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Niche Relationships of Carnivores in a Subtropical Primary Forest in Southern Taiwan

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Po-Jen Chiang, Kurtis Jai-Chyi Pei, Michael R. Vaughan, and Ching-Feng Li (2012) Niche relationships of carnivores in a subtropical primary forest in southern Taiwan. *Zoological Studies* **51**(4): 500-511. Carnivores are at the higher trophic levels and have garnered much attention in conservation and management efforts. In this study, we attempted to understand resource partitioning among sympatric carnivores existing in a primary forest with minimal human disturbance in southern Taiwan by camera trapping after the disappearance of the top carnivore, the clouded leopard (*Neofelis nebulosa*). Niche relationships were studied in terms of habitat, diet, and time dimensions. Six carnivore species were recorded, but the Asiatic black bear (*Ursus thibetanus formosanus*) was very rare. Canonical correspondence analysis of photographic rates and habitat factors of the other 5 carnivores showed that elevation was the strongest factor explaining the composition of the carnivore community in the habitat dimension. Carnivores could be divided into 3 groups. The low- to mid-elevation group consisted of the gem-faced palm civet (*Paguma larvata taivana*) and crab-eating mongoose (*Herpestes urva formosanus*) which had contrasting activity patterns and different diets; the mid- to high-elevation group consisted of yellow-throated marten (*Martes flavigula chrysospila*) and Siberian weasel (*Mustela sibirica taivana*). These 2 mustelids had similar diets, but Siberian weasels tended to avoid yellow-throated martens temporally. The Formosan ferret badger (*Melogale moschata subaurantiaca*) was more widely distributed along the elevational gradient. Ferret badgers partitioned resource use in either diet, activity patterns, or other habitat gradients from the other carnivores. Niche segregation and complementary resource use were observed in these 5 carnivores. http://zoolstud.sinica.edu.tw/Journals/51.4/500.pdf

Key words: Activity pattern, Complementary resource use, Niche segregation, Sympatric carnivores.

When ecologically similar species are in sympatry, different species often partition the use of resources, resulting in niche differentiation to facilitate species coexistence (Schoener 1974, Gordon 2000). Sympatric carnivores were found to have different habitat uses (Fedriani et al. 1999, Loveridge and Macdonald 2003, Vieira and Port 2007), different prey sizes (Karanth and Sunquist 2000, McDonald 2002, Scognamillo et al. 2003), different prey species (Karanth and Sunquist 2000), or different activity patterns (Fedriani et al. 1999, Loveridge and Macdonald 2003, Vieira and Port 2007). Schoener (1974) found that resource partitioning was principally along 3 dimensions (i.e., habitat, diet, and time) and that the habitat dimension was the relatively most important axis followed by food-type and then by temporal dimensions. When species were similar in 1 dimension, complementary resource use would imply dissimilarity in other dimensions to reduce interspecific competition (Schoener 1974 1983).

There are 11 wild carnivore species in Taiwan, including 2 felids, 5 mustelids, 2 viverrids, 1 herpestid, and 1 ursid. These 11 carnivores

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variably occur from coastal to alpine areas in Taiwan, and most are sympatric. However, the largest felid, the Formosan clouded leopard (*Neofelis nebulosa*) (Chiang 2007), and the largest mustelid, Eurasian otter (*Lutra lutra chinensis*) (Lin 2000), are likely extirpated from the wild in Taiwan. The largest carnivore in Taiwan, the Asiatic black bear (*Ursus thibetanus formosanus*), has also become very rare compared to its historical distribution and abundance (Hwang et al. 2006). The remaining larger carnivores in Taiwan are the leopard cat (*Prionailurus bengalensis chinensis*) with a body weight of 2.7-5.5 kg and the yellow-throated marten (*Martes flavigula chrysospila*) with a body weight of up to 3 kg. Disappearance of top carnivores may result in increased smaller carnivores, i.e., mesopredator release (Terborgh et al. 1999). 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 to assess reintroduction plans of the disappeared top carnivores (Terborgh et al. 1999) and also provide baseline information for conservation and management of these mesopredators.

However, only a few studies were conducted on carnivores in Taiwan and most focused on individual species. Very few studies addressed niche relationships of sympatric carnivores in Taiwan. Chuang and Lee (1997) studied food habits of the Formosan ferret badger (*Melogale moschata subaurantiaca*), crab-eating mongoose (*Herpestes urva formosanus*), and lesser Oriental civet (*Viverricula indica pallida*) in sympatry and found that these 3 species all mainly fed on invertebrates but that different invertebrate taxa had dissimilar relative importance values. Wu (1999) also found substantial diet overlap, with some degree of food-type segregation, between the Siberian weasel (*Mustela sibirica taivana*) and ferret badger. On the other hand, scat analysis revealed that the yellow-throated marten and Siberian weasel had similar diet niche breadths, and their diets overlapped to a high degree (Tsai 2007). However, their complementary resource use in other niche dimensions was not addressed. The only study involving temporal dimensions showed that the crab-eating mongoose was diurnal in contrast to the nocturnal ferret badger, lesser Oriental civet, and gem-faced palm civet (*Paguma larvata taivana*) (Chen et al. 2009). Chen et al. (2009) also studied habitat characteristics affecting the presence and absence and found some differences among these 4 sympatric carnivores in secondary forests in southern Taiwan.

Taiwan is an orogenic island with the highest elevation of 3952 m. Rapid development has encroached upon most lowland areas. The Tawu Mountain (TWM) area in southeastern Taiwan contains the largest remaining preserved primary rainforest with minimum human disturbance. Thus, it provides a good area to study sympatric carnivores under the most natural conditions which are little studied in Taiwan. The objective of this study was to investigate niche relationships of carnivores currently living in the TWM area to provide information for conservation and management of these carnivores in the changing landscape of Taiwan. We predicted that niche segregation and complementary resource use would be observed for sympatric carnivores.

MATERIALS AND METHODS

Study area

The study site in the TWM area in southern Taiwan consists of 2 adjacent protected areas, i.e., the Tawu Mountain Nature Reserve (48,000 ha) and Twin Ghost Lake Important Wildlife Area (45,000 ha). The elevation ranges 130-3100 m, and the area is primarily comprised of pristine rainforests, e.g., from tropical, subtropical, to temperate forest types along the elevational gradient consisting of the 4 major forest types of *Ficus*-*Machilus*, *Machilus*-*Castanopsis*, *Quercus*, and Taiwan hemlock (*Tsuga chinensis* var. *formosana*) (Su 1984). All of the forests are evergreen and have minimal human disturbance and hunting activities.

Camera trapping

Intensive camera trapping effort with 185 camera trapping sites were conducted in the TWM area in 2001-2004 (Fig. 1). Camera trap sites were selected based on stratified sampling of the 4 elevation ranges of < 1200 (72 sites), 1200-1900 (43 sites), 1900-2500 (49 sites), and 2500-3100 m (21 sites), corresponding to the 4 major forest types mentioned above. The photographic rate of each carnivore species was used as a surrogate of the relative population abundance as it was shown to be representative (Carbone et al. 2001, O'Brien et al. 2003, Liang 2005, Rovero and Marshall 2009). Higher occurrence rates at a camera trap site also indicate a higher usage of that particular habitat. Identifiable individuals were counted as different occurrence events (O'Brien et al. 2003). To avoid dependency of consecutive photos due to lingering animals, consecutive photographs of the same individual within 1 h were counted as single occurrence event (Yasuda 2004, Chiang et al. 2007). However, yellow-throated martens often formed small groups of 2 or 3 individuals. Their photographic events were counted in groups even though there were multiple distinguishable individuals in the same or consecutive photographs.

Habitat-use patterns

A canonical correspondence analysis (CCA) (Ter Braak 1986) was used to describe the carnivore community structure and its relationship with habitat characteristics using the R software (R Development Core Team 2009) with the "vegan" package (Oksanen et al.

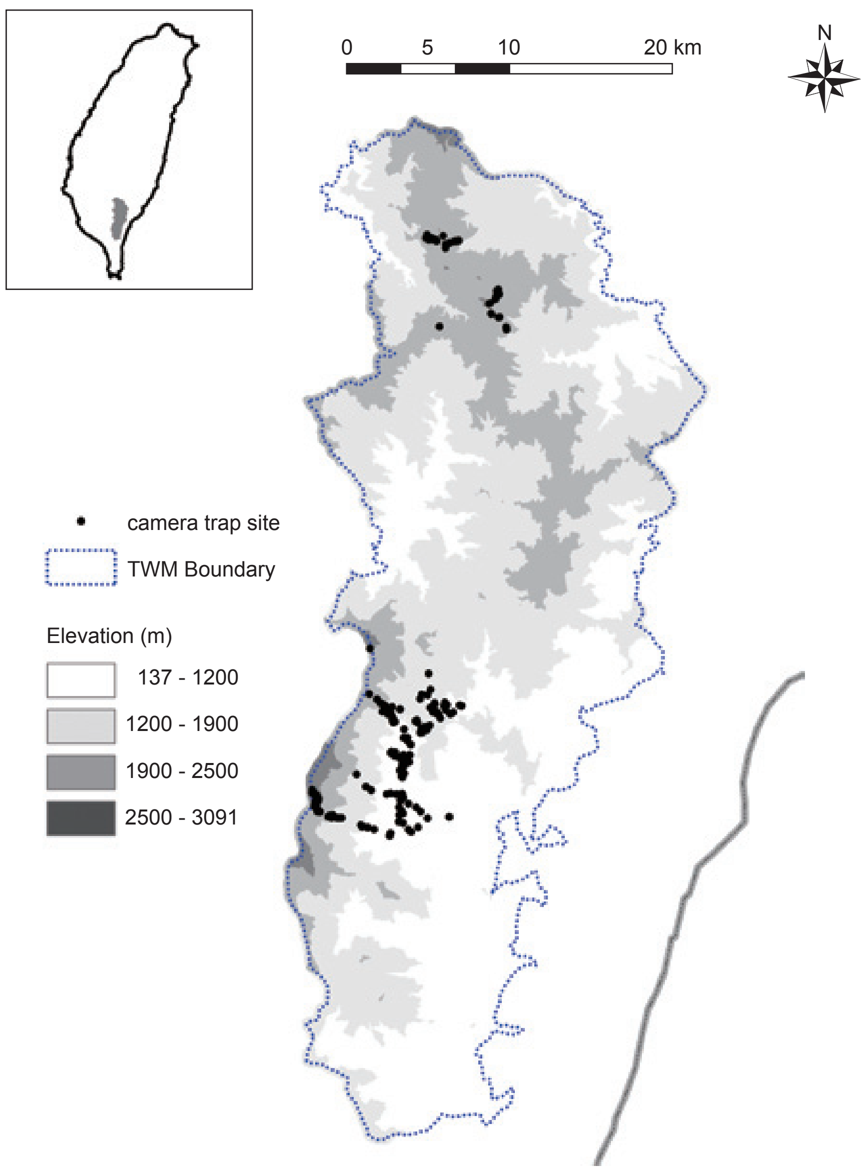

Fig. 1. Locations of camera trap sites in the Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area (at Tawu Mountain (TWM)). Four stratified elevation ranges are illustrated in the TWM area, and camera trap sites were sampled in these 4 stratified elevation ranges corresponding to 4 major vegetation types.

2008). Thirty-one habitat variables belonging to 4 categories, of 1) elevation, greenness, wetness, and terrain shape, 2) ruggedness, 3) forest understory, and 4) forest structure, were derived from a 40 × 40-m digital elevation model and measured in the field within a 17.8-m radius of the camera trap site (Table 1). A factor analysis was separately conducted on the 4 categories of habitat variables based on a correlation matrix using orthogonal rotation to reduce the number

Table 1. Four categories of habitat variables in the Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area (Tawu Mountain), Taiwan (2001-2004). The elevation and terrain categories were derived from a 40 × 40-m digital elevation model (DEM) as meso-scale habitat variables (except EVEN). EVEN in the terrain category and other habitat variables were measured within a 17.8-m radius of the camera trap sites as micro-scale habitat variables

Category	Habitat covariate	Description
Elevation/greenness/wetness	ALT	Elevation (m) from a global positioning system and differential post processing
	NDVI	Normalized difference vegetation index based on SPOT 4 satellite images (at a 12.5-m resolution).
	MOISTGRD	Moisture gradient based on DEM aspect and proximity to rivers and valleys, 10 levels: 1 (wettest)- 10 (driest on south-facing slopes)
	ASR	Annual solar radiation based on Fu and Rich (2002), which considered atmospheric conditions, elevation, aspect, and influences of the surrounding topography
	RIVERDIST	Distance to the nearest rivers or lakes
Terrain shape/ruggedness	SLOPEPOS	Slope position 0 (valley)- 100 (ridge), ratio of elevation difference to the valley and ridge
	SLOPEDEM	Slope from DEM in percentage (ArcGIS 9.2)
	SLOPESTD	Standard deviation of slopes (in percentage) within neighboring 3 × 3 cells (i.e., 120 × 120 m)
	CLIFFDIST	Distance to nearest cliff, defined as a slope of > 45° with an area of > 1.44 ha (i.e., 3 × 3 cells or 120 × 120 m)
	CLIFFCOUNT	Number of cliff cells (slope > 45°) within a 25 × 25 cell window (i.e., 1 × 1 km or 100 ha)
	TSI	Terrain shape index (Mcnab 1989) based on neighboring 3 × 3 DEM cells (i.e., 120 × 120 m). Positive values indicate a concave surface, negative values indicate a convex surface, 0 indicates a linear (not necessarily level) surface
	EVEN	Terrain evenness: standard deviation of terrain shape indices calculated for 2, 4, and 8 m
Forest understory/ground cover	HERBCO	Herbaceous cover (%)
	SHRUBCO	Shrub cover (%)
	SHRUBHT	Average shrub height (m)
	SHRUBDEN	Shrub density log(natural)-transformed
	SHRUBCV	Coefficient of variation (CV) of shrub distances at the 4 quadrants
	ROCKCO	Rock cover (%)
	VO	Average visual obscurity of 4 directions at 0.5-2 m (total 32 values) (%)
	VOSTD	Standard deviation of visual obscurity among 4 directions
Forest structures	STREEDEN	Tree density (diameter at breast height (DBH) of 1-20 cm), log-transformed
	LTREEDEN	Tree density (DBH of > 20 cm), log-transformed
	TREEDENCV	CV of tree densities among 3 size classes (DBHs of 1-5, 5-20, and > 20 cm)
	BASAL	Total basal area, log-transformed
	STREEHT	Average tree height (DBH of 1-20 cm)
	LTREEHT	Average tree height (DBH of > 20 cm)
	TREEHTCV	CV of tree heights among 3 size classes (DBHs of 1-5, 5-20, and > 20 cm)
	STRATUM	Number of forest strata (2-5)
	CANOPYHT	Canopy height (m)
	CANOPYCO	Average of 8 measurements of canopy cover (%)
	CANOPYGAP	CV between 8 measurements for canopy patchiness (gaps)

of habitat variables and collinearity. For each category, principal components were selected so that these components cumulatively explained at least 70% of the habitat variation. Components with eigenvalues of > 1 were also retained, even though the cumulative variation explained already exceeded 70%. These principal components were thereafter orthogonally rotated for ease of interpretation. Factor scores were used as habitat variables for each camera trap site in the habitat matrix of the CCA, and photographic rates of each carnivore at each camera trap site were used in the abundance matrix of the CCA.

Temporal patterns

Camera trapping is widely used to study diel activities of animals (see review in Cutler and Swann 1999). An index of the activity level for each hour was calculated by dividing the hourly number of occurrence events by the total number of occurrence events for each species. Hourly activity levels are expressed as percentages and depicted across 24 h.

Diet patterns

Diet was summarized according to published studies conducted in Taiwan or nearby Southeast Asian countries. Food types were divided into 5 categories: invertebrates, smaller mammals, other smaller vertebrates (amphibians, reptiles, birds, etc.), larger vertebrates (> 1 kg), and plants. A food category was assigned as a “major food item” if the average reported relative importance was > 40%, a “secondary food item” if it was 15%-40%, and an “occasional food item” if it was 5%-15%. Food categories with an average reported relative importance of < 5% were ignored for simplicity of comparison.

RESULTS

The total number of camera trap days for all 185 camera trap sites was 7812. Thirty-nine of 185 camera trap sites documented no carnivores. Six carnivore species were photographed by the other 146 camera trap sites, including Formosan black bear, Formosan ferret badger, Siberian weasel, yellow-throated marten, crab-eating mongoose, and gem-faced palm civet. Of the other existing carnivores of Taiwan not documented in this study, the leopard cat and lesser Oriental civet prefer more-disturbed lowland habitats (Pei and Chen 2007), and the least weasel (*Mustela nivalis formosana*) is currently found only in central and northern Taiwan (Lin et al. 2010). Thus, all carnivores of Taiwan that live in primary forests across a large elevation range were completely documented in this study. However, the black bear was very rare and was photographed at only a few sites. Thus, only the other 5 more widely distributed species were included in the CCA. In addition, the 39 camera trap sites at which no carnivores were documented were excluded from the CCA. Wilcoxon rank-sum tests showed that there were no significant differences in photographic rates between the dry and wet seasons for these 5 smaller carnivores (p = 0.16-0.9) in the study area. Thus, photographic rates were calculated for each camera trap site without separating dry and wet seasons for the analysis.

Habitat patterns

The factor analysis extracted 14 factors in total from 31 habitat variables belonging to 4 categories (Table 2) to be used in the CCA. For the CCA, the total inertia was 1.8111, while the constrained axes explained 23.1% of the total variability. The 1st 3 axes (with eigenvalues of 0.2193, 0.1136, and 0.0573) accounted for 52.3%, 27.1%, and 13.7% of the total variation explained (Fig. 2). The yellow-throated marten was located near the center of the ordination space with nearly 0 correlations with axes 1 and 2 suggesting that it may be a generalist in the study area.

A permutation test on the trace statistic showed that the measured habitat factors significantly explained the species composition ($p < 0.0001$ based on 10^4 permutations). The elevation(+)/greenness(-)/ASR(+) (A1) factor had the strongest relationship to the carnivore community. This factor was likely an overall effect of elevation change, because higher elevations tend to receive more solar radiation and are comprised of more conifers (less leaf area causing a lower normalized difference vegetation index (NDVI)). The Siberian weasel occupied the highest elevation, while gem-faced palm civets preferred the lowest elevation with higher NDVI and less solar radiation. For the other 3 carnivores, yellow-throated marten’s optimum was above the average along this elevational gradient, while that of the crab-eating mongoose was lower than the average. The optimum for the ferret badger was nearly at the average and was widely distributed across the elevation range.

The "river distance/slope position" factor (A2) and "smaller tree density/heterogeneity" factor (F3) also had strong relationships with the carnivore community. Gem-faced palm civets and crab-eating mongooses had a preference for rivers/valleys, which also usually receive less solar radiation and are at lower elevations, and forests with a lower density of trees with diameter at breast height (DBH) of < 20 cm and more homogeneous tree densities of different sizes. In contrast, the 3 mustelids had a converse pattern. These 2 habitat factors separated ferret badgers and crab-eating mongooses, which had similar optima on the elevation gradient (A1).

In terms of the forest structure, gem-faced palm civets and ferret-badgers occurred more often in forests with a lower canopy and a lower tree height of large trees with DBHs of > 20 cm (F1) and a higher tree height of small trees with DBHs of < 20 cm (F5). Such a trend may imply a preference for younger forests instead of old-growth forests which have large trees with high canopy cover. But the other 3 carnivores exhibited a contrasting trend. Moreover, ferret-badgers utilized habitats with more-densely spaced smaller trees (F3) while gem-faced palm civets preferred habitats with less-densely spaced smaller trees.

Forest understory and terrain characteristics generally had lower correlations with the carnivore community than the major gradients in the

Table 2. Factors extracted by Varimax rotation from the factor analysis of the 31 habitat variables in 4 categories in the Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area (Tawu Mountain), Taiwan (2001-2004)

Category	Code	Factor	High loadings (> 0.5) of habitat variables	Variation explained for each category
Elevation/greenness/wetness	A1	Elevation	0.74*ALT -0.83*NDVI 0.85*ASR	0.39
	A2	River distance/slope position	0.87*RIVERDIST 0.91*SLOPEPOS 0.61*MOISTGRD	0.39
Terrain shape/ruggedness	T1	Cliff/steepness	0.89*CLIFFCOUNT -0.89*CLIFFDIST 0.59*SLOPEDEM	0.32
	T2	Ruggedness/convex terrain	0.8*SLOPESTD -0.79*TSI	0.22
	T3	Uneveness (micro)	0.97*EVEN	0.17
Forest understory	U1	Dense shrub/less rocky	0.6*SHRUBCO 0.81*SHRUBDEN -0.66*SHRUBCV -0.63*ROCKCO	0.26
	U2	Visual obscurity	0.71*VO 0.85*VOSTD	0.17
	U3	Shrub height/cover	0.92*SHRUBHT 0.55*SHRUBCO	0.15
	U4	Herbaceous cover	0.96*HERBCO	0.13
Forest structure	F1	Forest height	0.84*LTREEHT 0.88*TREEHTCV 0.73*CANOPYHT	0.23
	F2	Canopy cover	0.91*CANOPYCO -0.91*CANOPYGAP	0.16
	F3	Tree density of DBH < 20 cm and heterogeneity	0.83*STREEDEN 0.82*TREEDENCV	0.14
	F4	Tree density of DBH > 20 cm and basal area	0.87*LTREEDEN 0.62*BASAL	0.13
	F5	Tree height of DBH < 20 cm and forest stratum	0.88*STREEHT 0.69*STRATUM	0.13

elevation and forest-structure categories. Shrub height/cover (U3) was slightly stronger and mostly associated with mustelids in contrast to the gem-faced palm civet and crab-eating mongoose, which did not seem to be related to the major food items (tree fruits and crustaceans, respectively).

Activity patterns

Yellow-throated martens (Fig. 3A) and crab-eating mongooses (Fig. 3B) were basically diurnal with few nocturnal activities. But crab-eating mongooses would extend their activities into nighttime, usually within 2 h of sunrise and sunset. Nocturnal species included ferret-badgers (Fig. 3A) and gem-faced palm civets (Fig. 3B). They also extended their activities to the daytime, most of which were within 0.5 h of sunrise and sunset. Siberian weasels (Fig. 3A) were active day and night with a significant tendency for more-nocturnal activities between 18:00 and 06:00 the following morning (84.6%, Chi-squared goodness of fit test, $p < 0.0001$).

Diet summary

Based on the types of major food items, diets of the 5 carnivores could be divided into 3 groups: invertebrates, small mammals, and plants (Table 3). Fruits were the major food items of gem-faced palm civets. Yellow-throated martens and Siberian weasels took a lot of small mammals. Ferret badgers and crab-eating mongooses fed mostly on invertebrates, including earthworms, crustaceans, and insects.

Niche relationship

When habitat patterns, activity patterns, and diet patterns were simultaneously examined, segregation among the carnivore community was more pronounced than when considering habitat patterns alone (Fig. 2). In the TWM area, when gem-faced palm civets and crab-eating mongooses shared some similar spatial patterns, they exhibited completely reversed activity patterns (i.e., nocturnal vs. diurnal). They also differed in

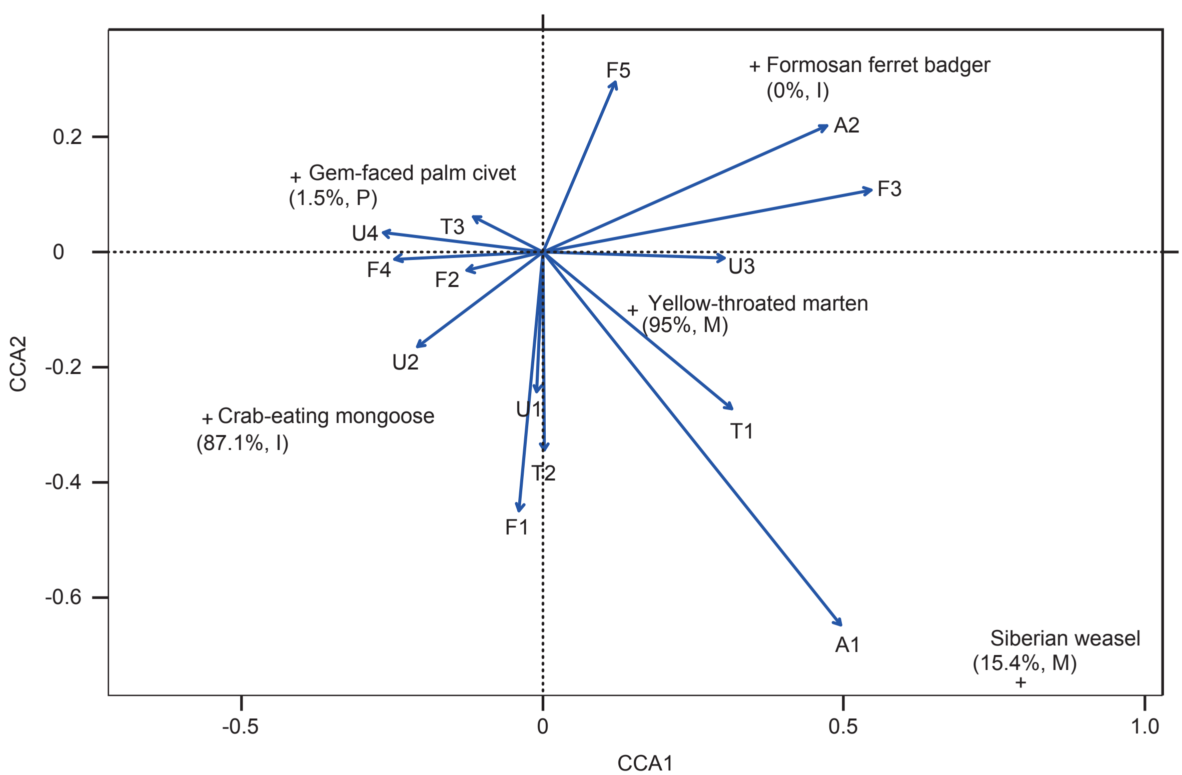

Fig. 2. Joint biplot of the canonical correspondence analysis based on axes 1 and 2 of the carnivore community (species in '+') of Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area (at Tawu Mountain (TWM)), Taiwan in relation to habitat factors (radiating lines). See table 3 for codes of habitat factors. Data were based on 146 camera trap sites (at an average elevation of 1572 m) collected in 2001-2004. Ordination scores were optimized for species. Parentheses after a species name gives its percentage of diurnal (06:00-18:00) activity and major food item type (P, fruits; I, invertebrates; M, small mammals).

the major food items (e.g., plants vs. invertebrates, Table 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 major A1, A2, and F3 habitat factors (lower than the average values for those factors for civets vs. higher than the average values for those factors for martens). Furthermore, yellow-throated martens fed on small mammals while gem-faced palm civets fed on fruits (Table 3).

Similarly, yellow-throated martens and ferret badgers, which were close to each other in the ordination space, were segregated in the temporal and diet dimensions. Although crab-eating mongooses and ferret badgers occupied similar optima along the elevation (A1) gradient, they had contrasting preferences in habitat factors A2 and F3 and also exhibited reversed activity patterns. Siberian weasels were active day and night and were away from the other 4 carnivores in the CCA

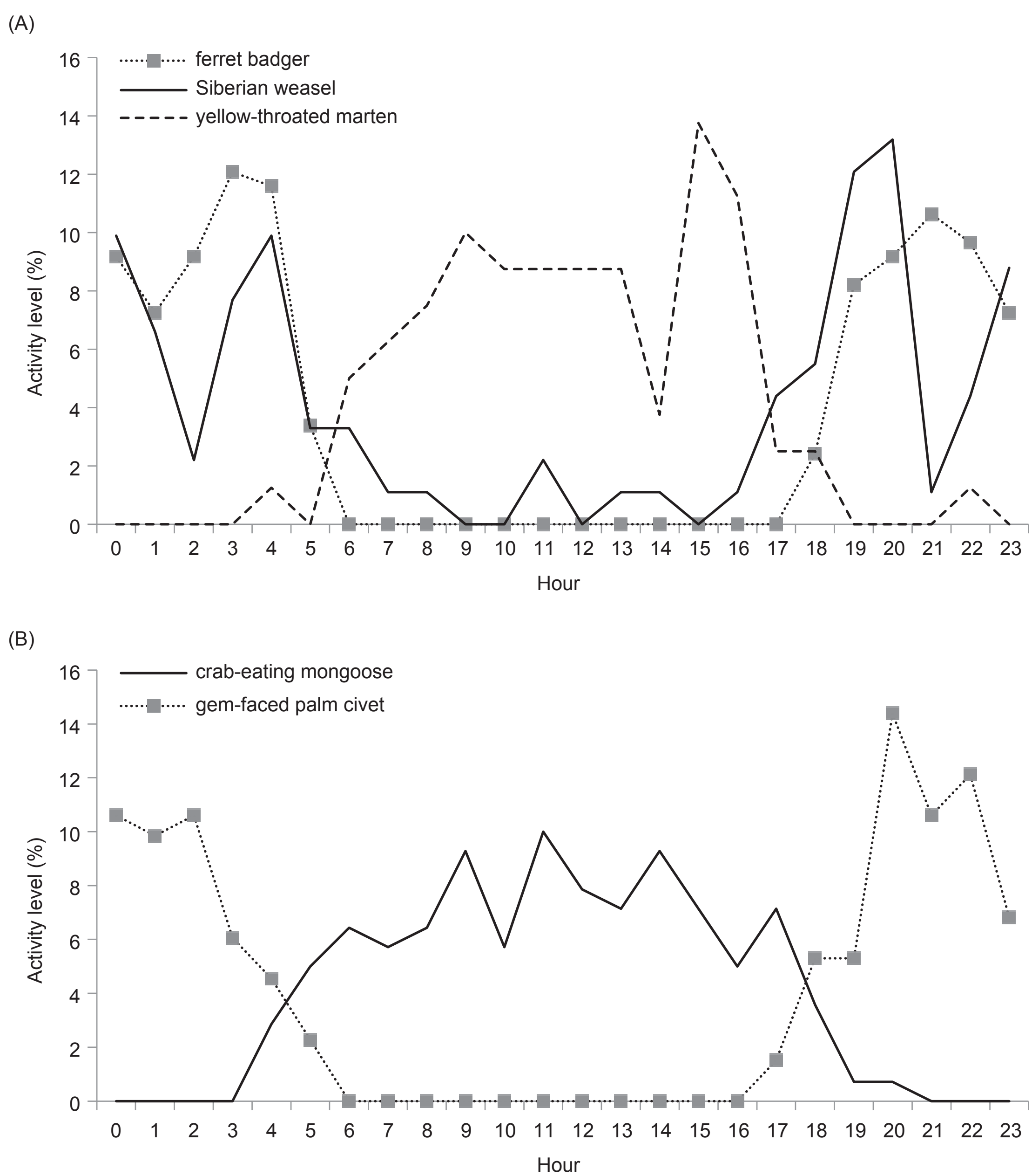

Fig. 3. Activity patterns of (A) the 3 mustelids of the ferret-badger (*n* = 207), yellow-throated marten (*n* = 80), and Siberian weasel (*n* = 91); and (B) the crab-eating mongoose (*n* = 140) and gem-faced palm civet (*n* = 132) at Tawu Nature Reserve and Twin Ghost Lake Important Wildlife Area (Tawu Mountain), Taiwan based on camera trapping data in 2001-2004.

ordination community space (Fig. 2). Even with the more closely related yellow-throated marten having similar major food item with Siberian weasels (Table 3), they seemed to be temporally separated (Fig. 3A). For the nocturnal species pair (gem-faced palm civet vs. ferret badger) and the diurnal species pair (crab-eating mongoose vs. yellow-throated marten) showing less segregation in time budget and along the elevation gradient (A1), prey differences (Table 3) seemed to be the major mechanism of niche segregation (Fig. 2), while habitat patterns also differed along the A2 and F3 gradients.

DISCUSSION

Analysis of the activity patterns and spatial patterns by the CCA based on camera trapping data provided an effective way to study niche segregation in time and space for carnivores in Taiwan which has never been explored before. When diets of these carnivores based on previous studies in Taiwan were considered for food-type partitioning, we observed complementary resource use (Schoener 1974 1983) through partitioning in terms of space (on microhabitat and landscape scales), food-type, and temporal dimensions. Species closer to each other in the ordination space were more likely to be sympatric and thus differed in time of activity or prey to facilitate coexistence.

The CCA revealed that elevation, which is analogical to latitude with respect to vegetation and weather patterns, was the strongest gradient explaining the composition of the carnivore community under natural conditions. The CCA biplot generally divided the Mustelidae from the other 2 lower-elevation species (Fig. 2). This pattern may reflect some of the phylogenetic aspects and evolutionary histories of these species. The Mustelidae is a Holarctic group, while the Viverridae and Herpestidae originated from tropical Asia of the Oriental Region (Ewer 1973).

Sympatric populations of Siberian weasels and yellow-throated martens at an elevation range of 2700-3700 m were found to have similar diet niche breadths and a high degree of diet overlap, mostly on small mammals (Tsai 2007). Interspecific competition for food therefore may occur. Within the TWM area where yellow-throated martens were more abundant at elevations of < 2500 m, Siberian weasels were significantly more active at night (nocturnal activities between 18:00 and 06:00 the following morning, 94.2%) at elevations of < 2500 m than at elevations of > 2500 m (nocturnal activities between 18:00 and 06:00 the following morning, 71.8%, Chi-squared test of independence, *d.f.* = 1, χ^2 = 6.98,

Table 3. Comparison of food-type dimensions for the 5 carnivores in the Tawu Mountain area of Taiwan. Summary of diets were based on literature in Taiwan and a few from nearby countries (i.e., for the gem-faced palm civet). Relative importance levels 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%). A relative importance level of < 5% was not included in the diet summary

Species	Invertebrates	Smaller vertebrates		Larger vertebrates	Plants	Source
		Others (reptiles, amphibians, birds)	Small mammals			
Yellow-throated marten		O	M	S		Tsai 2007
Siberian weasel	S	O	M	O (scavenge)		Ma 1990, Wu 1999, Tsai 2007
Formosan ferret badger	M	O				Chuang and Lee 1997, Wu 1999
Crab-eating mongoose	M	S			O	Chuang and Lee 1997
Gem-faced palm civet	O		O		M	Wang and Fuller 2003, Hwang 2008

$p < 0.01$). Similarly, radio-collared male Siberian weasels exhibited more diurnal activity (diurnal activities between 06:00 and 18:00, 71.5%) in a lower-elevation area (520-1230 m) in northeastern Taiwan without sympatric yellow-throated martens (Wong 1997).

Predators separate more often in diel activity patterns than do other groups of animals (Schoener 1974). Carnivores competing for similar prey were also observed to exhibit different activity patterns (Ray 1997, Fedriani et al. 1999, Karanth and Sunquist 2000, Vieira and Port 2007). The smaller Siberian weasel may be avoiding the larger, diurnal yellow-throated marten by being more active at night, since they are often sympatric and have a high degree of diet overlap (i.e., small mammals). St-Pierre et al. (2006) found that the smaller *Mustela erminea* avoided the larger *M. frenata*, which was related 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 (with a body weight difference up to 5-10-fold). Remains of smaller weasel (*Mustela*) species were found in the scat of other larger mammalian carnivores, including larger weasel and marten (*Martes*) species (Erlinge 1981, Zielinski et al. 1999, Fedriani et al. 2000, Edwards and Forbes 2003). Although yellow-throated marten's predation on Siberian weasels has not yet been documented, remains of a ferret badger, which is larger than Siberian weasel, were found in yellow-throated marten feces (Chung-Yi Lin, personal communication).

Lower elevations of the TWM area, which is comprised of primary forest, contained only 1 *Niviventer* rat species. This may have caused the yellow-throated marten and Siberian weasel to inhabit higher elevations in the TWM area (Fig. 2). However, yellow-throated marten's optimal habitat being lower than Siberian weasel along the elevation(+)/greenness(-) gradient within the TWM area (Fig. 2) suggests that it may be using its optimum habitat with more-abundant food including small mammals and larger ungulates (e.g., muntjacs), which yellow-throated martens have been observed to hunt (Matyushkin 1987, Sathyakumar 1999, Koh 2007). As forests at lower elevations tend to have fewer rodents, competition between Siberian weasels 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 limited small mammals, Siberian weasels were still found to adjust their food habits to forage for more invertebrates at lower elevations in Taiwan, which is likely due to the scarcity of small mammals (Tatara and Doi 1994, Wu 1999). In other words, Siberian weasels at low to mid-elevations in Taiwan would need to compete with yellow-throated martens for scarce small mammals and possibly compete with the larger, similarly nocturnal ferret badgers and lesser Oriental civets for invertebrates. But Wu (1999) observed that sympatric Siberian weasels and ferret badgers still differentiated their habitat and food dimensions to a certain degree. Our biplots (Fig. 2) also showed habitat segregation between Siberian weasels and ferret badgers.

Gem-faced palm civets and ferret badgers seem to be tolerant of human-altered landscapes to a certain degree and were found to be omnipresent in many areas across Taiwan, even very close to human encroachment. In the TWM area with minimal human disturbance, these 2 carnivores preferred lower forest heights (habitat factor F1 in Fig. 2), suggesting their adaptation to secondary forests near human encroachment, which usually have lower forest heights due to frequent human disturbances. In addition, they were both nocturnal and could avoid humans by being active at night.

Carbone et al. (2001) suggested that 1000 camera trap days could detect tiger (*Panthera tigris*) presence at very low densities (0.4-0.7 tigers/100 km^2). Our study area is about 930 km^2. If there was only 1 tiger in such a large area, the predicted camera-trapping effort to detect tiger presence would be around 5000 trap days. The fact that clouded leopards, Eurasian otters, leopard cats, and lesser Oriental civets were not detected in TWM's contiguous primary forests suggests their true absence given our extensive camera trapping effort of 7812 camera trap days. Current habitat types where lesser Oriental civets and leopard cats are mostly found in Taiwan are at elevations of < 1200 m in secondary forest mosaics with farmlands or adjacent to human encroachment (Chen 2002, Liu and ChangChien 2004, Pei and Chen 2006). In contrast to only 1 rat species occurring in contiguous primary forests at lower elevations, many other small rodents occur in lowlands closer to human encroachment (Lin 1982, Lin and Lin 1983). Such places are usually a mosaic of forests and agricultural lands which provides suitable prey (e.g., small mammals and Formosan hares that favor non-forest habitats) for leopard cats. Scarce small mammals in contiguous forests at low to mid-elevations would make competition for small mammal prey even greater for leopard cats in such pristine habitats where Siberian weasels and yellow-throated martens occur. Interspecific competition with other small mammal predators and a lack of prey are likely the mechanisms deterring leopard cats from using primary montane forests in Taiwan.

Our findings support the hypothesis of the leopard cat and lesser Oriental civet not preferring primary forests in contrast to populations in other Southeast Asia countries. Furthermore, of the 3 conservation categories in Taiwan's *Wildlife Conservation Law*, leopard cats are listed in category I as "endangered", while lesser Oriental civets are in category II, "valuable". Their habitats in Taiwan are undergoing rapid human encroachment, fragmentation, and shrinkage. Conservation actions are urgently needed for leopard cats and lesser Oriental civets in Taiwan. In addition, our camera trapping revealed abundant prey in the study area for clouded leopards. Since Taiwan is an island, and it is unlikely to be naturally recolonized by other clouded leopard populations, the TWM area could be a potential candidate for the reintroduction of clouded leopards. With the niche information of meso-carnivores presented in this paper, a clouded leopard reintroduction plan could be carefully conducted and monitored to assess any population or behavioral changes of other sympatric carnivores.

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