakeholders. However, caution must be taken when relating OI to population abundance (Anderson 2001, Jennelle et al. 2002) and relating population abundance to habitat quality (Van Horne 1983).

Even with hunting to control populations, Formosan macaques are not target game species of most hunters and the damage they cause to orchards increases every year. Pest problems of Formosan macaques usually occur at orchards adjacent to forests. It might be helpful to create a buffer zone, which Formosan macaques do not like, between the orchards and forests. Since Formosan macaques had lower occurrence rates at lower shrub cover and visual obscurity (Table 3.4), clearance of forest understory nearby orchards could be practiced before and during the fruiting season (but unnecessary after harvest) to reduce the occurrences of Formosan macaques. As wild boars also cause crop damage and prefer high shrub/grassland, clearance of forest understory might also reduce damages by wild boars. Most other environmental characteristics in Table 3.4 and 3.12 are not manageable except NDVI. Reducing NDVI would involve forest alteration (e.g. thinning or clear cut). But, this is controversial in terms of conservation of biodiversity and erosion control. Although creating buffer zones provides an option for pest management, it needs more research and experiments to assess the costs, performance, and influences on other species.

In addition to human hunting and habitat management, regulation by natural predation could possibly be accomplished by reintroduction of clouded leopards. Since Formosan macaques are the preferred prey of clouded leopards, reintroduction of clouded leopards could impose predation pressures on all of these herbivores including Formosan macaques. It is helpful to identify suitable reintroduction areas or preservation hot spots of abundant prey in a finer scale. For example, assuming the study area is the target reintroduction site, Fig. 3.8 illustrated the probability of occupancy of all the 5 large herbivore prey (multiply probabilities of occupancy of all species and average with neighboring 48 cells), one using the logit models of all 5 species and the other one assuming wild boars are omni-present. However, differences in population abundance at high occupancy were not obvious on maps. When needed, analysis could be conducted again by using only covariates obtainable in GIS so that maps of abundance could be produced. This could be easily extended to all of Taiwan for the area determined in Fig. 2.6 or 2.7 depicting the current available habitat for clouded leopards. However, such predictions do not consider the influence of human hunting on the prey base and need revision based on the extents and amplitudes of human hunting. Furthermore, choices of reintroduction sites may conflict with hunters’ expectations. Final decisions of reintroduction would need to include social and cultural factors together. Although camera trapping provided data on patterns of occupancy and abundance, our data covered only forest habitat within an altitude range of 350m~3,100m. In the future, more research is needed to understand the ecology of these large herbivores in different habitats, at different altitudes, and under different human hunting pressure.

Table 3.1 Covariates in the logit part of zero-inflated negative binomial regression or zero-inflated Poisson regression to model species distribution mechanism. Covariates were chosen in a larger scale and hypothesized to affect species presence or occupancy. Except season, covariates were derived from a 40m X 40m digital elevation model (DEM) and a SPOT 4 satellite image (details see Table 1.4).

Category	Variable	Method of calculation
Season	SEASON	Dry (1) or wet (0) season
	ALTSEASON[1]	Interaction of season and altitude (SEASON X ALT)
Altitude temperature wetness vegetation	NDVI	Normalized difference vegetation index from a satellite image. An index of greenness.
	ALT	Altitude (m)
	RIVERDIST	Distance to nearest river or mountain lakes (in TGLIWA)
	ASR	Annual solar radiation (hundred J/m^2)
Ruggedness / terrain	SLOPEDEM	Slope from DEM in percentage (ArcGIS 9.2)
	SLOPESTD	Standard deviation of slopes (in percentage) within neighboring 3x3 cells (i.e. 120mX120m)
	CLIFFDIST[2]	Distance to nearest cliff. Cliff is defined as slope>45° with area>1.44ha (i.e., 3x3 cells or 120mX120m)
	CLIFFCOUNT[2]	Number of cliff cells (slope>45°) within 25x25 cell window (i.e., 1kmX1km or 100ha).

[1] ALTSEASON was used for Formosan macaques and Reeve's muntjacs in the logit part only because they may practice altitudinal migration, i.e. move to higher altitudes during wet season.

[2] CLIFFCOUNT and CLIFFDIST are highly correlated. Use of either one depended on which fitted better or was free from difficulties in convergence during maximum likelihood estimation.

Table 3.2 (Continued to next page) Covariates in the negative binomial part of zero-inflated negative binomial regression or in the Poisson part of zero-inflated Poisson regression to model mechanisms influencing species occurrences conditional on presence. Except season and some from Table 3.1 (italicized), covariates were determined within 17.8m radius of the camera trap site (see Table 1.3 for details).

Category	Habitat covariate	Description
Photoarea	PHOTOAREA	Square of distance from the camera trap to the photo center
Season	SEASON	Dry (1) or wet (0) season
Altitude/ vegetation	ALT	Altitude (m)
	RHO	1 for rhododendron forest, 0 for other vegetation types
	NDVI	An index of greenness.
Terrain shape/ Ruggedness	SLOPE_FIELD	Slope in percentage measured in the field
	SLOPESTD	Standard deviations of slopes (percentage) within neighboring 3x3 cells (120mX120m)
	CLIFFDIST	Distance to nearest cliff. Either this of CLIFFCOUNT was used.
	CLIFFCOUNT	Number of cliff cells (slope>45°) within 1km^2. Range 0-625.
	TSIMIC	Average values of terrain shape indices calculated for 2m, 4m, and 8m. The average is highly correlated to the 3 indices at different distances (correlation 0.85, 0.98, and 0.96, respectively).
	EVEN	Terrain evenness: standard deviation of terrain shape indices calculated for 2m, 4m, and 8m.

Table 3.2 (Continued from previous page) Covariates in the negative binomial part of zero-inflated negative binomial regression or in the Poisson part of zero-inflated Poisson regression to model mechanisms influencing species occurrences conditional on presence. Except season and some from Table 3.1 (italicized), covariates were determined within 17.8m radius of the camera trap site (see Table 1.3 for details).

Category	Habitat covariate	Description
Forest understory/ ground cover	HERBCO	Herbaceous cover in percentage
	SHRUBCO	Shrub cover in percentage
	SHRUBHT	Average shrub height (m)
	SHRUBDEN	Shrub density log(natural) transformed
	SHRUBCV	CV of shrub distances at the 4 quadrants
	ROCKCO	Rock cover in percentage
	VO	Average visual obscurity of 4 directions from 0.5m to 2m (total 32 values) in percentage
	VOSTD	Standard deviation of visual obscurity among 4 directions
Forest structures	STREEDEN	Tree density (DBH 1-20cm), log transformed
	LTREEDEN	Tree density (DBH >20cm), log transformed
	TREEDENCV	CV of tree densities between 3 size classes
	BASAL	Total basal area, log transformed
	STREEHT	Average tree height (DBH 1-20cm)
	LTREEHT	Average tree height (DBH >20cm)
	TREEHTCV	CV of tree heights between 3 size classes
	SBRAHT	Average branch height (DBH 1-20cm), used for macaques only
	LBRAHT	Average branch height (DBH >20cm), used for macaques only
	STRATUM	Number of forest stratum (2-5)
	CANOPYHT	Canopy height
	CANOPYCO	Average of 8 measurements of canopy cover in percentage
	CANOPYGAP	CV between 8 measurements for canopy patchiness (gaps).
Moisture gradient /wetness	MOISTGRD	Moisture gradient based on field aspect, 10 levels: 1 (wettest) ~ 10 (driest in south-facing slopes)
	ASR	Annual solar radiation (hundred J/m^2)
	RIVERDIST	Distance to nearest river or mountain lakes (in TGLIWA)

Table 3.3 Model comparisons for habitat use of Formosan macaques in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area of southern Taiwan using zero-inflated negative binomial regression. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence. See Table 3.1 and 3.2 for definitions of covariates. Akaike weights were derived from ΔAIC_c. '+' indicates positive coefficient, '-' indicates negative coefficient, while empty indicates variable not included in the model.

Supported models		1	2	3
Number of covariates		13	12	14
ΔAIC_c		0.00	0.01	0.95
Akaike weight		0.38	0.38	0.24
Logit variable	ALTSEASON	+	+	+
	SLOPESTD	-	-	-
	ALTGPS	+	+	+
	CLIFFDIST	-	-	-
	CONSTANT	-	-	-
NB variable	SEASON	-	-	-
	NDVI	+	+	+
	PHOTOAREA	+	+	+
	SLOPEFIELD	-	-	-
	TSIMIC	-	-	-
	EVEN	-	-	-
	SHRUBCO	+		+
	VO	+	+	+
	MOISTGRD	+	+	+
	CANOPYCO			-
	CONSTANT	-	-	-

Table 3.4 Average coefficients and factor changes of covariates based on model averaging 3 supported zero-inflated negative binomial (ZINB) models in Table 3.3 using Akaike weights derived from ΔAIC_c for distribution and occurrences patterns of Formosan macaques in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence.

Model	**Covariate**	**Standard deviation**	**Averaged coefficient**	**Factor change**[1]
Logit	ALTSEASON	694.88	0.00149	2.808[2]
	SLOPESTD	6.31	-0.24211	0.217
	ALT	694.88	0.00178	3.436
	CLIFFDIST	331.19	-0.01043	0.032
	CONSTANT	N/A	-2.31393	N/A
Negative Binomial	SEASON	1[3]	-0.63878	0.528[3]
	NDVI	0.04	4.27759	1.198
	PHOTOAREA	1.65	0.09874	1.176
	SLOPEFIELD	0.37	-0.62872	0.793
	TSIMIC	0.13	-1.62801	0.803
	EVEN	0.05	-3.14456	0.845
	SHRUBCO	0.19	0.35627	1.071
	VO	0.19	1.03597	1.218
	MOISTGRD	3.07	0.03865	1.126
	CANOPYCO	0.05	-0.40235	0.980
	CONSTANT	N/A	-5.34191	N/A

[1] Exponent of the coefficient multiplied by the standard deviation of this covariate within the observations (except the dummy variable SEASON with value 0 or 1) to reflect the factor changes in the odds of absence (always 0) and factor changes in the expected occurrences for those presence sites (not always 0) when the covariate is increased by 1 standard deviation holding the others in constant.

[2] Calculated using standard deviation of ALT assuming in dry season relative to wet season.

[3] Calculated to reflect factor change in dry season relative to wet season.

Table 3.5 Model comparisons for habitat use of Reeve's muntjacs in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area of southern Taiwan using zero-inflated negative binomial regression. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence. See Table 3.1 and 3.2 for definitions of covariates. Akaike weights were derived from ΔAIC_c. '+' indicates positive coefficient, '-' indicates negative coefficient, while empty indicates variable not included in the model.

Supported models		1	2	3	4	5	6	7
Number of covariates		11	12	8	13	10	9	14
ΔAIC_c		0.00	0.12	0.57	0.85	1.35	1.57	1.76
Akaike weight		0.21	0.20	0.16	0.14	0.11	0.10	0.09
Logit variable	NDVI	-	-	-	-	-	-	-
	SLOPESTD	-	-	-	-	-	-	-
	SLOPEDEM	+	+		+	+	+	+
	ALT	+	+		+	+		+
	CLIFFCOUNT	+	+	+	+	+	+	+
	RIVERDIST	-	-		-	-		-
	CONSTANT	+	+	+	+	+	+	+
NB variable	ALT	-	-	-	-	-	-	-
	CLIFFCOUNT	-	-	-	-		-	-
	RHO		-		-			-
	SLOPEFIELD	-	-	-	-	-	-	-
	VOSTD							-
	TREEDENCV	-	-	-	-	-	-	-
	CANOPYCO				+			+
	CANOPYHT	-	-	-	-	-	-	-
	CONSTANT	+	+	+	+	+	+	+

Table 3.6 Average coefficients and factor changes of covariates based on model averaging 7 supported zero-inflated negative binomial (ZINB) models in Table 3.5 using Akaike weights derived from ΔAIC_c for distribution and occurrences patterns of Reeve's muntjacs in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence.

Model	**Covariate**	**Standard deviation**	**Averaged coefficient**	**Factor change**[1]
Logit	NDVI	0.04	-64.86004	0.064
	SLOPESTD	6.31	-0.28449	0.166
	SLOPEDEM	20.74	0.09228	6.778
	ALTGPS	694.88	0.00793	247.465
	CLIFFCOUNT	65.59	0.08641	289.308
	RIVERDIST	232.36	-0.01196	0.062
	CONSTANT	N/A	13.24799	N/A
Negative Binomial	ALT	694.88	-0.00090	0.536
	CLIFFCOUNT	65.59	-0.00298	0.822
	RHO	1[2]	-0.72484	0.484[2]
	SLOPEFIELD	0.37	-0.41533	0.858
	VOSTD	0.09	-0.06644	0.994
	TREEDENCV	0.29	-0.56192	0.850
	CANOPYCO	0.05	0.33152	1.017
	CANOPYHT	4.27	-0.03958	0.844
	CONSTANT	N/A	1.04311	N/A

[1] Exponent of the coefficient multiplied by the standard deviation of this covariate within the observations (except the dummy variable RHO with value 0 or 1) to reflect the factor changes in the odds of absence (always 0) and factor changes in the expected occurrences for those presence sites (not always 0) when the covariate is increased by 1 standard deviation holding the others in constant.

[2] Calculated to reflect factor change in rhododendron forest relative to non-rhododendron forest.

Table 3.7 Model comparisons for habitat use of Formosan serows in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area of southern Taiwan using zero-inflated negative binomial regression. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence. See Table 3.1 and 3.2 for definitions of covariates. Akaike weights were derived from ΔAIC_c. '+' indicates positive coefficient, '-' indicates negative coefficient, while empty indicates variable not included in the model.

Supported models		1	2	3	4	5	6	7	8	9
Number of covariates		13	12	14	10	11	15	9	16	8
ΔAIC_c		0.00	0.36	0.82	1.09	1.20	1.50	1.60	1.92	1.98
Akaike weight		0.19	0.16	0.13	0.11	0.10	0.09	0.08	0.07	0.07
Logit variable	NDVI	-	-	-	-	-	-	-	-	-
	CLIFFCOUNT	-	-	-	-	-	-	-	-	-
	CONSTANT	+	+	+	+	+	+	+	+	+
NB variable	ALT	-	-	-	-	-	-	-	-	-
	CLIFFDIST	-	-	-	-	-	-	-	-	-
	RIVERDIST	+	+	+	+	+	+	+	+	+
	TSIMIC	-	-	-			-		-	
	EVEN								-	
	SHRUBCO	-	-	-	+	-	-	-	-	-
	ROCKCO			+			+		+	
	VO						+		+	
	LTREEDEN	-	-	-		-	-		-	
	TREEDENCV	-	-	-	-	-	-	-	-	
	BASAL	+	+	+	+	+	+	+	+	+
	LTREEHT	-	-	-	-	-	-		-	
	STRATUM	+		+			+		+	
	CANOPYGAP	+	+	+	+	+	+	+	+	+
	CONSTANT	-	-	-	-	-	-	-	-	-

Table 3.8 Average coefficients and factor changes of covariates based on model averaging 9 supported zero-inflated negative binomial (ZINB) models in Table 3.5 using Akaike weights derived from ΔAIC_c for distribution and occurrences patterns of Formosan serows in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence.

Model	Covariate	Standard deviation	Averaged coefficient	Factor change[1]
Logit	NDVI	0.04	-43.90562	0.156
	CLIFFCOUNT	65.59	-0.09114	0.003
	CONSTANT	N/A	25.63355	N/A
Negative Binomial	ALT	694.88	-0.00043	0.744
	CLIFFDIST	331.19	-0.00078	0.773
	RIVERDIST	232.36	0.00076	1.192
	TSIMIC	0.13	-0.59074	0.923
	EVEN	0.05	-0.14912	0.992
	SHRUBCO	0.19	-0.57764	0.895
	ROCKCO	0.15	0.19804	1.030
	VO	0.19	0.10945	1.021
	LTREEDEN	0.65	-0.18288	0.887
	TREEDENCV	0.29	-0.52828	0.859
	BASAL	0.77	0.24877	1.212
	LTREEHT	3.04	-0.05111	0.856
	STRATUM	0.62	0.09437	1.099
	CANOPYGAP	0.06	2.88786	1.181[2]
	CONSTANT	N/A	-1.59111	N/A

[1] Exponent of the coefficient multiplied by the standard deviation of this covariate within the observations to reflect the factor changes in the odds of absence (always 0) and factor changes in the expected occurrences for those presence sites (not always 0) when the covariate is increased by 1 standard deviation holding the others in constant.

[2] Calculated to reflect factor change by increasing 1 layer of forest stratum.

Table 3.9 Model comparisons for habitat use of sambar deer in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area of southern Taiwan using zero-inflated negative binomial regression. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence. See Table 3.1 and 3.2 for definitions of covariates. Akaike weights were derived from $\Delta\mathrm{AIC_c}$. '+' indicates positive coefficient, '-' indicates negative coefficient, while empty indicates variable not included in the model.

	Supported models	1	2	3	4	5	6
	Number of covariates	18	20	17	19	16	15
	$\Delta\mathrm{AIC_c}$	0.00	0.86	0.99	1.13	1.30	1.63
	Akaike weight	0.26	0.17	0.16	0.15	0.14	0.12
Logit variable	ALT	+	+	+	+	+	+
	CLIFFDIST	-	-	-	-	-	-
	CONSTANT	-	-	-	-	-	-
NB variable	NDVI	-	-	-	-	-	-
	ASR	-	-	-	-	-	-
	ALT	+	+	+	+	+	+
	RIVERDIST	-	-	-	-	-	-
	PHOTOAREA		+		+		
	RHO	-	-	-	-	-	-
	TSIMIC	-	-	-	-		
	EVEN	-	-	-	-	-	-
	SHRUBHT	-	-		-		
	SHRUBDEN	+	+	+	+	+	+
	ROCKCO	-	-	-	-	-	-
	STREEDEN	-	-	-	-	-	-
	LTREEDEN	+	+	+	+	+	+
	TREEDENCV	+	+	+	+	+	
	STREEHT	-	-	-	-	-	-
	TREEHTCV		-				
	STRATUM	-	-	-	-	-	-
	MOISTGRD	+	+	+	+	+	+
	CONSTANT	+	+	+	+	+	+

Table 3.10 Average coefficients and factor changes of covariates based on model averaging 11 supported zero-inflated negative binomial (ZINB) models in Table 3.7 using Akaike weights derived from ΔAIC_c for distribution and occurrences patterns of sambar deer in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence.

Model	**Covariate**	**Standard deviation**	**Averaged coefficient**	**Factor change**[1]
Logit	ALT	694.88	0.00672	106.965
	CLIFFDIST	331.19	-0.00514	0.182
	CONSTANT	N/A	-13.27401	N/A
Negative Binomial	NDVI	0.04	-6.92356	0.746
	ASR	24.99	-0.01229	0.736
	ALT	694.88	0.00123	2.353
	RIVERDIST	232.36	-0.00105	0.784
	PHOTOAREA	1.65	0.02544	1.043
	RHO	1[2]	-20.11970	0.000[2]
	TSIMIC	0.13	-1.50180	0.816
	EVEN	0.05	-7.59969	0.666
	SHRUBHT	0.28	-0.32921	0.912
	SHRUBDEN	0.81	0.24065	1.216
	ROCKCO	0.15	-1.96197	0.746
	STREEDEN	0.90	-0.70306	0.529
	LTREEDEN	0.65	0.37355	1.277
	TREEDENCV	0.29	0.67637	1.215
	STREEHT	0.77	-0.40738	0.732
	TREEHTCV	0.11	-0.25057	0.972
	STRATUM	0.62	-0.50012	0.606
	MOISTGRD	3.07	0.10312	1.372
	CONSTANT	N/A	6.47116	N/A

[1, 2] See explanations in Table 3.6.

Table 3.11 Model comparisons for habitat use of wild boars in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area of southern Taiwan using zero-inflated negative binomial regression. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence. See Table 3.1 and 3.2 for definitions of covariates. Akaike weights were derived from ΔAIC_c. ‘+’ indicates positive coefficient, ‘-‘ indicates negative coefficient, while empty indicates variable not included in the model.

Supported models		1	2	3	4	5	6
Number of covariates		9	8	6	10	11	12
ΔAIC_c		0.00	0.72	1.05	1.13	1.28	1.82
Akaike weight		0.26	0.18	0.16	0.15	0.14	0.11
Logit variable	SLOPESTD	+	+	+	+	+	+
	NDVI	-	-		-	-	-
	RIVERDIST	-	-		-	-	-
	CONSTANT	+	+	-	+	+	+
NB variable	NDVI	-			-	-	-
	ASR				-	-	-
	SHRUBHT	+	+	+	+	+	+
	SHRUBCV						-
	ROCKCO	+	+	+	+	+	+
	VO	-	-	-	-	-	-
	STREEHT	-	-	-	-	-	-
	CANOPYHT	-	-	-	-	-	-
	MOISTGRD					+	+
	CONSTANT	+	-	-	+	+	+

Table 3.12 Average coefficients and factor changes of covariates based on model averaging 6 supported zero-inflated negative binomial (ZINB) models in Table 3.3 using Akaike weights derived from ΔAIC_c for distribution and occurrences patterns of wild boars in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. This mixture model consisted of two parts: logit model (L) for probability of absence (always 0) and negative binomial model (NB) for expected frequency of occurrences conditional on presence.

Model	**Covariate**	**Standard deviation**	**Averaged coefficient**	**Factor change[1]**
Logit	SLOPESTD	6.31	20.52374	$1.65 \times 10^{+56}$
	NDVI	0.04	-2690.52910	3.74×10^{-50}
	RIVERDIST	232.36	-0.16044	6.45×10^{-17}
	CONSTANT	N/A	1215.03847	N/A
Negative Binomial	NDVI	0.04	-5.60081	0.789
	ASR	24.99	-0.00374	0.911
	SHRUBHT	0.28	0.93700	1.298
	SHRUBCV	0.17	-0.11886	0.980
	ROCKCO	0.15	1.73403	1.296
	VO	0.19	-2.45264	0.626
	STREEHT	0.77	-0.49108	0.687
	CANOPYHT	4.27	-0.07742	0.718
	MOISTGRD	3.07	0.02055	1.065
	CONSTANT	N/A	2.73904	N/A

[1] Exponent of the coefficient multiplied by the standard deviation of this covariate within the observations to reflect the factor changes in the odds of absence (always 0) and factor changes in the expected occurrences for those presence sites (not always 0) when the covariate is increased by 1 standard deviation holding others in constant.

Table 3.13 (Continued to next page) Habitat segregations in occupancy and occurrences of Formosan macaques, Reeve's muntjacs, Formosan serows, sambar deer, and wild boars in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan. Positive signs imply higher values increase probability of occupancy or have higher expected number of occurrences conditional on presence and vice versa for negative signs. Signs were based on model averaged coefficients.

Model	Habitat type	Habitat	Macaque	Muntjac	Serow	Sambar	Wild Boar
Occupancy	Season	ALTSEASON	-				
	Temperature wetness/ altitude vegetation	ALT	-	-		-	
		NDVI		+	+		+
		RIVERDIST		+			+
	Terrain/ Ruggedness	SLOPEDEM		-			
		SLOPESTD	+	+			-
		CLIFFCOUNT		-	+		
		CLIFFDIST	+			+	
Occurrences	Season	SEASON	-				
	Altitude/ vegetation	ALT		-	-	+	
		RHO		-		-	
		NDVI	+			-	-
	Terrain shape/ Ruggedness	SLOPE_FIELD	-	-			
		SLOPESTD					
		CLIFFDIST			-		
		CLIFFCOUNT		-			
		TSIMIC	-		-	-	
		EVEN	-		-	-	
	Moisture gradient /wetness	MOISTGRD	+			+	+
		ASR				-	-
		RIVERDIST			+	-	

Table 3.13 (Continued from previous page) Habitat segregations in occupancy and occurrences of Formosan macaques, Reeve’s muntjacs, Formosan serows, sambar deer, and wild boars in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan. Positive signs imply higher values increase probability of occupancy or have higher expected number of occurrences conditional on presence and vice versa for negative signs. Signs were based on model averaged coefficients.

Model	**Habitat type**	**Habitat**	**Macaque**	**Muntjac**	**Serow**	**Sambar**	**Wild Boar**
Occurrences	Forest understory/ ground cover	HERBCO					
		SHRUBCO	+		-		
		SHRUBHT				-	+
		SHRUBDEN				+	
		SHRUBCV					-
		ROCKCO			+	-	+
		VO	+		+		-
		VOSTD		-			
	Forest structures	STREEDEN				-	
		LTREEDEN			-	+	
		TREEDENCV		-	-	+	
		BASAL			+		
		STREEHT				-	-
		LTREEHT			-		
		TREEHTCV				-	
		STRATUM			+	-	
		CANOPYHT		-			-
		CANOPYCO	-	+			
		CANOPYGAP			+		

Table 3.14 Pearson correlations between estimated occupancy and 3 forms of abundance indices based on photographic rates (OI) for Formosan macaque, Reeve's muntjac, Formosan serow, sambar deer, and wild boar at 4 altitude zones (i.e. n=4) in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004. OI indicated GOI (group occurrence index) for Formosan macaque and SOI (species occurrence index) for the other 4 ungulate species. The highest significant correlation coefficient was in bold.

Species	**OI**	**1/OI**	**ln(OI)**
Formosan macaque (dry season)	**0.991****	-0.975*	0.988**
Formosan macaque (wet season)	0.481	-0.405	0.448
Reeve's muntjac	0.703	**-0.984***	0.980*
Formosan serow	0.999**	-0.9947**	**0.999****
Sambar deer	0.890	-0.921	0.916
Wild boar	0.344	-0.196	0.266

* p<0.05

** p<0.01

Table 3.15 Observed and estimated occupancy, photographic rates from camera trapping (GOI: group occurrence index, SOI: species occurrence index, see chapter 2), and overall false absence rate (FAR) and occurrence index (OI: GOI or SOI) for Formosan macaque, Reeve's muntjac, Formosan serow, sambar deer, and wild boar at 4 altitude zones in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

Species		**350-1,200m**	**1,200-2,000m**	**2,000-2,500m**	**2,500-3,100m**	**Overall FAR and OI**
Formosan macaque (dry season)	Observed occupancy	62.1%	57.1%	63.0%	13.3%	27.1% (FAR)
	Estimated occupancy	99.0%	87.1%	78.4%	18.4%	
	GOI	2.72	2.59	1.93	0.12	2.22
Formosan macaque (wet season)	Observed occupancy	89.3%	82.1%	80.8%	70.6%	13.9% (FAR)
	Estimated occupancy	100%	98.3%	99.4%	78.7%	
	GOI	5.51	5.69	2.71	3.08	4.41
Reeve's muntjac	Observed occupancy	97.2%	91.8%	74.4%	9.5%	3.0% (FAR)
	Estimated occupancy	100%	94.3%	79.2%	10.8%	
	SOI	25.76	8.35	5.08	0.30	13.45
Formosan serow	Observed occupancy	77.8%	73.5%	58.1%	100%	18.4% (FAR)
	Estimated occupancy	95.7%	98.8%	78.3%	100%	
	SOI	3.32	3.75	1.68	3.78	3.11
Sambar deer	Observed occupancy	41.7%	49.0%	46.5%	4.8%	37.9% (FAR)
	Estimated occupancy	100.0%	93.0%	61.5%	5.2%	
	SOI	1.09	1.45	1.23	0.07	1.10
Wild boar	Observed occupancy	23.6%	12.2%	27.9%	38.1%	68.2% (FAR)
	Estimated occupancy	97.6%	90.2%	82.7%	91.0%	
	GOI	0.39	0.17	0.31	0.39	0.31

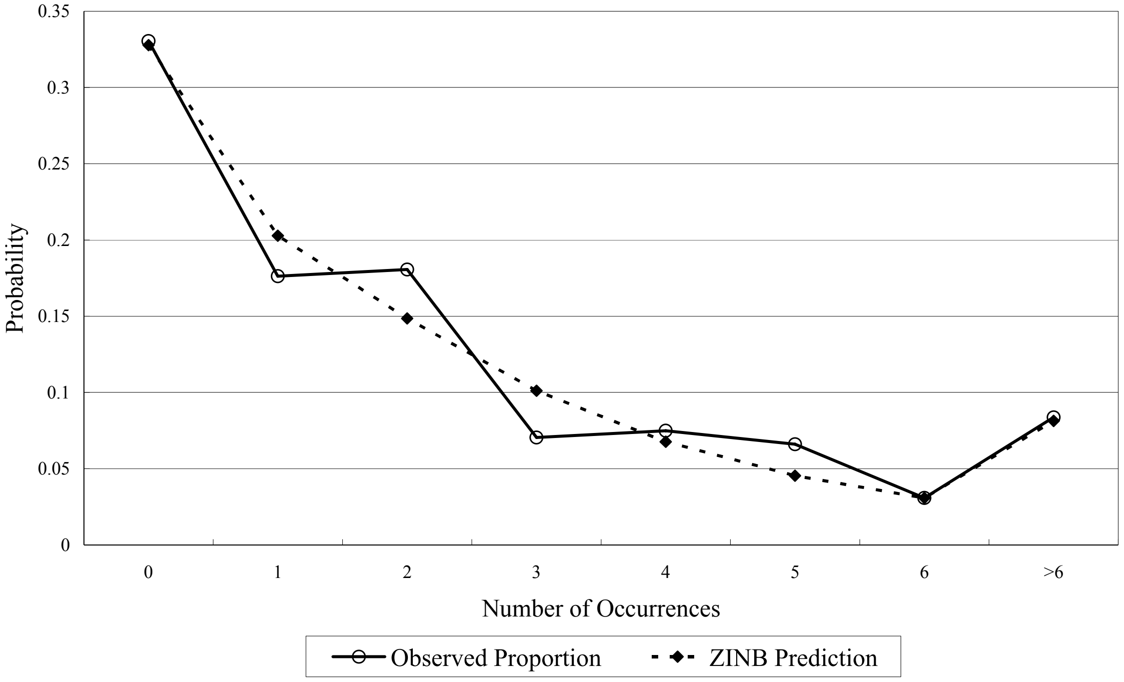


Figure 3.1 Predicted probabilities of different number of Formosan macaque group occurrences from the average of 3 supported zero-inflated negative binomial models (ZINB) and observed proportions of different number of Formosan macaque group occurrences from the original camera trapping data collected in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

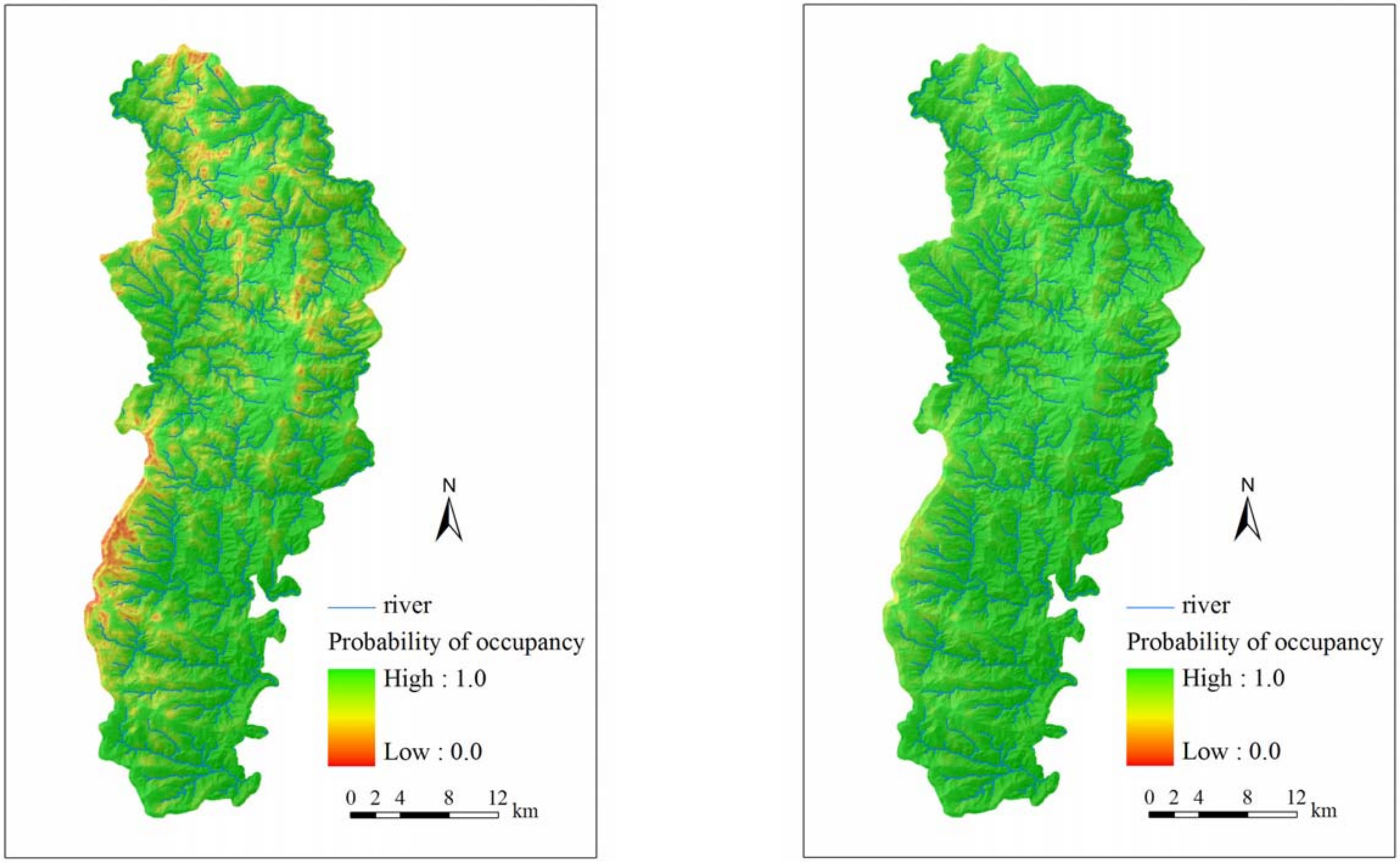


Figure 3.2 Predicted probabilities of occupancy for Formosan macaques in dry season (left) and wet season (right) in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, shown in shaded terrain relief (valley is darker).

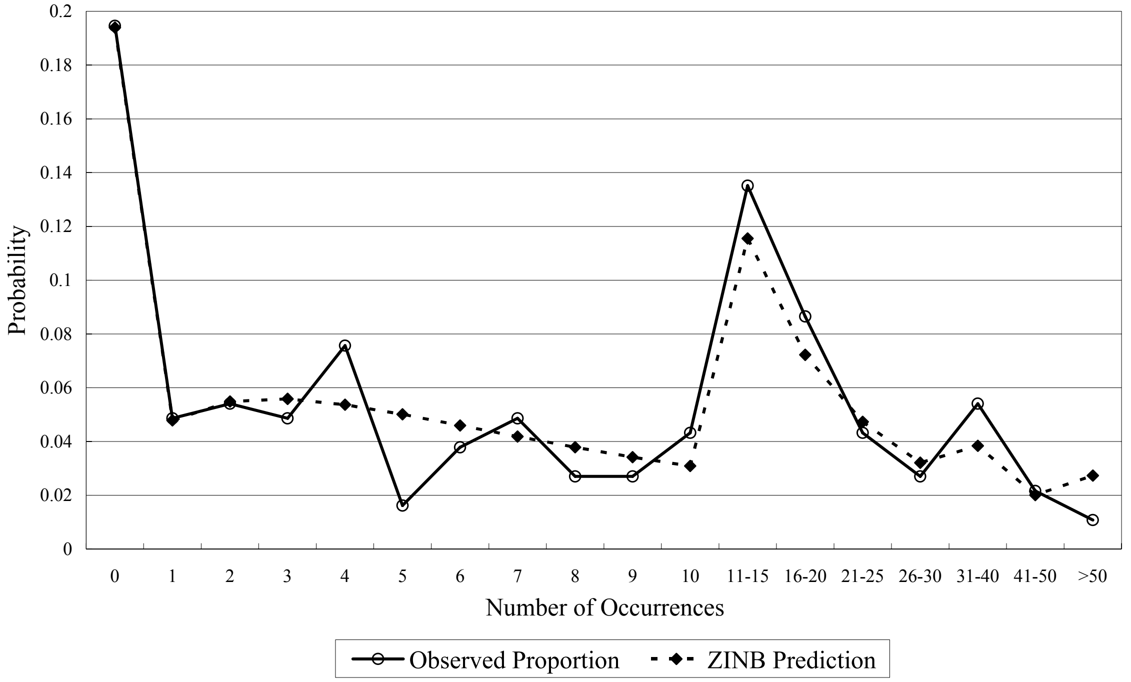
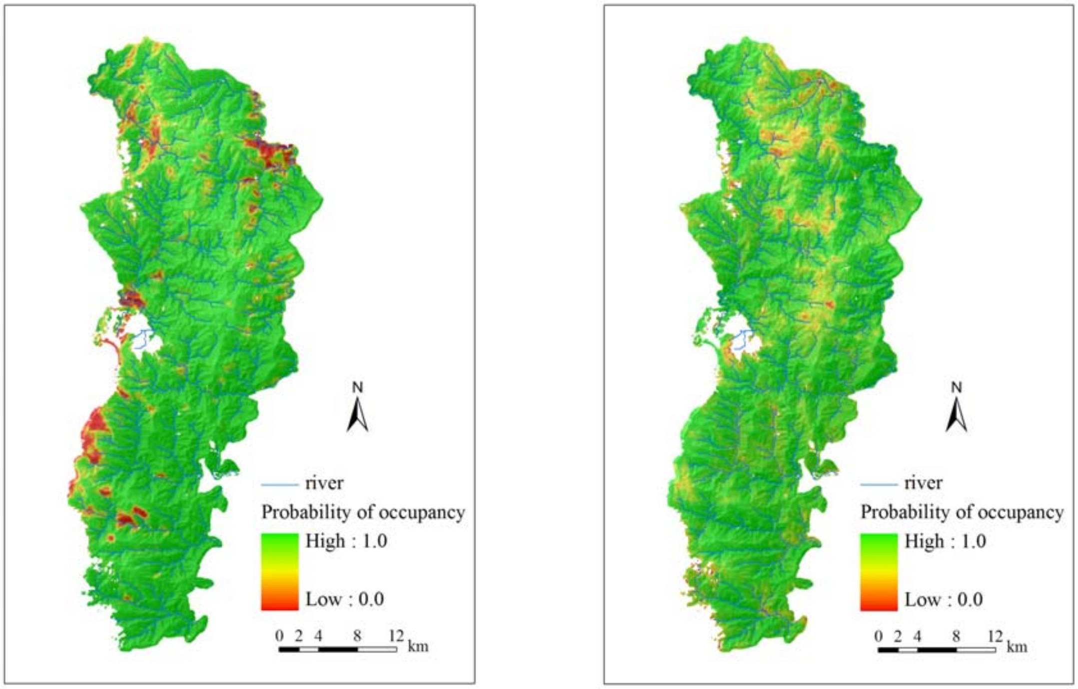
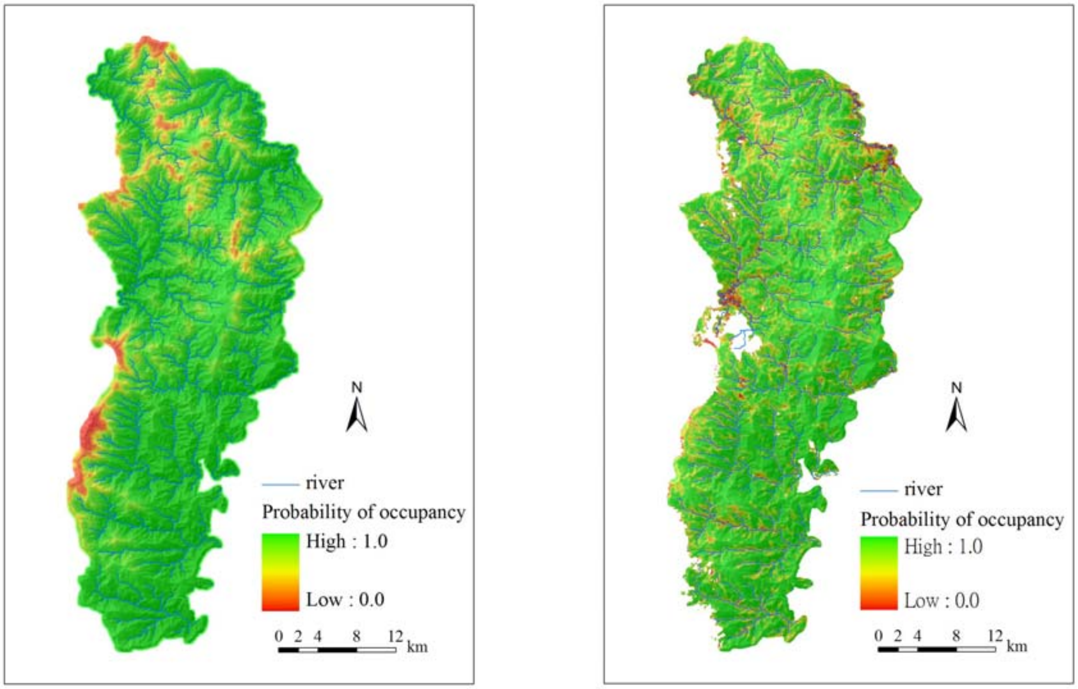


Figure 3.3 Predicted probabilities of different number of Reeve's muntjac occurrences from the average of 7 supported zero-inflated negative binomial models (ZINB) and observed proportions of different number of Reeve's muntjac occurrences from the original camera trapping data collected in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.



(a) Reeve's muntjac (b) Formosan serow



(c) Sambar deer (d) Wild boar

Figure 3.4 Predicted probabilities of occupancy for (a) Reeve's muntjacs, (b) Formosan serows, (c) sambar deer, and (d) wild boars in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, shown in shaded terrain relief (valley is darker). In (a), (b) and (d), some area could not be predicted because of missing NDVI data.

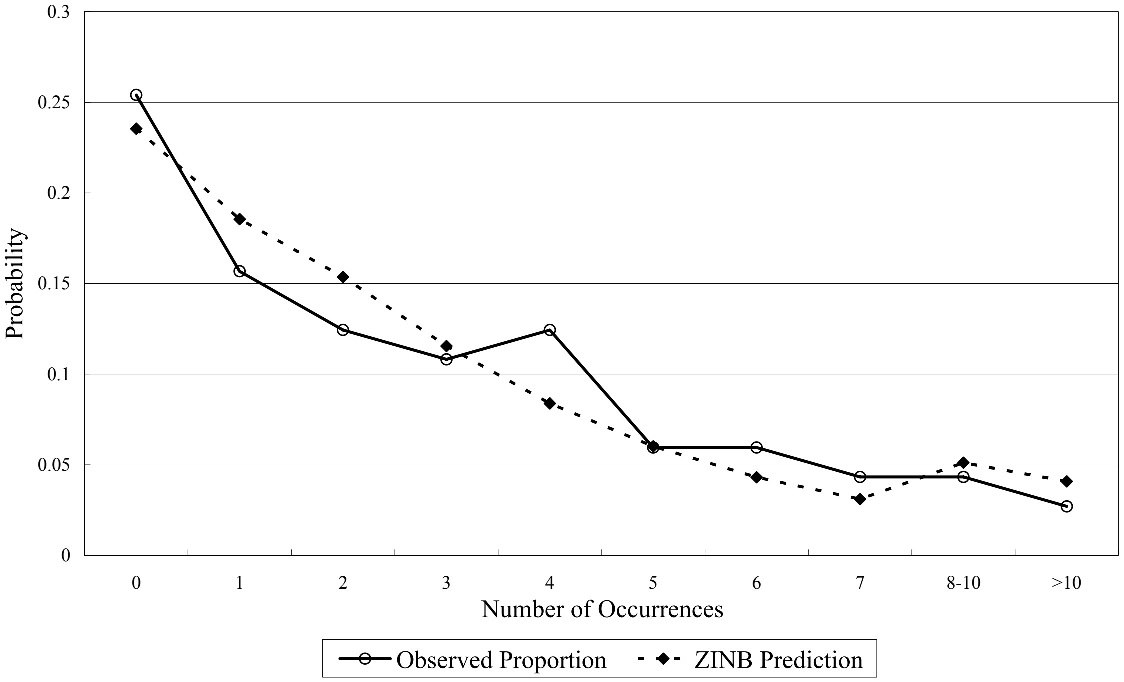


Figure 3.5 Predicted probabilities of different number of Formosan serow occurrences from the average of 9 supported zero-inflated negative binomial models (ZINB) and observed proportions of different number of Formosan serow occurrences from the original camera trapping data collected in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

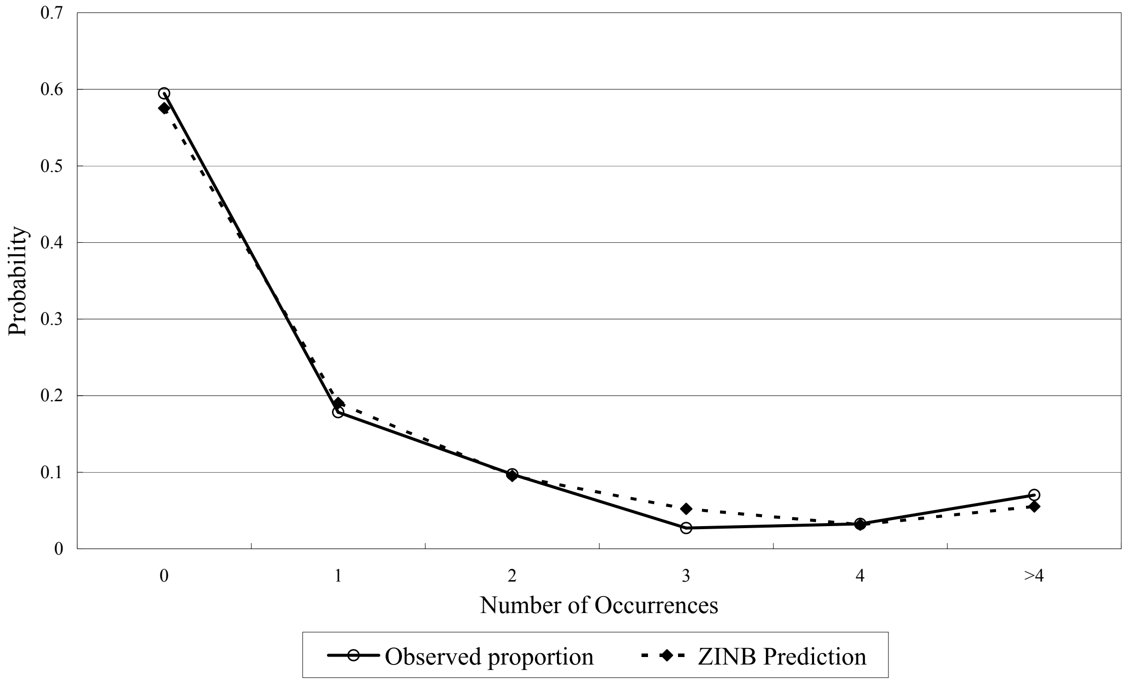


Figure 3.6 Predicted probabilities of different number of sambar deer occurrences from the average of 6 supported zero-inflated negative binomial models (ZINB) and observed proportions of different number of sambar deer occurrences from the original camera trapping data collected in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

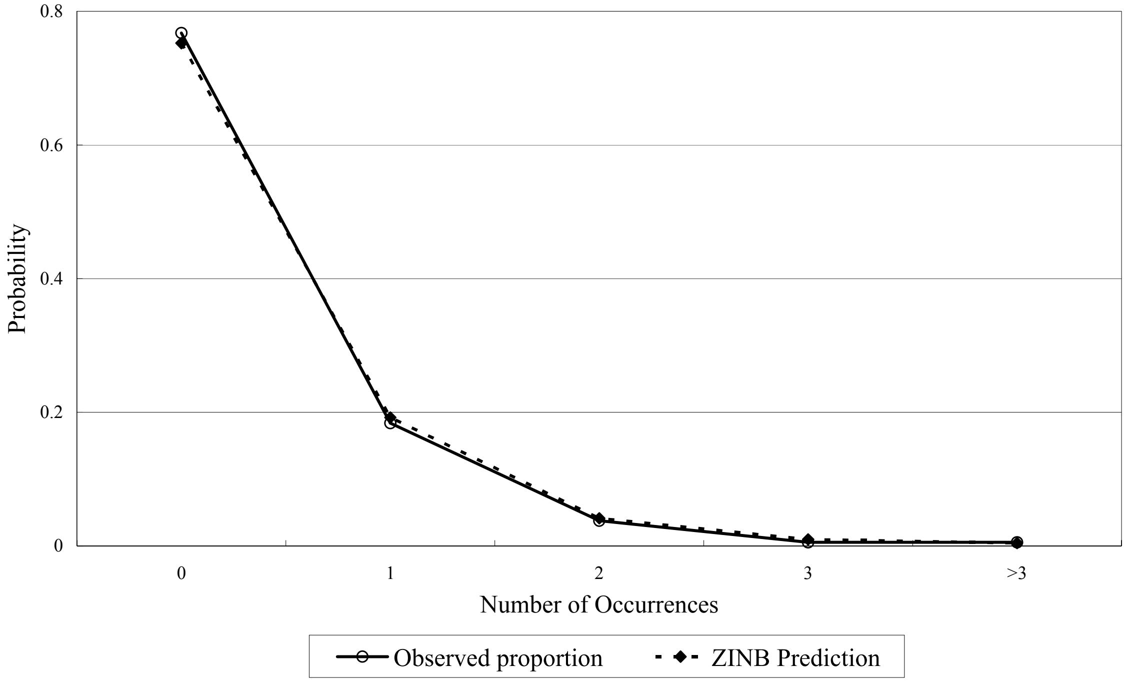


Figure 3.7 Predicted probabilities of different number of wild boar occurrences from the average of 11 supported zero-inflated negative binomial models (ZINB) and observed proportions of different number of wild boar occurrences from the original camera trapping data collected in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, 2001-2004.

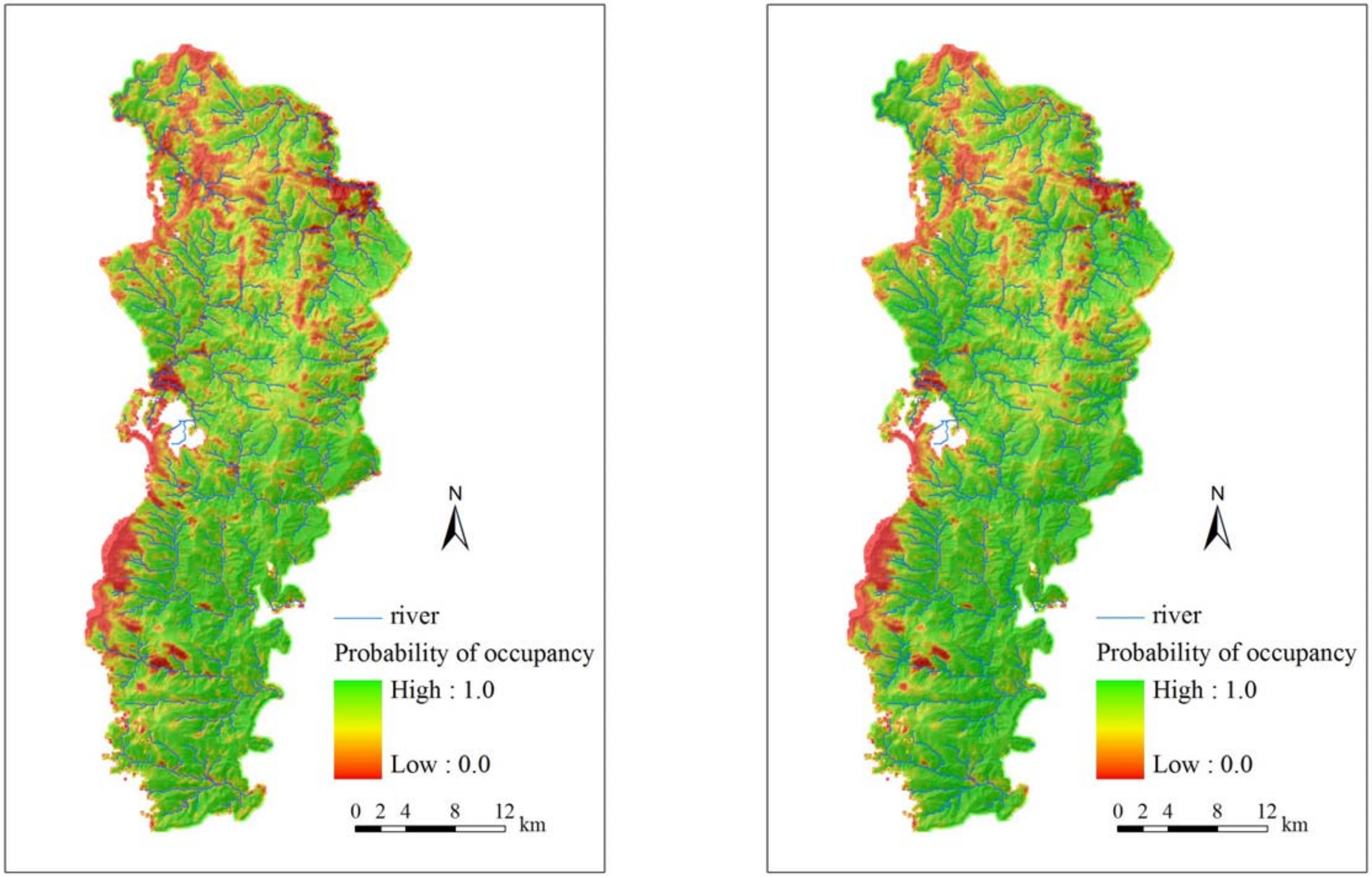


Figure 3.8 Predicted probability of occupancy of all 5 herbivores (left: using wild boars' logit model, right: assume wild boars are omnipresent) in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, shown in shaded terrain relief (valley is darker). Some area could not be predicted because of missing NDVI data.

Chapter 4: Diversity and niche relationships of carnivores in Taiwan

Introduction

When ecologically similar species are in sympatry, different species often partition use of resources, resulting in niche differentiation to facilitate species coexistence (Schoener 1974, Gordon 2000). For example, sympatric carnivores were found to have different habitat uses (Fedriani et al. 1999, Loveridge and Macdonald 2003, Vieira and Port 2007), different prey size (Karanth and Sunquist 2000, McDonald 2002, Scognamillo et al. 2003), different prey species (Chuang and Lee 1997, Karanth and Sunquist 2000), or different activity patterns (Fedriani et al. 1999, Chen 2002, Loveridge and Macdonald 2003, Vieira and Port 2007). Schoener (1974) found that resource partitioning was principally along these 3 dimensions (i.e. habitat, diet, and time) and that the habitat dimension was relatively the most important axis followed by food-type and then by temporal dimensions. When species were similar in one dimension, complimentary resource use would imply dissimilarity in other dimensions to reduce interspecific competition (Schoener 1974;1983).

There are 11 wild carnivore species in Taiwan (Table 1.1), including 2 felids, 5 mustelids, 2 viverrids, crab-eating mongoose in the Herpestidae, and Asiatic black bear in the Ursidae. Mongooses had been classified in the family Viverridae (Ewer 1973), but recent evidence has put them into a separate family, Herpestidae (Nowak 2005). These 11 carnivores occur variably from coastal plain to the highest mountain tundra (altitude 3,952m) in Taiwan and many are sympatric in forested environments. However, the largest felid (Formosan clouded leopard, see chapter 2) and the largest mustelid (Eurasian otter, Lin 2000) are likely extinct in Taiwan. The largest carnivore, Asiatic black bear, has also become very rare compared to historical distribution and abundance (Hwang et al. 2006). The remaining larger carnivores in Taiwan are the leopard cat with body weight 2-4kg (Nowell and Jackson 1996) distributed in low lands close to human encroachment (Pei and Chen 2006) and the yellow-throated marten with body weight up to 3kg (C. Chen personal communication and Grassman et al. 2005a) distributed mostly in remote primary forests at higher altitudes. Disappearance of top carnivores may result in increased smaller carnivores, i.e. mesopredator release (Terborgh et al. 1999), and thus cause declines of prey (e.g. birds and small vertebrates) of these mesopredators (Soule et al. 1988, Palomares et al. 1995, Crooks and Soule 1999). Understanding the niche relationships of carnivores may shed light on how these species coexist or avoid one another. But, the cascading impacts of vanishing top carnivores in Taiwan are unknown and do not get much attention. On the other hand, human encroachment and economic development has tremendously altered the habitat and has incurred forest fragmentation and disappearance. Suitable habitats for these carnivores may be reduced, while information regarding how human activities affect the carnivores is limited in Taiwan.

Investigating the resource utilization of these mesopredators and how they partition resources could help understand the mechanisms influencing the vertebrate community, particularly the current niche relationships of these mesopredators living in areas without top carnivores. Such information could be used in assessing the reintroduction plans of the disappearing top carnivores (Terborgh et al. 1999) and also provide baseline information for conservation and management of these mesopredators. However, only a few studies (excluding local inventory surveys) have been conducted on carnivores in Taiwan and most focused on individual species. Very few studies addressed the niche relationships of sympatric carnivores in Taiwan. Chuang and Lee (1997) studied the food habits of Formosan ferret badger, crab-eating mongoose, and lesser oriental civet in sympatry and found these 3 species all fed mainly on invertebrates but had dissimilar relative importance among different invertebrate taxa. In contrast, scat analysis revealed that yellow-throated martens and Siberian weasels had similar diet niche breadth and overlapped diet in high degree (Tsai 2007a). But, their complimentary resource use in other niche dimensions was not addressed. Wu (1999) also found substantial diet overlap between Siberian weasels and Formosan ferret badgers. However, they had different occurrence frequencies among various prey species and exhibited some degree of habitat segregation. The only study involving temporal dimension showed that crab-eating mongoose was diurnal in contrast to the nocturnal Formosan ferret badger, lesser oriental civet, and gem-faced palm civet (Chen 2002). Chen (2002) also studied habitat characteristics affecting presence and absence and found some differences among these 4 sympatric carnivores in southern Taiwan.

The influence of human activities on carnivore communities in Taiwan has not been studied. It could be beneficial, neutral, or detrimental to some species, or it could reduce carnivore diversity due to hunting or forest practices causing habitat loss. Taiwan is an island, and geographic constraints from sea and mountain peaks could limit species distribution and may produce a mid-domain pattern of species diversity along the altitude gradient (Colwell and Lees 2000). Understanding spatial patterns of species diversity had been a central theme of ecology and may provide some conservation insights in local regions. The objectives of this study were to investigate the niche relationships of mesopredators currently living in the absence of carnivores (e.g. Formosan clouded leopard, Eurasian otter, and also possibly Asiatic black bear) in Taiwan, to understand the spatial patterns of carnivore diversity, and to understand how these carnivores are coping with human activity and its influences on the carnivore community. We predicted that 1) complimentary resource use would be observed for sympatric carnivores, 2) human activity could influence some species and adversely reduce carnivore diversity, and 3) a mid-domain effect (hump-shaped) of carnivore diversity would occur along the altitude gradient.

Methods

Niche relationships were investigated along 3 dimensions (i.e. habitat, diet, and time). To study their activity patterns and spatial patterns, camera trapping was used to collect data on relative abundance of carnivores. Micro-habitat and meso-habitat of the camera trap sites were measured at each site (see chapter 1 for details). Spatial patterns were analyzed in 2 scales. The first is within the study area in southern Taiwan (for details see chapter 1, Fig. 1.2). The second scale is for the spatial patterns across Taiwan, and data were based on other published literature of camera trapping studies in Taiwan. Taiwan is an orogenic island of approximate 36,000 km^2 located in Southeast Asia (Fig. 1.1). The highest mountain peak is 3,952m. Due to the alternating monsoons and typhoons, annual precipitation is high (generally 1,500m-2,500m in plains and 2,000m-3,500m in mountains) making the natural vegetation types mostly evergreen forests (Su 1984). High altitude ranges had created a vegetation gradient of broad-leaf trees at lower altitudes, coniferous trees at higher altitudes, and transitions at altitudes between 1,500m and 2,500m (Su 1984).

Activity patterns

Camera trapping has been used widely to study animal diel activities (see review in Cutler and Swann 1999). It assumes that the more active animals are during a time period, the higher the probability of being photographed during that time period. I calculated the number of photographic occurrence events (see chapter 1) for each hour. The index of activity level for each hour was calculated by dividing the hourly number of group occurrence events by the total number of group occurrence events. Hourly activity levels were expressed as percentages and depicted across 24 hours (regular activity pattern). However, camera trapping lasted a whole year. Activity levels at crepuscular hours were ambiguous when classifying as diurnal or nocturnal. Before sunrise and after sunset, there is still some light scattered through the atmosphere. Thus, I used civil twilight hours in the morning and in the evening to distinguish between day and night instead of using regular sunrise and sunset time. Civil twilight is defined as "…to begin in the morning, and to end in the evening when the center of the Sun is geometrically 6 degrees below the horizon. This is the limit at which twilight illumination is sufficient, under good weather conditions, for terrestrial objects to be clearly distinguished…In the morning before the beginning of civil twilight and in the evening after the end of civil twilight, artificial illumination is normally required to carry on ordinary outdoor activities." (Astronomical Applications Department, U.S.A. Naval Observatory (USNO), http://aa.usno.navy.mil/faq/docs/RST_defs.php#top). However, this definition is for humans in open environments without obstruction by terrain. In the study area where forest canopy is dense and mountains are steep and high, it felt like complete dark around civil twilight hours in the morning and in the evening based on our field experiences. Civil twilight hours were obtained using USNO's online program (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Coordinates used to calculate civil twilight hours for 2001-2004 were based on the center of the study area (Longitude 120°

47’ E, Latitude 22˚ 37’N). Differences of civil twilight hours between the other locations within the study area and the coordinates used were within 1 minute. To further illustrate the activity pattern relative to twilight hours (twilight activity pattern), I defined the time within the civil twilight hours (i.e. begin in the morning and end in the evening) as daytime and vice versa for nighttime. “Daytime” was classified into 12 equal-length “virtual hours” and assigned as 6 to 18 o’clock. “Nighttime” was also similarly classified into 12 “virtual hours” and assigned as 18 in the evening to 24 (or 0 for midnight) and then to 6 o’clock in the morning. Activity (an occurrence event) was recorded by virtual hour. Hourly activity level was then calculated for each virtual hour and overlaid with the regular activity pattern for comparison. However, the virtual hour is not necessarily 60 minutes and varied throughout the year. Approximately from 2/5 to 11/4, daytime is longer than night time and the largest difference is around the summer solstice (862 vs. 578 minutes). Daytime is shorter than nighttime for the remaining days and the largest difference occurs around the winter solstice (694 vs. 746 minutes). But, equal daytime and night time does not occur around equinoxes. Activity within the civil twilight hours (i.e. daytime) was classified as diurnal and assigned a value of 1; while nocturnal activity was assigned a value of -1. An overall index of diurnal activity (DI) was calculated by summing these values (i.e. 1 or -1) for all occurrence events and dividing this sum by the total number of occurrence events. That is, 0 indicated even diurnal and nocturnal activities; while 1 implied completely diurnal and -1 implied completely nocturnal. This index (DI) was used as one of the niche dimension for comparison of temporal segregation.

Because of the dependency of animals occurring in groups (e.g. pairs or adults with young), group occurrences (see chapter 1) were used. To avoid the influences of lures, only pictures from trail sets were included. Pictures from the incomplete first day of camera trapping in each roll of film were also excluded so that sampling effort for every hour was the same (i.e. camera trapping days for each roll of film was controlled to be an integer multiplier of a day or 24 hours). For species not recorded from our camera trapping in the study area, DI was calculated based on other camera trapping studies in Taiwan, but was neither adjusted according to twilight hours nor based on group occurrences.

Spatial patterns

I conducted canonical correspondence analysis (CCA) (Ter Braak 1986) to describe the carnivore community structure and its relationship with habitat characteristics using the software PC-ORD (MjM Software Design, Gleneden Beach, OR, U.S.A.). Species abundance was based on photographic rates from camera trapping (OI, i.e. number of occurrences standardized for camera trapping effort, see method in chapter 3). CCA were conducted at 2 scales.

1. <u>within the study area</u>:

I calculated a group occurrence index (GOI, see chapter 2) for yellow-throated martens because they were sometimes photographed or observed in groups of 2-3 individuals (this study). For the other carnivores, species occurrence index (SOI, see chapter 2) based on identifiable individuals was used as they were mostly solitary. Wilcoxon rank-sum tests showed that there were no significant differences of OI between dry and wet seasons for 5 smaller carnivores (Formosan ferret badger, Siberian weasel, yellow-throated marten, crab-eating mongoose, and lesser oriental civet, p=0.16-0.9) in the study area. Thus, OI was calculated for each camera trap site without separating dry and wet seasons for analysis. Only trail sets were used to avoid effects from lures and other factors. Only camera trap sites that documented at least one carnivore were used for analysis of community. Although camera trap sites may include many zeros for some of the less common species and the distribution of species abundance could be skewed, CCA is quite robust to skewed species distribution, quantitative noise in abundance data, and unusual sampling design (Palmer 1993).

Habitat variables were measured at two scales, meso-scale landscape variables derived from 40mX40m digital elevation model and micro-scale variables measured within 17.8m radius of the camera trap site. The 31 habitat variables were divided into 4 categories: altitude/greenness/wetness, terrain shape/ruggedness, forest understory, and forest structure (Table 4.1, see chapter 1 for details). Because of the large number of habitat variables and collinearity, I conducted factor analysis using orthogonal rotation to reduce the number of habitat variables and collinearity. I used STATA 9.2 to perform factor analysis based on principal component analysis on a correlation matrix. Factor analysis was conducted on the 4 categories of habitat variables (Table 4.1) separately instead on the whole set of variables alone so that each factor was a linear combination of a few variables in the same category and was easier to interpret. For each category, principal components were selected so that these components explained at least 70% of habitat variation cumulatively. Components with eigenvalues >1 were also retained even though cumulative variation explained already exceeded 70%. These principal components were thereafter orthogonally rotated (varimax with Horst normalization to maximize dispersion of the ordination) for ease of interpretation of the rotated factors. Factor scores were used as habitat variables for each camera trap site in CCA.

2. <u>landscape scale across Taiwan</u>:

Instead of using individual camera trap sites as the sampling units in the previous scale, I conducted a meta-analysis and used individual areas of all camera trapping studies in Taiwan as sampling units. Averaged OI of each area were extracted from published studies conducted in Taiwan including this study. Because of the large altitude ranges (150-3,100m) of the study area, our data were separated into 5 zones by altitudes and hunting pressure. Areas from other camera trapping studies covering wide altitude ranges were also divided into narrower altitude ranges similarly. However, other camera trapping studies only reported SOI for yellow-throated martens and GOI could not be obtained. But, total group occurrences and total species occurrences of yellow-throated marten in the study area were 103 and 95, respectively. The difference was small because different individuals were hard to differentiate in consecutive photos. Thus, GOI and SOI of yellow-throated marten in the study area did not differ a lot. After averaging for different altitude zones, influence of using GOI for yellow-throated marten from this study could be ignored in this landscape scale of analysis of Taiwan as a whole.

Variables in the environment matrix of CCA for each area included average altitude, human activity, and level of forest alterations. Average altitude was calculated if altitudes of camera trap sites were reported in the literature. Otherwise, mid point of the altitude range of the study area was used. Human activity was based on 2 values: proximity (5km) to paved roads and villages (0 or 1) and levels of human hunting (0: no hunting, 1: occasional hunting, 2: seasonal hunting, 3: consistent hunting). Levels of forest alterations were ranked from 0 to 5 with 0 indicating contiguous primary forest and 5 being the extreme side of fragmented (mosaic with farmlands or human encroachment) secondary forests in early succession stages and plantation forests after clear cut. Proximity to roads and villages was examined by overlaying areas with road and village coverages on a GIS. Levels of human hunting and forest alterations were determined subjectively based on information from the original literature and corresponding authors in combination with personal field experiences in those areas. The 2 values of proximity to roads and villages and levels of human hunting were each scaled to 10 and summed to form an overall index of human activity (0-20).

Diet patterns

Diet was summarized according to published studies conducted in Taiwan. If no local information was available, studies in nearby Southeast Asian countries were used instead. I divided food types into 5 categories: invertebrate, smaller mammals, other smaller vertebrate (amphibians, reptiles, birds, etc.), larger vertebrate (>1kg), and plant. Importance of each category was assigned as major food items if average reported relative importance was greater than 40%, secondary food items if average reported relative importance was between 15% and 40%, occasional food items if average reported relative importance was between 5% and 15%. Food category having average reported relative importance <5% was ignored for ease of comparison.

Diversity of carnivores

Similar to the meta-analysis of the carnivore community at the landscape scale of all of Taiwan, individual areas from camera trapping studies in Taiwan were the sampling units and the associated altitude, index of human activity (HA), and level of forest alteration (FORALTER) were used as covariates. Carnivore richness was simply the number of carnivore species documented based on all camera trap sites in the area. Since the number of camera trap sites and the camera trapping effort in an area were usually large enough, I believed that the species list for each area was complete except for extremely rare species, which I would not consider a resident species. However, feral cats were excluded and only wild carnivores were included for analysis. I hypothesized that 1) carnivore diversity was lower at high levels of human activity, and 2) carnivore diversity exhibited a mid-domain pattern along the altitude gradient. A set of *a priori* models were chosen based on first-order and quadratic terms of altitude, HA, FORALTER, and the interaction term of altitude and HA (ALT*HA). I used multiple linear regression and AIC_c to rank the models and test the hypotheses.

Results

Camera trapping success

Thirty-nine of all 185 trail sets with >10 camera trap days in the study area did not document any carnivores. These 39 sites were excluded in later analysis. Seven carnivore species were documented by camera trapping in the study area (see Table 1.1). The lesser oriental civet was recorded only near the southern boundary of the study area by another team. Asiatic black bears were photographed at 5 camera trap sites, including 1 trail set, 1 site beside a cavity, and 3 lure sets. Signs of Asiatic black bears were also rarely encountered. Asiatic black bears seemed to be very rare in the study area and concentrated at higher altitudes in the northern part of the study area. The other 5 carnivores, the crab-eating mongoose, gem-faced palm civets, and 3 mustelids including the yellow-throated marten, Siberian weasel, and Formosan ferret badger, were more commonly distributed throughout the study area (Table 4.2). Other camera trapping studies documented these 7 carnivore species as well, plus the leopard cat. For comparison with leopard cats, feral cats (*Felis catus*) were also included in the analysis.

Activity patterns

Yellow-throated martens (DI=0.95, Fig. 4.1) and crab-eating mongooses (DI=0.88, Fig. 4.2) were basically diurnal with few nocturnal activities. Nocturnal activities of the crab-eating mongoose were 2 “virtual hours” within civil twilight time (Fig. 4.2). That is, crab-eating mongooses extended activities to nighttime when necessary and rested throughout the night without interruption. But, yellow-throated martens could occur in the middle of the night (1 occurrence at 22 o’clock, Fig. 4.1). Nocturnal species included Formosan ferret-badgers (DI=-0.98, Fig. 4.3) and gem-faced palm civets (DI=-0.90, Fig. 4.4). Similar to the crab-eating mongoose, these 2 carnivores extended activities to daytime (but less, compared to the crab-eating mongoose) when necessary and rested throughout the day. For species showing the same type of activity patterns, there was significant association between the 2 nocturnal species (e.g. gem-faced palm civet and Formosan ferret badger, chi-square test of independence, df=13, χ^2=23.4, p=0.038) while no association was found between the 2 diurnal species (e.g. yellow-throated marten and crab-eating mongoose, chi-square test of independence, df=14, χ^2=8.9, p=0.84) based only on active hours. Siberian weasels were active day and night (DI=-0.66, Fig. 4.5) with a tendency of more nocturnal activities (chi-square test of goodness, χ^2=56.5, *df*=1, p<0.0001, expected occurrences based on average length of daytime and nighttime). Only 6 occurrences of Asiatic black bears were recorded. Four of the five occurrences with identifiable time of day were in daytime (but 2 of the 4 diurnal occurrences were close to civil twilight time in the evening). The only nighttime occurrence was an adult with a yearling. Because of the small sample size, the DI of Asiatic black bear from this study (0.60) was averaged with a radio telemetry study (0.2 from Hwang and Garshelis 2007) as the overall DI (i.e. 0.40) of Asiatic black bears, while DI's of lesser oriental civets, leopard cats, and feral cats were based on other camera trapping studies in Taiwan (Table 4.3).

Twilight activity patterns more accurately illustrated activities around crepuscular hours. The twilight activity patterns also tended to have fewer ups and downs than the regular activity patterns (cf. Fig. 4.1-4.5). More exaggeration in regular activity patterns may due to different sampling time of the year. General consistency between regular and twilight activity patterns suggested that twilight activity pattern may be a better option in illustrating diel activity patterns relative to daytime and nighttime.

Factor analysis of habitat characteristics within the study area

1. Altitude/greenness/wetness category:

   Two factors were retained and explained 78% of the variation (Table 4.4). From the rotated factor loadings (Table 4.4), factor 1 (altitude/greenness) had strong emphasis on altitude, NDVI, and annual solar radiation. As altitude gets higher, coniferous trees become more dominant and thus NDVI becomes lower (Pearson correlation coefficient of altitude and NDVI = -0.60, $p<0.0001$, $n=146$). Higher altitude also tends to receive more solar radiation compared to lower altitude, where surrounding higher mountains block solar radiation (Pearson correlation coefficient of altitude and ASR = 0.75, $p<0.0001$, $n=146$). Factor 1 described a pattern of altitude and greenness (i.e. higher altitude and smaller greenness of forests). Factor 2 was related to being distant from rivers/creeks and relatively closer to ridges. It also correlated slightly with moisture gradient (MOISTGRD, factor loading 0.61) and altitude (factor loading 0.46) because being closer to ridges implies higher in altitude and will render moisture gradient greater than 3 (the lowest values of MOISTGRD, e.g. 1 or 2, occurred only at deep valley bottom and river side receiving less sunlight regardless of aspect).

2. Terrain shape/ruggedness category:

   Three factors were retained and explained 70% of the variation (Table 4.5). From the rotated factor loadings (Table 4.5), factor 1 (cliff/steep pattern) indicated areas close to cliffs (cliff >1.5ha), cliffy area within 1km^2, and areas associated with steep terrain (SLOPEDEM). Factor 2 (ruggedness/convex terrain pattern) was associated with higher SLOPESTD and convex terrain (negative loading of TSI) in the scale of 120mX120m area. This often occurs near ridge tops. EVEN almost solely represented factor 3 (unevenness pattern). But, this was measured within 17.8m of camera trap sites in contrast to the other factors by a DEM model.

3. Forest understory category:

   Four factors were retained and explained 72% of the variation (Table 4.6). From the rotated factor loadings (Table 4.6), factor 1 (dense shrub/less rocky pattern) was mostly related to shrub density and higher shrub cover, plus smaller heterogeneity of shrub distribution. Rocky ground cover may be unlikely to support lush shrub growth. But, this factor is not related to shrub height, which is represented by factor 3 (shrub height pattern). Although factor 2 describes visual obscurity pattern, positive high loadings of VOSTD and VO suggests that factor 2 is related to high visual obscurity, but with higher variation among different directions. Factor 4 implies higher herbaceous cover.

4. Forest structure category:

   Five factors were retained and explained 79% of the variation (Table 4.7).

From the rotated factor loadings (Table 4.7), factor 1 (forest height pattern) describes the height of the upper layer of forest including large trees (DBH>20cm) and canopy. High loading of TREEHTCV in factor 1 suggests the forest has higher heterogeneity in tree heights among different tree size categories. Factor 2 (canopy cover pattern) implies dense canopy cover without gaps. Factor 3 (tree density heterogeneity pattern) is associated with denser smaller trees (DBH<20cm tree density and heterogeneity) and higher heterogeneity of tree densities among 3 tree size categories. This may indicate forests in earlier succession or in harsh environments (see discussion in chapter 3). In contrast, factor 4 (DBH>20cm tree density and basal pattern) is related to denser large trees (DBH>20cm) and likely higher basal area. Factor 5 (DBH<20cm tree height and forest stratum pattern) describes taller smaller trees (DBH<20cm) and a tendency of more complex forests (more forest tree stratum).

Factor analysis extracted 14 factors in total from 31 habitat variables belonging to the above 4 categories. Correlations among these 14 factors were mostly < 0.3 and >-0.3 with only 2 correlations between 0.3 and 0.4 (Table 4.8). Only river distance/slope position pattern and cliff/steep pattern had a higher correlation (0.48) as cliffs sometimes occur near ridge tops. Observation of the histogram of these 14 factors suggested that they do not depart from a normal distribution substantially and most actually approximate a normal distribution reasonably well. Given the robustness of CCA to collinearity of habitat variables (Palmer 1993), we believed that the multiple linear regression conducted within the CCA should perform quite well for our data.

Spatial patterns from CCA

1. <u>Within the study area:</u>

The ordination biplot from CCA of 5 carnivore species in the study area and their relationships with 14 habitat factors is shown in Fig. 4.6 (axis 1 vs. 2) and Fig. 4.7 (axis 1 vs. 3). Appendix I lists the summary statistics and correlations of ordination axes with the habitat factors. The 3 axes explained 12.2%, 6.3%, and 2.9%, respectively, of variation in the species data and accounted for 21.4% of variation in total. The first axis separated gem-faced palm civets and crab-eating mongooses (previously in the same family Viverridae) from the 3 mustelids. Axis 2 further separated gem-faced palm civets from crab-eating mongooses and separated Formosan ferret-badgers from the weasel and marten group. Yellow-throated martens were separated from the Siberian weasel when axis 3 was considered.

Monte Carlo test showed that there was significant correlation between species and habitat (p=0.001 for axis 1). The altitude(+)/greenness(-) factor (A1) had the strongest relationship in the carnivore community. The Siberian weasel occupied the highest altitude, while gem-faced palm civets preferred the lowest altitudes. The other 3 carnivores were close to the average along the altitude(+)/greenness(-) (A1) gradient with yellow-throated marten's optimum being above the average and Formosan ferret badgers and crab-eating mongooses being lower than the average. River distance/slope position (A2) and smaller tree density/heterogeneity patterns (F3) also had strong relationships with the carnivore community. Gem-faced palm civets and crab-eating mongooses had a preference for rivers/valleys and forests with more smaller trees and more homogeneous tree densities of different sizes. In contrast, the 3 mustelids had a converse pattern. These 2 habitat factors (A2 and F3) separated Formosan ferret badgers and crab-eating mongooses, which had similar optimum in the altitude(+)/greenness(-) gradient. However, yellow-throated martens were located near the center of the ordination space suggesting that it may be a generalist, which may be seen from their nearly 0 correlations with axis 1 and axis 2 (Appendix I). Yellow-throated martens had a higher correlation with axis 3 and were associated with terrain ruggedness (i.e. uneven terrain shape in the micro scale, but linear surfaces in the meso scale, Fig. 4.7). Linear surfaces (lower standard deviation of slopes within 120mX120m neighbor) generally occurred in the mid mountain slope instead of ridge (convex terrain) or valley (concave terrain) and were therefore close to the average of the river distance/slope position gradient (yellow-throated marten's optimum habitat in Fig. 4.6). Gem-faced palm civets had patterns similar to yellow-throated martens in axis 3 and they both were famous for their arboreality (Nowak 1999). However, axis 3 explained the least variance and this pattern may not be significant.

2. <u>Landscape scale across Taiwan:</u>

Forty-one areas were identified from camera trapping studies in Taiwan (including this study) (T. Y. Lin, unpublished data, Chen 2002, Pei 2002b, Liu 2003, Pei et al. 2003, Hwang and Chian 2004, Hwang and Pei 2004, Pei 2004a, Wang 2004, Wu et al. 2004, Lai 2005, Wang and Hsu 2005, Wang and Huang 2005, Pei and Chen 2006), ranging from coastal forests to coniferous forests as high as 3,100m (average altitude of 41 areas=992m). Levels of forest alterations ranged from primary forests (0) to fragmented early succession forest or plantation forests after clear cuts or fire (5). Human activity also ranged from remote areas without hunting to areas close to roads with heavy hunting pressure. Pearson's correlations among these 3 variables were -0.48 between altitude and human activity, -0.69 between altitude and level of forest alteration, and 0.78 between human activity and level of forest alteration. Areas at lower altitudes were close to human encroachment and tended to have higher levels of human activity and forest alteration. All these camera trapping studies were all still within forests. No camera trapping studies in completely open habitat were included.

The ordination biplot from CCA of all carnivores (9 species including feral cats) and their relationships with 3 habitat factors is shown in Fig. 4.8 (axis 1 vs. 2). Appendix II lists the summary statistics and correlations of ordination axes with the habitat factors. Monte Carlo test showed that there was significant correlation between species and habitat ($p=0.001$ for axis 1). Similarly, the altitude gradient has the strongest relationship in the carnivore community. The general pattern of the 5 carnivores (i.e. yellow-throated marten, Siberian weasel, Formosan ferret badger, crab-eating mongoose, and gem-faced palm civet) was similar to the result in the smaller scale (i.e. within the study area) analyzed previously except that gem-faced palm civets and Formosan ferret badgers were closer to each other and moved to a lower altitude along the gradient as they were still commonly found in much lower altitudes with higher levels of human activity and forest alteration.

The 3 axes explained 23.2%, 8.5%, and 1.8% of variation, respectively, in the species data and accounted for 33.5% of variation in total. The first axis separated gem-faced palm civets, Formosan ferret badgers, leopard cats, and feral cats from the other carnivores as they occurred more at the lower altitudes with higher levels of human activity and forest alteration. Crab-eating mongooses and lesser oriental civets preferred slightly higher altitude. But, they had contrast tolerance of human activity and forest alteration and were separated by axis 2. Similarly, Asiatic black bears and yellow-throated martens were separated from the smaller Siberian weasel by axis 2 and these 3 carnivores occupy higher altitudes than the other species. Siberian weasels appeared mode likely to occur at places with some human disturbance than the 2 larger carnivores (i.e. Asiatic black bear and yellow-throated marten), which preferred more pristine and intact forest.

Diet summary

Six studies on diets of Asiatic Black bears, yellow-throated martens, Siberian weasels, Formosan ferret badgers, crab-eating mongooses, and feral cats were conducted in Taiwan (Table 4.3). Detailed information on diets of gem-faced palm civets and leopard cats in Taiwan was not available and their diet summary was based on studies conducted geographically near Taiwan (Table 4.3). Based on types of major food items (Table 4.3), diets of the 9 carnivores in Taiwan could be divided into 3 groups: invertebrates, small mammals, and plants. Plant fruits were the major food items of Asiatic black bears and gem-faced palm civets. Yellow-throated martens, Siberian weasels, leopard cats, and feral cats took a lot of small mammals. Formosan ferret badgers, crab-eating mongooses, and lesser oriental civets fed mostly on invertebrates, including earthworms, crustaceans, and insects.

Niche relationship

1. <u>Five carnivores within the study area</u>:

When activity patterns, spatial patterns, and diet patterns were examined together, niche segregation among the carnivore community was more pronounced. Gem-faced palm civets and crab-eating mongooses sharing similar spatial patterns had completely reversed activity patterns (i.e. nocturnal vs. diurnal). They also differed in the major food items (e.g. plant vs. invertebrate, Table 4.3). Gem-faced palm civets also had a reversed activity pattern with the diurnal yellow-throated marten and differed in the optimum habitat along the 3 habitat factors (lower than factors' average vs. marten's higher than factors' average). Similarly, yellow-throated martens fed on small mammals while gem-faced palm civets fed on plant fruits (Table 4.3). Although crab-eating mongooses and Formosan ferret badgers occupied similar optimum along the altitude(+)/greenness(-) gradient, they had contrasting preference in habitat factors A2 and F3 (Table 4.4 and 4.7) and also exhibited reversed activity patterns. Siberian weasels were active day and night and departed most from the other 4 carnivores in the CCA ordination community space (Fig. 4.6). Even with the more closely related yellow-throated marten having similar major food item with Siberian weasels (Table 4.3), they seemed to separate temporally (DI=0.95 for yellow-throated martens vs. DI=-0.66 for Siberian weasels, Fig. 4.1 vs. 4.4). For the nocturnal species pair (gem-faced palm civet vs. Formosan ferret badger) and the diurnal species pair (crab-eating mongoose vs. yellow-throated marten) showing less temporal segregation, they were further apart from each other in the CCA ordination community space (Fig. 4.6) than species pairs with contrasting activity patterns (i.e. mongoose/palm civet and badger/marten except mongoose/badger). Even for species showing the same type of activity patterns, peaks of activity still differed in some degrees and showed some temporal segregation. Activity patterns of the 2 diurnal species were independent. Crab-eating mongooses extended more activities to night time than yellow-throated martens. Crab-eating mongooses also had more even activity levels throughout the day and activity peaked at different time (e.g. 14) compared to yellow-throated martens (Fig. 4.1 and 4.2). Although activity patterns of the 2 nocturnal species did not differ significantly, Formosan ferret badgers started higher activity earlier after sunset, were less active before midnight, and their activity peaked close to sunrise (Fig. 4.3). In contrast, gem-faced palm civets had higher activity levels later (e.g. 20, Fig.

4.4) and lowered activity levels gradually after midnight without peaks before sunrise.

2. Nine carnivores in a landscape scale across Taiwan:

Altitude was the most important environmental gradient that separated the 9 carnivores in Taiwan (Fig. 4.8). Five carnivores (i.e. Formosan ferret badger, gem-faced palm civet, lesser oriental civet, leopard cat, and feral cat) that occurred more at lower altitudes with higher levels of human activity and forest alteration were either nocturnal or had a tendency of nocturnal behavior (Table 4.3). Resource partitioning was observed more in diet among these 5 carnivores. Formosan ferret badgers and lesser oriental civets ate mostly invertebrates. Gem-faced palm civets fed on plant fruits, while leopard cats and feral cats occurred at even lower altitudes and preyed on small mammals. However, the two felids overlapped a lot on all 3 niche dimensions (Fig. 4.8, Table 4.3). Crab-eating mongooses, which were on a slightly higher altitude gradient with similar major food items (i.e. invertebrate) with lesser oriental civets and Formosan ferret badgers, had contrasting activity patterns (diurnal vs. nocturnal, Table 4.3) to all the other carnivores at lower altitudes. Similarly, Asiatic black bears and yellow-throated martens were more diurnal while Siberian weasels, occupying the similar high altitude gradient (Fig. 4.8), were more nocturnal (Table 4.3). Yellow-throated martens and Siberian weasels had similar diets, but different activity patterns. Yellow-throated martens were close to Asiatic black bears in the carnivore community space and had similar activity patterns, but differed in diet (small mammal vs. plant, Fig. 4.8 and Table 4.3).

Diversity of carnivores in Taiwan

The carnivore richness showed a hump-shaped pattern along the altitude gradient (Fig. 4.9). The quadratic model of altitude (i.e. altitude and its square term) was significant ($F_{2,38}$=7.65, p=0.002) in explaining the relationships between altitude and carnivore richness in contrast to the non-significant first-order linear altitude model (altitude as independent variable only, $F_{1,39}$=1.41, p=0.243). For the *a prioi* models (Table 4.9) based on the variables altitude, HA (human activity), and FORALTER (level of forest alteration), the model of quadratic altitude effect plus the interaction term of altitude and HA was substantially better than all the other models (ΔAIC_c of all the other modes > 2, Table 4.9). Although HA was not in the best model, the interaction term of altitude and HA suggested lower carnivore richness at higher levels of human activity (Table 4.10). However, intermediate forest disturbance did not seem to maintain higher carnivore diversity (the 5th model with quadratic term of FORALTER, ΔAIC_c=4.81, Table 4.9).

Discussion

Activity pattern

Although small carnivores were adaptable in diel activity patterns due to influences of food, weather, or other factors (Zielinski 1988), activity patterns of the 5 carnivores in the study area except Siberian weasels (i.e. yellow-throated marten, Formosan ferret badger, gem-faced palm civet, and crab-eating mongoose) were consistent among various parts of Taiwan (K. J. C. Pei unpublished data, Hwang 1995, Chen 2002, Pei 2002b, Liu 2003, Wang 2004, Wang and Hsu 2005, Pei and Chen 2006). Activity patterns of nocturnal lesser oriental civets also were consistent in different areas of Taiwan (K. J. C. Pei unpublished data, Chen 2002, Liu and ChangChien 2004). Thus, using our DI's of these carnivores for the temporal comparison of niche relationships in the landscape scale across Taiwan should not produce any problems. In summary, strict diurnal or nocturnal species were relatively consistent across regions. Species, which were active day and night, were found more frequently to adjust their diel activity patterns under different situations. Leopard cats (Liu and ChangChien 2004, Pei and Chen 2006) and Asiatic black bears (this study and Hwang and Garshelis 2007) also were active day and night and DI varied among different areas.

Small mammal predators

Four carnivores in Taiwan were classified as small mammal predators (Table 4.3), i.e. the low-mid altitude group of 2 felids and the mid-high altitude group of 2 mustelids. Yellow-throated martens and Siberian weasels had almost non-overlapping distribution with leopard cats and feral cats in Taiwan. This likely was related to the altitudinal bimodal pattern of species richness and abundance of their major small mammal prey (e.g. mice, rats, and voles), excluding squirrels, in Taiwan. Many small rodents occur in lowlands close to human encroachment (Lin 1982, Lin and Lin 1983). However, only 1 rat species, i.e. spinous country rat (*Niviventer coxingi*), was distributed in forests at lower altitudes (<1,500m) away from human encroachment (this study and Yu 1993, Yu 1994, Wu and Yu 2000). At altitudes higher than 1,500m, another *Niviventer* species started to occur and the spinous country rat decreased (this study and Yu 1993, Yu 1994, Wu and Yu 2000). At even higher altitudes, small mammals were more diverse and more abundant (Lin and Shiraishi 1992, Yu 1993, Yu 1994, Adler 1996).

Sympatric populations of Siberian weasels and yellow-throated martens at a altitude range of 2,700m-3,700m in Taiwan were found to have similar diet niche breadth and a high degree of diet overlap, mostly on small mammals (Tsai 2007a). Interspecific competition for food may occur as they both occupied higher altitudes and exhibited less habitat partition (Fig. 4.6 and 4.8). Siberian weasels and yellow-throated martens separated in the temporal dimension (0.95 vs. -0.66 of DI, Fig. 4.1 vs. 4.4) and this would support the complimentary resource use principle (Schoener 1974;1983). Within the study area at altitudes>2,500m, Siberian weasels tended to be diurnal (DI=-0.44), but below 2,500m where yellow-throated martens were more abundant (ref. Table 2.5 in chapter 2), they were significantly more active at night (DI=-0.79) than at altitudes>2,500m (chi-square test of independence, df=1, χ^2=5.35, p=0.02). In northeastern Taiwan (1,200-1,850m) where yellow-throated martens were rare (OI=0.02, nearly 1/40 of the OI at the similar altitudes of our study area), Siberian weasels (DI=-0.36) were not as nocturnal as the Siberian weasel population in our study area (DI=-0.79 at altitudes <2,500m) where yellow-throated martens were more abundant. Furthermore, radio-collared male Siberian weasels exhibited more diurnal activity (DI=0.43) in a lower altitude area (520-1,230m) in northeastern Taiwan without yellow-throated marten in sympatry (Wong 1997). Carnivores competing for similar prey also have been observed to differ in activity patterns to favor co-occurrence (Ray 1997, Fedriani et al. 1999, Karanth and Sunquist 2000, Vieira and Port 2007). The smaller Siberian weasel may be avoiding the diurnal, larger yellow-throated marten by being more active at night since they occupied a similar altitude gradient and had a high degree of diet overlap (i.e. compete for small mammals). St-Pierre et al. (2006) found the smaller *Mustela erminea* avoided the larger *M. frenata*. But, they found spatial avoidance and relate it to intraguild interactions including interspecific competition and intraguild predation. Intraguild predation (Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997) may be one of the mechanisms shaping the weasel/marten community in Taiwan as Siberian weasels are much smaller than yellow-throated martens (body weight difference up to a ratio of 5-10 times). Although yellow-throated marten's predation on Siberian weasels has not been documented, yellow-throated martens have been reported to kill the larger mustelid, Formosan ferret badger, in Taiwan (T. Y. Lin personal communication). And, remains of smaller weasel (*Mustela*) species had been found in the scats of other larger mammalian carnivores, including the larger weasel (*Mustela*) and marten (*Martes*) species (Erlinge 1981, Zielinski et al. 1999, Fedriani et al. 2000, Edwards and Forbes 2003). Intraguild interactions may be driving the temporal segregation between Siberian weasels and yellow-throated martens.

The biomass of small mammals in the study area is likely higher in the mid altitude range (1,200-2,000m) because that is where the 2 larger *Niviventer* rats overlapped (ref. Table 2.5 in chapter 2). Altitudes > 2,000m in the study area had relatively lower photographic rates of other smaller mice and voles because of the smaller high-altitude area and lack of Yushan cane grassland. Yellow-throated marten's optimum habitat close to the average along the altitude(+)/greenness(-) gradient within the study area (Fig. 4.6) suggested that it may be using the optimum habitat with more abundant food including small mammals and larger ungulates (e.g. muntjacs and serows), which yellow-throated martens has been observed to hunt (H. Wu personal communication, Matyushkin 1987, Sathyakumar 1999, Koh 2007). More diverse and abundant small mammal prey at the highest altitudes in the study area (>2,500m) may reduce competition for food resources between Siberian weasels and yellow-throated martens. These may explain why Siberian weasels and yellow-throated martens were more abundant at higher altitudes and why Siberian weasels used higher altitudes (Fig. 4.6 and 4.8) than yellow-throated martens.

As forests at lower altitudes tended to have fewer rodents, competition between

Siberian weasel and yellow-throated martens for small mammals may be higher. Even at places where yellow-throated martens were rare or did not occur and Siberian weasels may not need to compete for limiting small mammals, Siberian weasels still were found to adjust food habits to forage for more invertebrates at lower altitudes in Taiwan, which was likely due to the scarcity of small mammals (Tatara and Doi 1994, Wu 1999). In other words, Siberian weasels at low-mid altitudes of Taiwan would need to compete with yellow-throated martens for scarce small mammals and possibly compete with the larger, similarly nocturnal Formosan ferret badgers for invertebrates. Although Wu (1999) maintained that Siberian weasels and Formosan ferret badgers still differentiated in habitat and food dimensions to a certain degree, biplots (Fig 4.6 and 4.8) showed habitat segregation between Siberian weasels and Formosan ferret badgers along the altitude gradient. Siberian weasels may still use habitats at lower altitudes where Formosan ferret badgers were more abundant, but, the population size of Siberian weasels at lower altitudes of Taiwan is quite low (this study and Wong 1997). Habitat segregation between Siberian weasels and the other 2 larger mustelids was likely more pronounced in a scale covering a wider altitude range (Fig. 4.6 and 4.8).

The spatial segregation between leopard cats and the marten/weasel group along the altitude gradient (Fig. 4.8) may help reduce food competition between leopard cats and the mustelids with similar diet preference of small mammals (Clode and Macdonald 1995, Fedriani et al. 1999, Wu 1999, Vieira and Port 2007). The low richness and abundance of small mammals in the primary forests between the current distribution of leopard cats (altitude<700m) and the high altitudes (altitude>2,500m), plus the lack of other prey, such as non-forest Formosan hares, seemed to make the primary forest in this altitude range unsuitable habitat to leopard cats. In contrast, yellow-throated martens and

Siberian weasels were opportunist and generalist predators (Wu 1999, Tsai 2007a) and were still commonly found within the primary forests of this altitude range. Scarce small mammals would make competition for small mammal prey even greater for leopard cats in the mid-altitude range. This may be one of the reasons that leopard cats did not extend their distribution to altitudes>2,500m in Taiwan as high altitude populations of leopard cats would likely be separated from the main lowland population and have to compete with yellow-throated martens and Siberian weasels for small mammals and less alternate prey.

Niche relationships

Analysis of activity patterns and spatial patterns by CCA provided an effective description of niche segregation in time and space for the carnivores in Taiwan. They used different vegetation structure and terrain characteristics. When diets of these carnivores based on previous studies in Taiwan were considered for food-type partition (Table 4.3), we observed complimentary resource use (Schoener 1974;1983) through the partitions in terms of habitat, food-type, and temporal dimensions for both scales. For example, both the diurnal species-pair (crab-eating mongoose vs. yellow-throated marten) and the nocturnal species-pair (gem-faced palm civet vs. Formosan ferret badger) in the study area had very different diets but the same activity patterns. Predators separate more often in diel activity patterns than other groups of animals do (Schoener 1974). Similarly, we found that species with less difference in habitat or food-type dimensions usually were active at different times of the day. For example, crab-eating mongooses had a different activity pattern from the other 2 nocturnal invertebrate feeders (e.g. Formosan ferret badgers and lesser oriental civets). In the case of the 2 plant eating carnivores, Asiatic black bears were more diurnal while gem-faced palm civets were nocturnal.

The CCA biplot (Fig. 4.6) generally divided the mustelidae from the other 2 species with preference for low altitude, i.e. gem-faced palm civets and crab-eating mongooses, which also exhibited temporally nonsynchronous spatial overlap and diet differentiation. In addition, gem-faced palm civets could utilize the forest vertically for plant food (Nowak 1999), but crab-eating mongooses could not and instead used habitats closer to rivers or creeks to forage fro crustaceans and amphibians seldom taken by gem-faced palm civets. Siberian weasels and yellow-throated martens, which have a wide latitudinal distribution to Siberia (Nowak 1999), preferred higher altitudes where the environment and weather conditions may be more similar to the temperate regions.

This pattern of niche differentiation reflects some of the phylogenetic aspects and evolutionary histories of these species. Mustelidae is a holarctic group while Viverridae and Herpestidae were originated from the oriental region of tropical Asia (Ewer 1973). The CCA analysis revealed altitude, which is analogical to latitude with respect to vegetation and weather patterns, to be the strongest gradient to explain the composition of carnivore community under natural conditions within the study area. For the CCA analysis of the carnivore community across Taiwan, altitude also had the strongest relationships even under a human-altered landscape. Latitudinal distribution of these carnivores in the world was similar to their altitude ranges in Taiwan. That is, yellow-throated martens and Siberian weasels occupied the highest altitudes, while Viverridae, Herpestidae, Felidae, and the Formosan ferret badgers were at the lower altitudes.

Diversity of carnivores in Taiwan

Albeit only 8 species were considered, the carnivore richness in Taiwan demonstrated a hump-shaped curve, which suggested some support for the mid-domain effect (Rahbek 1995, Colwell and Lees 2000, Colwell et al. 2004). Similar patterns have been documented for breeding bird species in Taiwan (Lee et al. 2004, Koh et al. 2006) and many taxa in the world (Rahbek 1995, Colwell et al. 2004). Taiwan was connected to the Asia mainland during several glacial periods and separated again after the retreat of glaciers in the Pleistocene (Voris 2000). Thus, mammals of Taiwan consisted of Palearctic, Himalayan, and tropical Oriental species, and some Palearctic and Himalayan species were confined to the high altitudes of Taiwan after the retreat of glaciers (Kano 1940, Lin and Lin 1983).

Altitude ranges of the 8 carnivores may, in part, explain the mid-domain effect. These species roughly divide into 2 groups. The low-mid altitude group (generally <2,500m) consisted of leopard cats, gem-faced-palm civets, lesser oriental civets, crab-eating mongooses, and Formosan ferret badgers. The mid-high altitude group (generally >1,200m) included yellow-throated martens, Siberian weasels, and Asiatic black bears (Figs. 4.6 and 4.8). Altitude ranges of these 8 species overlapped in the mid-domain contributing to higher carnivore richness at mid altitudes. The altitude range in the analysis ranged up to 3,100m, but the highest peak in Taiwan reached 3,952m. Carnivores occurring at altitudes higher than 3,100m would include, at most, the Taiwan high mountain least weasel, which has limited distribution (Lin 2000), plus yellow-throated martens and Siberian weasels. Asiatic black bears seldom occur that high (Hwang et al. 2006). Even if we considered the complete altitude range (0-4,000m), we would not expect the hump-shaped pattern to differ.

Lower carnivore richness at lower altitudes could be the result of human activities (e.g. hunting and forest clearing and fragmentation). However, the best model with the interaction term of altitude and HA (ALT*HA) had substantial support over the model with simply the HA variable (the 4th model, ΔAIC_c=2.82, Table 4.9), suggesting an interaction between altitude and human activity (HA). Altitude was significantly correlated to HA (Pearson correlation=-0.48, p=0.001) and FORALTER (Pearson correlation=-0.69, p<0.0001). There was a tendency for higher levels of human activity and forest alteration at lower altitudes. Lower altitudes were highly populated and more fragmented and the forests were often secondary or plantation forests after clear cuts. Higher altitudes with similar HA values (e.g. close to major roads and high hunting pressure, but away from villages) were usually less populated, had less fragmented forest, and usually still had some patches of primary forest nearby. Larger mammals such as Asiatic black bears and yellow-throated martens may not find suitable habitats at lower altitudes even though they could move to lower altitudes (this study and Hwang et al. 2006). In contrast, leopard cats and lesser oriental civets were very limited to altitudes lower than 1,200m and were rarely found at altitudes over 1,500m (Liu and ChangChien 2004, Pei and Chen 2006). Influences of hunting may also differ between low and high altitudes. The interaction effect of altitude and HA seemed to suggest that the influence of human activity on carnivore richness at higher altitudes may be less extreme than at lower altitudes. However, the 2 extinct large carnivores (e.g. Formosan clouded leopard and Eurasian otter) were not included in the analysis. Prior to their extinction and at times when there was little human activity in the lowlands, Formosan clouded leopards and Eurasian otters would occur in some of the lower altitudes making the carnivore richness at lower altitudes higher than we have documented. However, coastal lowlands were usually plains with few trees and prey, and were unlikely suitable habitat for clouded leopard (see chapter 2). In addition, the meso-carnivore communities may have been affected by the 2 top carnivores due to competition or intraguild predation (Terborgh et al. 1999) in contrast to the current carnivore diversity under no top carnivores. We still expected a hump-shaped pattern, which may be asymmetrical, of carnivore diversity along the altitude gradient from the coast to the highest peak of Taiwan when Formosan clouded leopards and Eurasian otters still survived.

Albeit the influence of human activity on carnivore richness, the best model included the quadratic term of altitude with a much smaller AIC_c than the model without the quadratic term of altitude (differences>14, Table 4.9), implying strong support for the quadratic model over the first-order linear model of altitude. The pattern of carnivore richness along the altitude gradient in Taiwan was likely a synthesis of human activity and the mid-domain effect. But, even though mid-altitude had higher carnivore richness and may acquire more conservation attention, limited altitudinal distribution of lesser oriental civets and leopard cats plus the endangered status of leopard cats in Taiwan still warrants the importance of conservation of lowland habitat.

Human activity and forest alteration

Gem-faced palm civets and Formosan ferret badgers seemed to be tolerant of human-altered landscapes to a certain degree and were found in many areas close to human encroachment (personal observations). This may be related to their preference for lower forest height (habitat factor F1 in the Fig. 4.6 CCA biplot when the r^2 cutoff value was reduced to 0.15 instead of previously used 0.2, not shown in Fig. 4.6), as forests nearby human encroachment were usually low due to historical or frequent human disturbances. In addition, they were both nocturnal and could avoid humans by being active at night. Similarly, lesser oriental civets and leopard cats were also nocturnal (Chen 2002, Pei and Chen 2006) and used habitats close to human encroachment. In contrast, diurnal carnivores (e.g. yellow-throated marten, Asiatic black bear, and crab-eating mongoose) avoided human activities. Change of diel activity patterns by switching to more nocturnal activities due to human disturbance has been reported in Sumatra (Griffiths and Vanschaik 1993) and in Taiwan (this study in Pei 2002b, Liu and ChangChien 2004, Pei and Chiang 2004). Further research, particularly for the endangered leopard cat, is needed to see whether animals' switching to forage at different times of the day, which may not be optimal for them, could affect their fitness and thus their population dynamics.

Nondetection of lesser oriental civets, leopard cats, and Taiwan high mountain least weasels in the study area may suggest true absence given our extensive camera trapping effort. Lesser oriental civets are still found in many parts of Taiwan (Chen 2002, Liu and ChangChien 2004, Pei and Chen 2006). Taiwan high mountain least weasels are a newly found species and seem to have limited distribution at high altitudes around central Taiwan (Lin 1999). But, leopard cats are endangered and found only in western Taiwan, and seem to have fragmented populations (Liu and ChangChien 2004, Pei and Chen 2006). Current habitat types where lesser oriental civets and leopard cats are mostly found are at altitudes < 1,200m in secondary forests mosaic with farmlands or adjacent to human encroachment (Chen 2002, Liu and ChangChien 2004, Pei and Chen 2006). In the carnivore community ordination space (Fig. 4.8), lesser oriental civets and leopard cats were at the extreme side of the gradients of human activity and level of forest alteration. We also felt that these 2 species are not interior species of forest habitat and thus do not occur or are extremely rare in the primary forest of the study area and other parts of Taiwan (Chen 2002, Pei and Chen 2006). Yellow-throated martens and Siberian weasels were absent in the current range of leopard cats (Liu and ChangChien 2004, Pei and Chen 2006), and leopard cats seemed to utilize habitats with more abundant prey and less competitors. But, it is unclear why lesser oriental civets seldom used interior forests. We found less niche segregation in the 3 dimensions between lesser oriental civets and Formosan ferret badgers as they had similar spatial patterns (Fig. 4.8) and activity patterns (Table 4.3) and relied on invertebrates as major food items (Table 4.3), despite the fact that proportions of different food items differed in a finer scale (Chuang and Lee 1997) and micro-habitat use also differentiated in slope (Chen 2002). Even less niche segregation was observed for feral cats and leopard cats (Fig. 4.8 and Table 4.3). This is worth attention as current populations of leopard cats and possibly lesser oriental civets in Taiwan may not be in good condition (Chen 2002, Liu and ChangChien 2004, Pei and Chen 2006).

Although these carnivores occurred more at lower altitudes close to human encroachment, it does not necessarily mean that human activity and forest alteration was good for them as no survival and fitness information was available. Areas with the highest level of forest alteration in our data were fragmented secondary forests in early succession or plantation forests mosaic with farmlands and some human encroachment. It would not be applicable to extrapolate our results to conclude that more human activity, hunting and forest alteration would be beneficial to some carnivore populations and the overall diversity. Major habitat types for leopard cats and lesser oriental civets are lowlands close to human encroachment and they face extremely high pressure from development. Their current distributions are fragmented. Since current protected areas in

Taiwan consist of mostly higher altitudes, protection of lower altitudes does not seem sufficient. Given that gem-faced palm civets and Formosan ferret badgers had relatively stable populations in primary forests, we felt that further research of leopard cats and lesser oriental civets is urgently needed to understand their population dynamics in human landscape and the influence of habitat fragmentation.

Disappearance of large carnivores

Disappearance of Formosan clouded leopards (see chapter 2) and Eurasian otters (Lin 2000) and the extreme rarity of Asiatic black bears in the study area signified the lack of large carnivores in Taiwan. The diet and habitat requirement of Formosan clouded leopards and Asiatic black bears partially overlap. The Eurasian otter's diet and habitat was similar to crab-eating mongooses. Asiatic black bears and gem-faced palm civets share the same major food items (Table 4.3) and they are sympatric in primary forests away from human encroachment. Whether mesopredator release (Terborgh et al. 1999) occurred in our study area is unknown. But, we did document diverse and abundant carnivores. Our study area had the highest carnivore species richness (6 species or 7 species if lesser oriental civets documented by another team were included) among 41 areas of camera trapping studies throughout Taiwan. In the eastern part of Yushan National Park where Asiatic black bears seemed to be the most abundant in Taiwan, OI of gem-faced palm civets (overlap diet with bears in plant food) was nearly half of the gem-faced palm civets' OI in our study area. But, carnivore richness (6 species) in Yushan National Park also was high. Nevertheless, the population of Asiatic Black bears in Yushan National Park may be low and endangered (Hwang 2003), and is no where abundant in Taiwan (Hwang et al. 2006). It may be necessary to understand whether the mesopredators induced higher predation pressure on their prey (e.g. small vertebrates) due to vanishing top carnivores (Crooks and Soule 1999).

Table 4.1 (Continued to next page) Four categories of habitat variables in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004). The altitude and terrain categories were derived from 40mX40m digital elevation model (DEM) as meso-scale habitat variables (except EVEN). EVEN in the terrain category and the other habitat variables were measured within 17.8m radius of camera trap sites as micro-scale habitat variables. See Tables 1.3 and 1.4 for details.

Category	Habitat covariate	Description
Altitude/ greenness/ wetness	ALT	Altitude (m) (differentially processed with GPS)
	NDVI	An index of greenness.
	MOISTGRD	Moisture gradient based on DEM aspect and proximity to river and valley, 10 levels: 1 (wettest) ~ 10 (driest in south-facing slopes)
	ASR	Annual solar radiation (hundred J/m^2)
	RIVERDIST	Distance to nearest river or mountain lakes
	SLOPEPOS	Slope position 0(valley)-100(ridge), ratio of elevation difference to the valley and ridge
Terrain shape/ ruggedness	SLOPEDEM	Slope from DEM in percentage (ArcGIS 9.2)
	SLOPESTD	Standard deviation of slopes (in percentage) within neighboring 3x3 cells (i.e. 120mX120m)
	CLIFFDIST	Distance to nearest cliff. Cliff is defined as slope>45° with area>1.44ha (i.e., 3x3 cells or 120mX120m)
	CLIFFCOUNT	Number of cliff cells (slope>45°) within 25x25 cell window (i.e., 1kmX1km or 100ha).
	TSI	Terrain shape indices based on neighboring 3x3 cells (i.e. 120mX120m)
	EVEN	Terrain evenness: standard deviation of terrain shape indices calculated for 2m, 4m, and 8m.

Table 4.1 (Continued from previous page) Four categories of habitat variables used in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004). The altitude and terrain categories were derived from 40mX40m digital elevation model (DEM) as meso-scale habitat variables (except EVEN). EVEN in the terrain category and the other habitat variables were measured within 17.8m radius of camera trap sites as micro-scale habitat variables. See Tables 1.3 and 1.4 for details.

Category	Habitat covariate	Description
Forest understory/ ground cover	HERBCO	Herbaceous cover in percentage
	SHRUBCO	Shrub cover in percentage
	SHRUBHT	Average shrub height (m)
	SHRUBDEN	Shrub density log(natural) transformed
	SHRUBCV	CV of shrub distances at the 4 quadrants
	ROCKCO	Rock cover in percentage
	VO	Average visual obscurity of 4 directions from 0.5m to 2m (total 32 values) in percentage
	VOSTD	Standard deviation of visual obscurity among 4 directions
Forest structures	STREEDEN	Tree density (DBH 1-20cm), log transformed
	LTREEDEN	Tree density (DBH >20cm), log transformed
	TREEDENCV	CV of tree densities between 3 size classes
	BASAL	Total basal area, log transformed
	STREEHT	Average tree height (DBH 1-20cm)
	LTREEHT	Average tree height (DBH >20cm)
	TREEHTCV	CV of tree heights between 3 size classes
	STRATUM	Number of forest stratum (2-5)
	CANOPYHT	Canopy height
	CANOPYCO	Average of 8 measurements of canopy cover in percentage
	CANOPYGAP	CV between 8 measurements for canopy patchiness (gaps).

Table 4.2 Percentage of detection sites and average photographic rates (OI, number of pictures per 1,000 camera trap hours) of 146 camera trap sites with detection of at least 1 of the 5 carnivore species in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan, collected from 2001 to 2004.

Species	**Number of camera trap sites with detection**	**Percentage**	**Average OI**
Siberian weasel	50	34.2%	0.49
Yellow-throated marten	50	34.2%	0.55
Formosan ferret badger	75	51.4%	1.59
Gem-faced palm civet	60	41.1%	1.08
Crab-eating mongoose	60	41.1%	1.20

Table 4.3 Comparison of temporal and food-type dimensions for the 9 carnivores in Taiwan. Activity pattern (diurnal index, DI) was based on this study and other studies in Taiwan. Summary of diets were also based on studies in other parts of Taiwan except for gem-faced palm civets which were taken from a study in southeastern China and leopard cats which were taken from studies in Thailand and Tsushima islands (Japan). Relative importance of food types were averaged across studies and classified into 3 categories, i.e. M: major food items (>40%), S: secondary food items (15-40%), O: occasional food items (5-15%). Relative importance < 5% was left blank in the diet summary.

Species	Activity pattern		Diet summary					
	DI	Source	Invertebrate	Smaller vertebrate		Larger vertebrate	Plant	Source
				Others (reptiles, amphibians, birds)	Small mammals			
Asiatic black bear	0.40	(Hwang and Garshelis 2007) and this study				O	M	(Hwang et al. 2002)
Yellow-throated marten	0.95	This study		O	M	S		(Tsai 2007a)
Siberian weasel	-0.66	This study	S	O	M	O (scavenge)		(Ma 1990, Wu 1999, Tsai 2007a)
Formosan ferret badger	-0.98	This study	M	O				(Chuang and Lee 1997, Wu 1999)
Crab-eating mongoose	0.88	This study	M	S			O	(Chuang and Lee 1997)
Gem-faced palm civet	-0.90	This study	O		O		M	(Wang and Fuller 2003)
Lesser oriental civet	-1.00	(Chen 2002)	M		S		S	(Chuang and Lee 1997)
Leopard cat	-0.71	(Pei and Chen 2006)	O	S	M			(Rabinowitz 1990, Tatara and Doi 1994, Grassman 2000, Grassman et al. 2005c)
Feral cat	-0.02	(Pei and Chen 2006)	O	S	M			(Kuo 2006)

Table 4.4 Eigenvalues, proportions of variation explained, and cumulative variation explained of the 6 principal components and factor loadings of retained factors by Varimax rotation from the factor analysis of the 6 habitat variables of the altitude/greenness/wetness category in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004).

Principal component	Eigenvalue	Proportion of variation explained	Cumulative variation explained
1	3.91	0.65	0.65
2	0.77	0.13	0.78
3	0.56	0.09	0.87
4	0.42	0.07	0.94
5	0.20	0.03	0.98
6	0.14	0.02	1.00

Variable	Loadings of rotated factors	
	Factor 1 (A1)	Factor 2 (A2)
ALT	0.74	0.46
NDVI	-0.83	-0.20
ASR	0.85	0.32
MOISTGRD	0.47	0.61
RIVERDIST	0.33	0.87
SLOPEPOS	0.24	0.91
Proportion of variation explained	0.39	0.39
Factor pattern interpretation	Altitude(+)/greenness(-)	River distance/ slope position

Table 4.5 Eigenvalues, proportions of variation explained, and cumulative variation explained of the 6 principal components and factor loadings of retained factors by Varimax rotation from the factor analysis of the 6 habitat variables of the terrain shape/ruggedness category in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004).

Principal component	**Eigenvalue**	**Proportion of variation explained**	**Cumulative variation explained**
1	2.15	0.36	0.36
2	1.11	0.19	0.54
3	0.96	0.16	0.70
4	0.78	0.13	0.83
5	0.70	0.12	0.95
6	0.30	0.05	1.00

	Loadings of rotated factors		
Variable	**Factor 1 (T1)**	**Factor 2 (T2)**	**Factor 3 (T3)**
SLOPESTD	0.10	0.80	0.03
SLOPEDEM	0.52	0.17	0.27
TSI	-0.11	-0.79	-0.03
CLIFFCOUNT	0.89	0.10	0.03
CLIFFDIST	-0.89	-0.06	0.02
EVEN	0.08	0.02	0.97
Proportion of variation explained	0.32	0.22	0.17
Factor pattern interpretation	Cliff/steepness	Ruggedness/ convex terrain	Uneveness(micro)

Table 4.6 Eigenvalues, proportions of variation explained, and cumulative variation explained of the 8 principal components and factor loadings of retained factors by Varimax rotation from the factor analysis of the 8 habitat variables of the forest understory category in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004).

Principal component	**Eigenvalue**	**Proportion of variation explained**	**Cumulative variation explained**
1	2.22	0.28	0.28
2	1.31	0.16	0.44
3	1.23	0.15	0.60
4	0.96	0.12	0.72
5	0.72	0.09	0.81
6	0.70	0.09	0.89
7	0.48	0.06	0.95
8	0.37	0.05	1.00

Variable	**Loadings of rotated factors**			
	Factor 1 (U1)	**Factor 2 (U2)**	**Factor 3 (U3)**	**Factor 4 (U4)**
HERBCO	0.07	0.02	-0.06	0.96
SHRUBCO	0.60	-0.01	0.55	0.12
SHRUBHT	-0.10	0.02	0.92	-0.09
SHRUBDEN	0.81	0.22	-0.03	-0.02
SHRUBCV	-0.66	0.32	0.10	0.14
ROCKCO	-0.63	-0.10	-0.03	-0.23
VO	0.43	0.71	0.20	-0.18
VOSTD	-0.10	0.85	-0.09	0.12
Proportion of variation explained	0.26	0.17	0.15	0.13
Factor pattern interpretation	Dense shrub/ less rocky	Visual obscurity	Shrub height	Herbaceous cover

Table 4.7 Eigenvalues, proportions of variation explained, and cumulative variation explained of the 11 principal components from the factor analysis of the 11 habitat variables of the forest structure category in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004).

Principal component	**Eigenvalue**	**Proportion of variation explained**	**Cumulative variation explained**
1	3.16	0.29	0.29
2	1.74	0.16	0.45
3	1.44	0.13	0.58
4	1.35	0.12	0.70
5	1.02	0.09	0.79
6	0.75	0.07	0.86
7	0.54	0.05	0.91
8	0.44	0.04	0.95
9	0.30	0.03	0.98
10	0.22	0.02	1.00
11	0.04	0.00	1.00

	Loadings of rotated factors				
Variable	**Factor 1 (F1)**	**Factor 2 (F2)**	**Factor 3 (F3)**	**Factor 4 (F4)**	**Factor 5 (F5)**
STREEDEN	-0.21	-0.01	0.83	0.29	0.02
LTREEDEN	-0.27	0.06	-0.15	0.87	0.03
TREEDENCV	-0.07	-0.05	0.82	-0.39	-0.06
BASAL	0.44	0.21	0.25	0.62	0.02
STREEHT	-0.14	0.11	-0.11	-0.03	0.88
LTREEHT	0.84	0.20	-0.12	0.04	0.25
TREEHTCV	0.88	0.15	-0.11	0.04	-0.29
STRATUM	0.31	0.07	0.09	0.08	0.69
CANOPYCO	0.21	0.91	-0.01	0.03	0.09
CANOPYGAP	-0.12	-0.91	0.04	-0.13	-0.09
CANOPYHT	0.73	0.09	-0.12	-0.20	0.17
Proportion of variation explained	0.23	0.16	0.14	0.13	0.13
Factor pattern interpretation	Forest height	Canopy cover	DBH<20cm tree density and heterogeneity	DBH>20cm tree density and basal	DBH<20cm tree height and forest stratum

Table 4.8 Pearson correlation matrix of 14 habitat factors in 4 categories of habitat variables (see previous tables for abbreviations of factors) for 146 camera trap sites in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004). Habitat factors within the same category are orthogonal and are not shown. Pearson correlation coefficient > 0.3 is in bold.

		Altitude/greenness/ Wetness category		**Terrain shape/ ruggedness**			**Forest understory**			
		A1	A2	T1	T2	T3	U1	U2	U3	U4
Terrain shape/ ruggedness	T1	0.15	**0.48****							
	T2	-0.07	0.11							
	T3	0.03	0.13							
Forest understory	U1	0.01	0.18*	0.09	0.16*	0.02				
	U2	0.07	0.21**	0.28**	0.15	**0.39****				
	U3	0.11	0.06	-0.07	0.02	0.01				
	U4	-0.22**	-0.15	-0.11	0.14	-0.07				
Forest structure	F1	0.29**	-0.12	-0.04	-0.24**	-0.07	-0.18*	-0.24**	0.04	-0.03
	F2	-0.03	0.05	0.08	-0.01	-0.13	0.02	-0.07	-0.11	-0.13
	F3	**0.34****	0.26**	0.08	0.09	0.10	0.20*	0.14	-0.05	-0.23**
	F4	-0.06	0.18*	0.25**	0.15	0.25**	0.17*	0.26*	-0.09	-0.09
	F5	-0.11	-0.04	-0.13	-0.01	-0.11	-0.12	-0.19*	-0.08	-0.02

* $p<0.05$
** $p<0.01$

Table 4.9 Linear regression model comparison of carnivore richness (number of species) from camera trapping studies conducted in 41 (N) areas across Taiwan during 1998-2006. ALT: average altitude of the area, HA*: index of human activity, FORALTER*: level of forest alterations. A variable parenthesized with superscript of 2 indicates square of the variable for quadratic effect. This analysis excluded feral cat and consisted of 8 wild carnivores of Taiwan.

Model	**ΔAIC_c**	**Akaike weight**	**R-square**
ALT + $(ALT)^2$ + ALT*HA	0.00	0.52	0.59
ALT + $(ALT)^2$ + HA + ALT*HA	2.05	0.19	0.59
ALT + $(ALT)^2$ + HA	2.82	0.13	0.56
ALT + $(ALT)^2$ + HA + FORALTER	2.88	0.12	0.58
ALT + $(ALT)^2$ + HA + FORALTER + $(FORALTER)^2$	4.81	0.05	0.59
HA	13.27	0.00	0.38
ALT + HA	14.29	0.00	0.39
ALT + $(ALT)^2$ + FORALTER	18.77	0.00	0.36
ALT + $(ALT)^2$ + FORALTER + $(FORALTER)^2$	19.92	0.00	0.37
ALT + $(ALT)^2$	20.77	0.00	0.29
FORALTER	24.15	0.00	0.19
ALT	31.13	0.00	0.03

* HA was based on 2 values, i.e. within 5km from roads or villages (0 or 1) and levels of human hunting pressure (0-3). These 2 values were then scaled to 10 equally and summed to form an overall score of human activities, i.e. from 0 to 20. FORALTER is level of forest alterations (0-5).

Table 4.10 Linear regression summary of the best model (R-square=0.59) explaining carnivore diversity in Taiwan. Data were from camera trapping studies conducted in 41 (N) areas across Taiwan during 1998-2006. ALT: average altitude of the area (per hundred meter), HA*: index of human activity, ALT*HA: interaction term by multiplying ALT and HA. $(ALT)^2$ indicates square of the variable ALT for quadratic effect. This analysis excluded feral cat and consisted of 8 wild carnivores of Taiwan.

Source	SS	df	MS	F	p-value
Model	45.04	3	15.01	17.89	<0.0001
Residual	31.06	37	0.84		
Total	76.10	40	1.90		

Variable	Coefficient	p-value	95% confidence interval	
ALT	0.481	<0.001	0.337	0.634
$(ALT)^2$	-0.016	<0.001	-0.021	-0.010
ALT*HA	-0.007	<0.001	-0.009	-0.005
Constant	2.185	<0.001	1.524	2.847

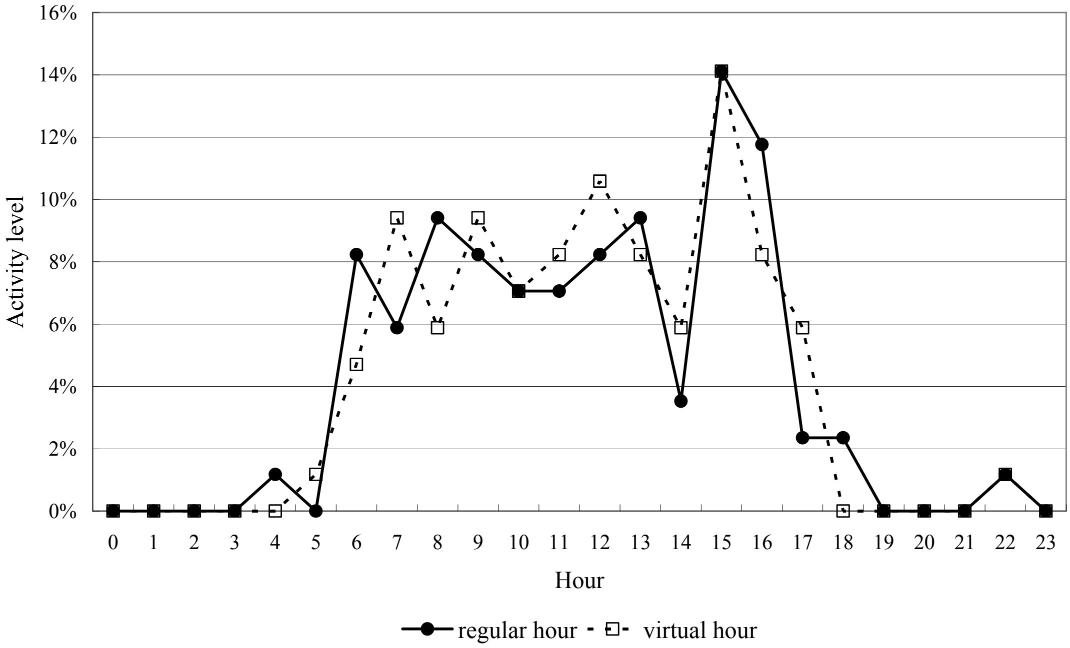


Figure 4.1 Diel activity pattern (N=85) of yellow-throated martens in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan during 2001-2004. The solid line is the regular activity pattern and the dotted line is the twilight activity pattern adjusted by civil twilight hours.

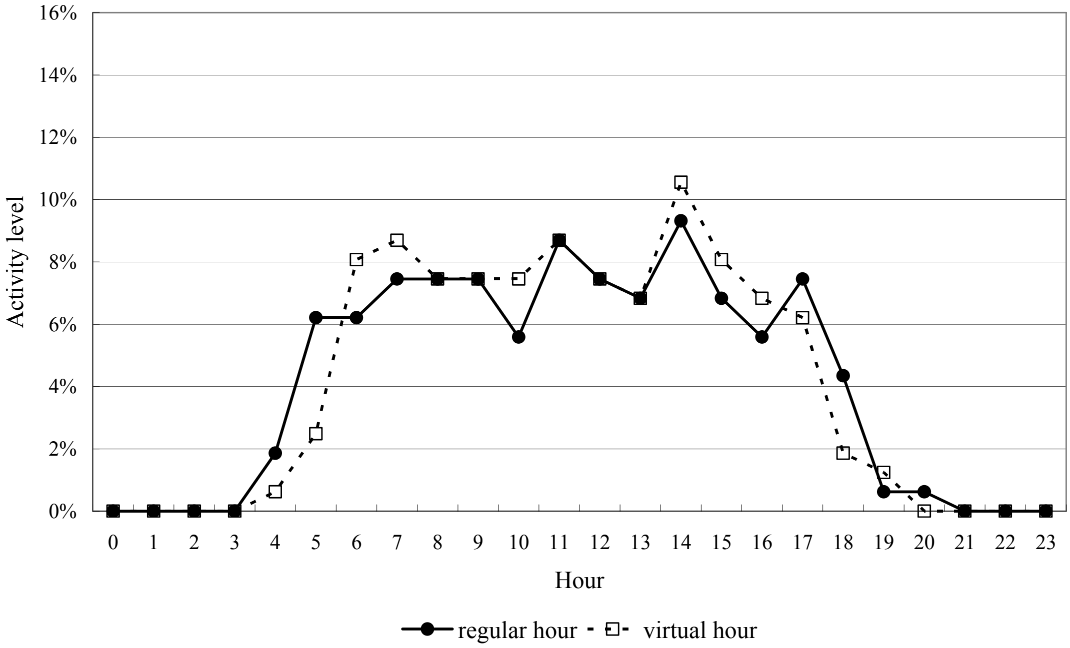


Figure 4.2 Diel activity pattern (N=161) of crab-eating mongooses in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan during 2001-2004. The solid line is the regular activity pattern and the dotted line is the twilight activity pattern adjusted by civil twilight hours.

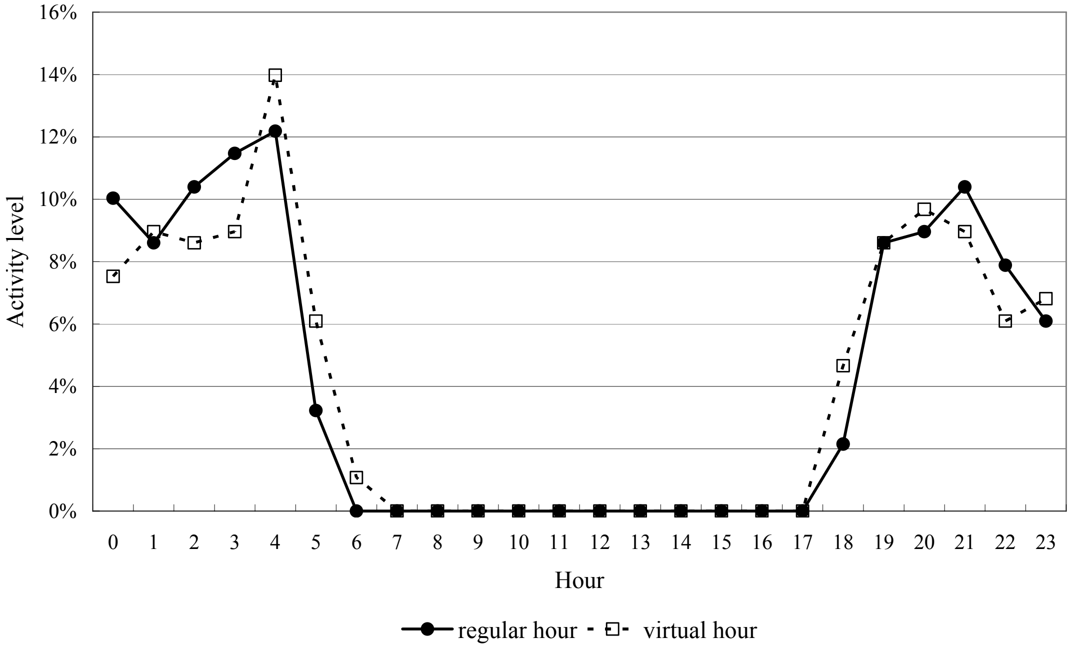


Figure 4.3 Diel activity pattern (N=279) of Formosan ferret badgers in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan during 2001-2004. The solid line is the regular activity pattern and the dotted line is the twilight activity pattern adjusted by civil twilight hours.

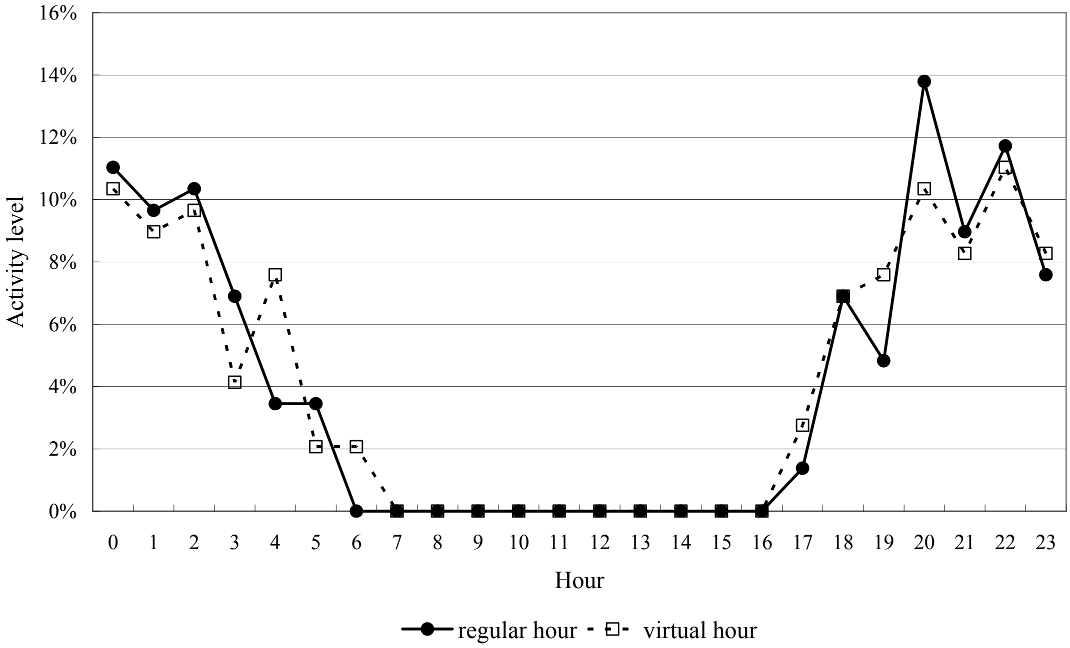


Figure 4.4 Diel activity pattern (N=145) of gem-faced palm civets in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan during 2001-2004. The solid line is the regular activity pattern and the dotted line is the twilight activity pattern adjusted by civil twilight hours.

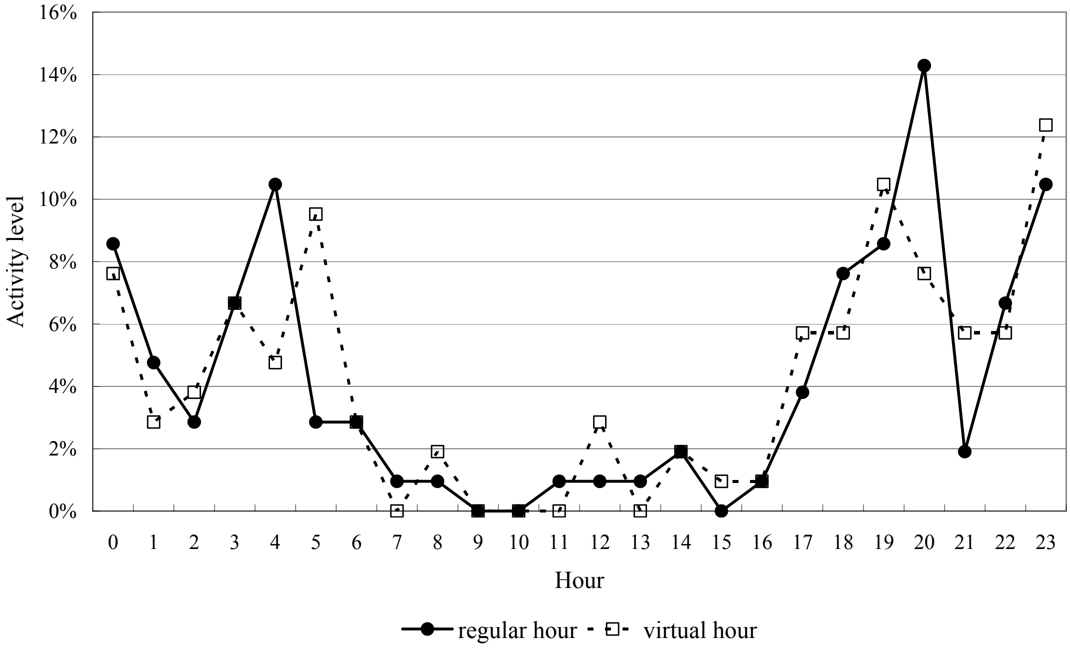


Figure 4.5 Diel activity pattern (N=105) of Siberian weasels in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan during 2001-2004. The solid line is the regular activity pattern and the dotted line is the twilight activity pattern adjusted by civil twilight hours.

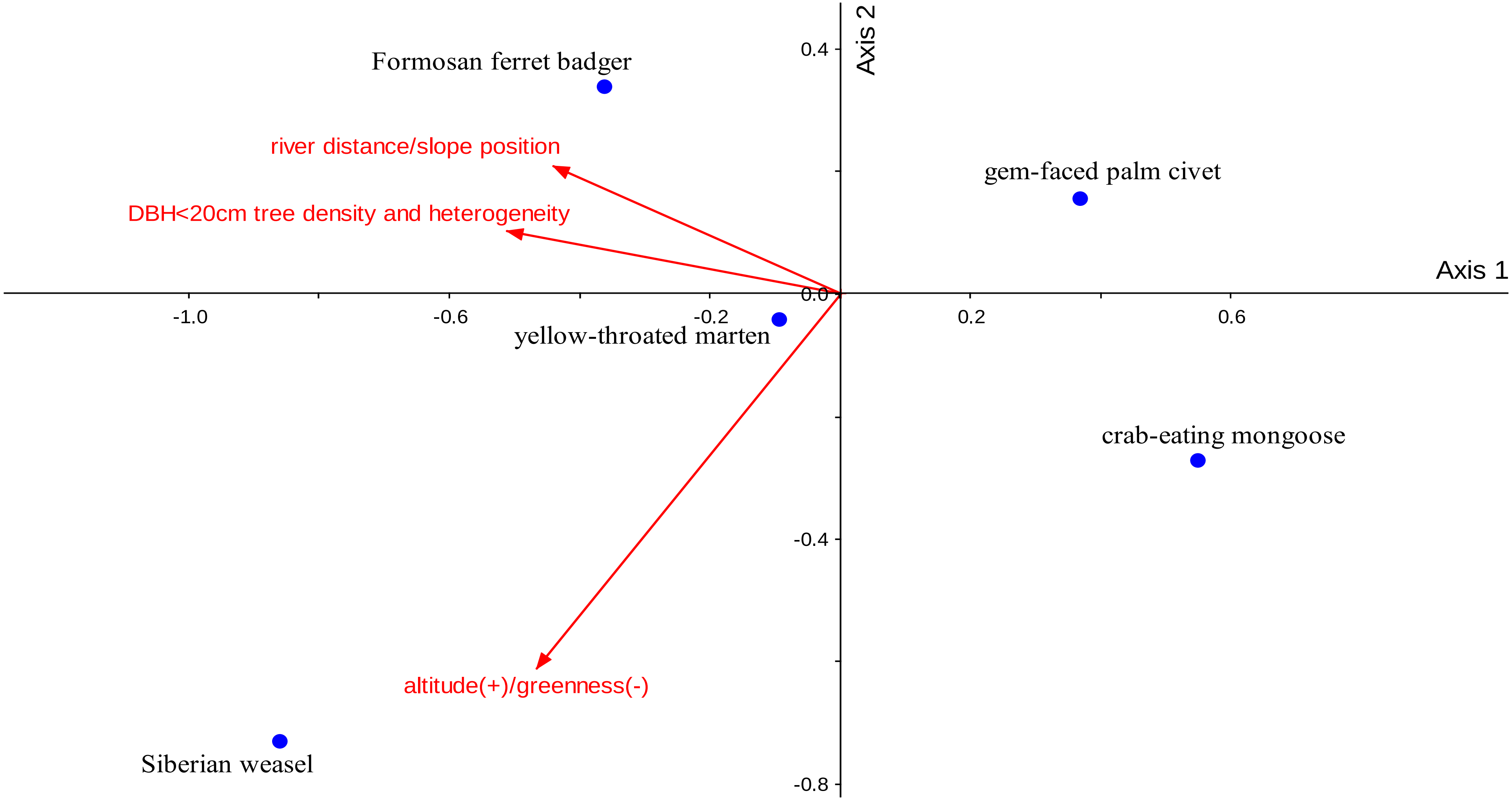


Figure 4.6 Joint biplot of canonical correspondence analysis based on axis 1 and axis 2 of the carnivore community (species in blue round points) of Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan in relation to habitat factors (red radiating lines). Data were based on 143 camera trap sites (average altitude 1,572m) collected from the 2001-2004. Ordination scores were optimized for species. Cutoff r^2 for habitat factors (coefficient of determinant with ordination axis scores) for display was 0.2.

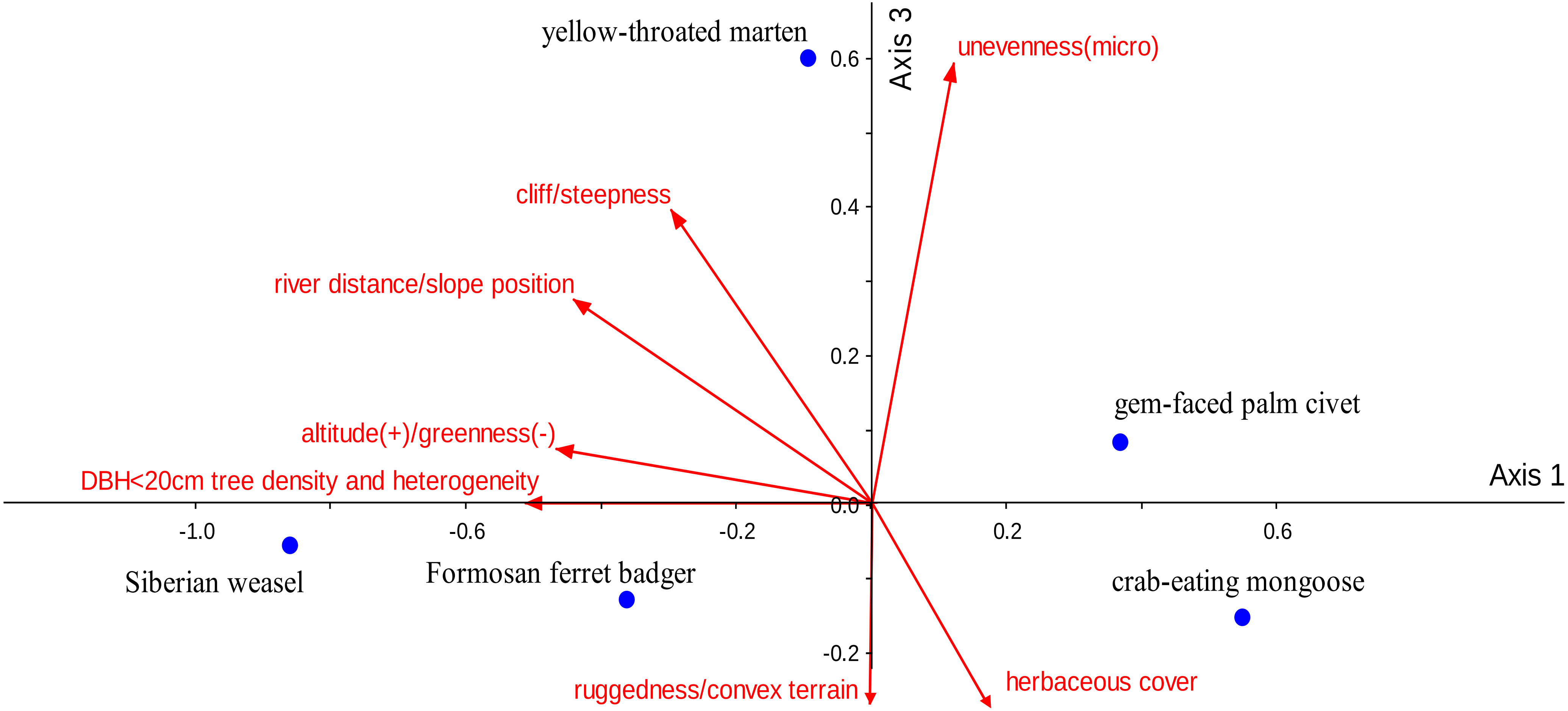


Figure 4.7 Joint biplot of canonical correspondence analysis based on axis 1 and axis 3 of the carnivore community (species in blue round points) of Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan in relation to habitat factors (red radiating lines). Data were based on 143 camera trap sites (average altitude 1,572m) collected from the 2001-2004. Ordination scores were optimized for species. Cutoff r^2 for habitat factors (coefficient of determinant with ordination axis scores) for display was 0.2.

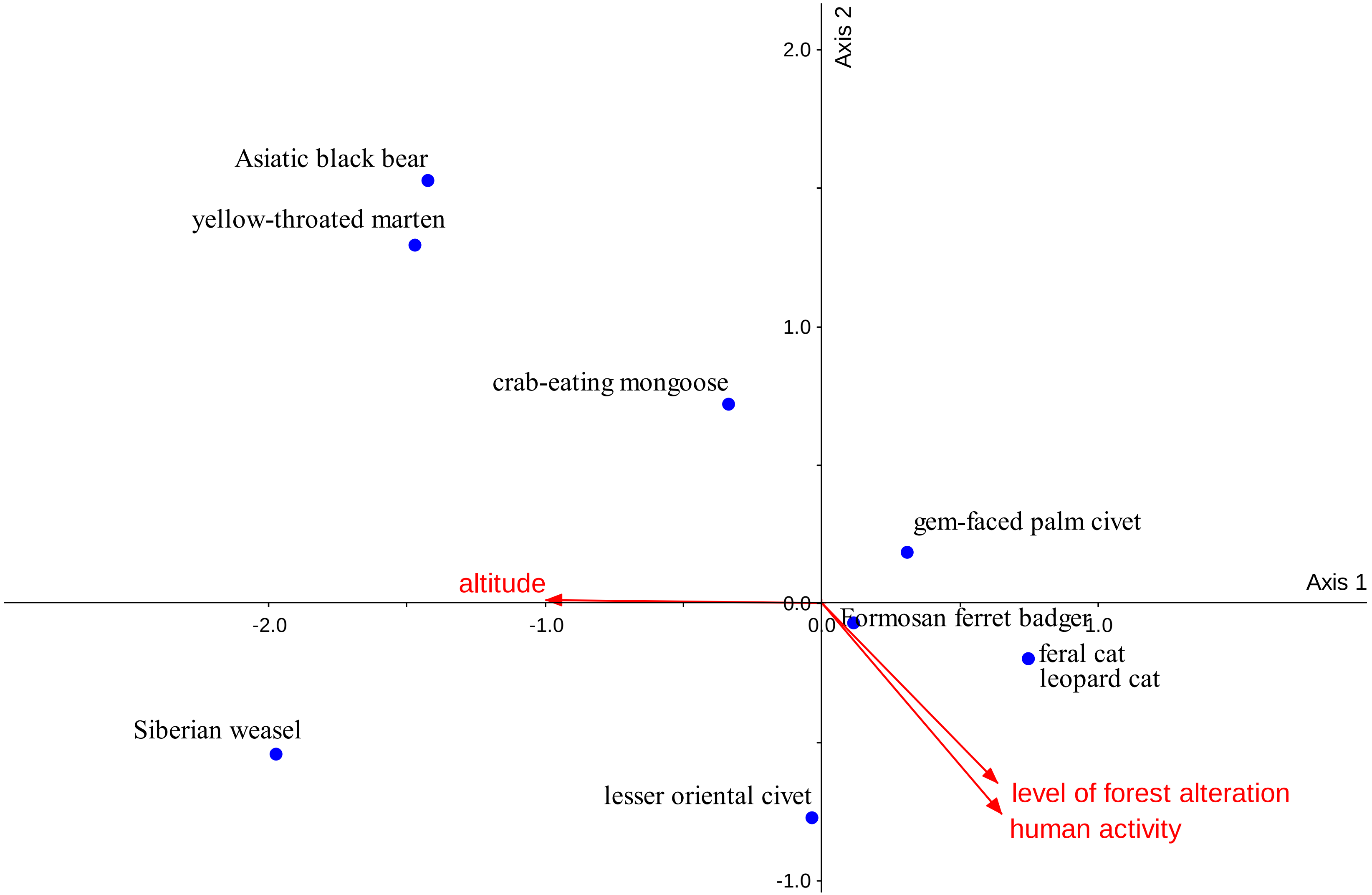


Figure 4.8 Joint biplot of canonical correspondence analysis based on axis 1 and axis 2 of the carnivore community (species in blue round points) of Taiwan in relation to habitat factors (red radiating lines). Data were based on all camera trapping studies collected during 1998-2006 (total 41 areas, average altitude 992m). Ordination scores were optimized for species. This was flipped vertically from original biplot produced by PC-ORD.

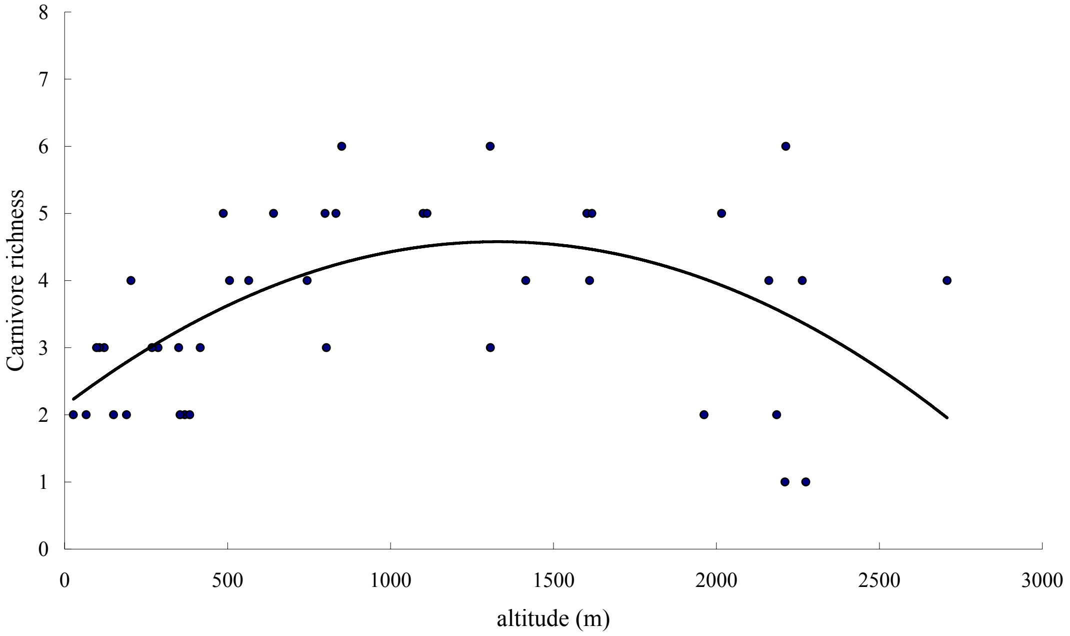


Figure 4.9 Mid-domain relationships of carnivore richness (number of species) and altitude. Quadratic curve was fitted using the altitude variable and its square term. Data were based on 41 areas from camera trapping studies collected in Taiwan during 1998-2006. This analysis excluded feral cat and consisted of 8 wild carnivores of Taiwan.

Appendix I. Summary statistics and correlations for the first 3 axes of the canonical correspondence analysis with the habitat factors and carnivore species for 146 camera trap sites in Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area, Taiwan (2001-2004).

Statistics	**Axis 1**	**Axis 2**	**Axis 3**
Eigenvalue	0.22	0.11	0.05
% variance explained in species data	12.2	6.3	2.9
Pearson correlation of species-habitat*	0.65	0.46	0.35
Kendall (rank) correlation of species-habitat*	0.39	0.24	0.10

* Correlation between sample scores for an axis derived from the species data and the sample scores that are linear combinations of the habitat factors

Habitat factors	**Intraset correlation**			**Interset correlation**		
	Axis 1	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 3**
Altitude(+)/greenness(-)	-0.47	-0.61	0.07	-0.30	-0.28	0.03
River distance/slope position	-0.44	0.21	0.27	-0.29	0.10	0.10
Cliff/steepness	-0.30	-0.25	0.39	-0.19	-0.12	0.14
Ruggedness/convex terrain	-0.01	-0.34	-0.40	0.00	-0.16	-0.14
Uneveness(micro)	0.12	0.08	0.59	0.08	0.04	0.20
Dense shrub/less rocky	0.01	-0.23	0.26	0.01	-0.11	0.09
Visual obscurity	0.20	-0.15	0.15	0.13	-0.07	0.05
Shrub height	-0.29	-0.02	-0.17	-0.19	-0.01	-0.06
Herbaceous cover	0.25	0.02	-0.39	0.16	0.01	-0.14
Forest height	0.04	-0.42	0.01	0.03	-0.20	0.00
Canopy cover	0.12	-0.03	-0.01	0.08	-0.02	-0.01
DBH<20cm tree density and heterogeneity of tree densities among 3 tree sizes	-0.51	0.10	0.00	-0.33	0.05	0.00
DBH>20cm tree density and basal	0.24	0.00	0.43	0.15	0.00	0.15
DBH<20cm tree height and forest stratum	-0.12	0.27	-0.33	-0.08	0.13	-0.11

Pearson and Kendall tau correlations of species with ordination axes

Habitat factors	**Axis 1**		**Axis 2**		**Axis 3**	
	r	**tau**	**r**	**tau**	**r**	**tau**
Siberian weasel	-0.35	-0.31	-0.34	-0.21	-0.01	0.04
Formosan ferret badger	-0.15	-0.09	0.28	0.25	-0.06	-0.05
Gem-faced palm civet	0.25	0.17	0.12	0.09	0.06	-0.01
Crab-eating mongoose	0.34	0.32	-0.11	0.05	-0.05	-0.03
Yellow-throated marten	0.02	-0.03	0.01	0.01	0.28	0.17

Appendix II Summary statistics and correlations for the first 3 axes of the canonical correspondence analysis with the habitat factors and carnivore species for 41 areas from camera trapping studies conducted during 1998~2006 in Taiwan.

Statistics	**Axis 1**	**Axis 2**	**Axis 3**
Eigenvalue	0.31	0.10	0.02
% variance explained in species data	25.0	8.0	1.4
Pearson correlation of species-habitat*	0.84	0.67	0.33
Kendall (rank) correlation of species-habitat*	0.65	0.22	0.07

* Correlation between sample scores for an axis derived from the species data and the sample scores that are linear combinations of the habitat factors

Habitat factors	**Intraset correlation**			**Interset correlation**		
	Axis 1	**Axis 2**	**Axis 3**	**Axis 1**	**Axis 2**	**Axis 3**
Altitude	-1.00	-0.01	0.07	-0.83	-0.01	0.02
Human activity	0.65	0.76	0.03	0.54	0.51	0.01
Level of forest alteration	0.64	0.65	-0.42	0.53	0.44	-0.14

Pearson and Kendall tau correlations of species with ordination axes						
Habitat factors	**Axis 1**		**Axis 2**		**Axis 3**	
	r	**tau**	**r**	**tau**	**r**	**tau**
Yellow-throated marten	-0.33	-0.38	0.51	0.43	-0.21	-0.10
Siberian weasel	-0.62	-0.69	-0.11	-0.02	-0.12	0.00
Formosan ferret badger	0.44	0.29	0.17	0.14	-0.18	-0.14
Gem-faced palm civet	0.64	0.55	0.40	0.34	-0.24	-0.08
Crab-eating mongoose	0.05	-0.07	0.48	0.22	0.01	0.03
Lesser oriental civet	0.12	0.04	-0.14	-0.25	-0.01	-0.03
Leopard cat	0.35	0.37	0.03	0.00	-0.15	-0.16
Asiatic black bear	-0.20	-0.29	0.37	0.24	-0.17	-0.13
Feral cat	0.49	0.53	0.04	0.06	-0.23	-0.21

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