ECOLOGY OF THREE SYMPATRIC FELIDS IN A MIXED EVERGREEN FOREST IN NORTH-CENTRAL THAILAND

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We report on the natural history of 3 rare and mostly unstudied felids, the clouded leopard (*Neofelis nebulosa*), Asiatic golden cat (*Catopuma temminckii*), and marbled cat (*Pardofelis marmorata*), in Phu Khieo Wildlife Sanctuary, Thailand. From February 1999 to February 2003, 4 clouded leopards (2 males and 2 females), 2 Asiatic golden cats (1 male and 1 female), and 1 female marbled cat were captured, radiocollared, and tracked for 1–17 months. Clouded leopards exhibited annual ranges (95% minimum convex polygon) of 22.9–45.1 km^2, traveled an average of 1,932 m each day, and were active during 58% of diel activity readings. Asiatic golden cats ranged 32.6–47.7 km^2, traveled an average of 1,597 m each day, and exhibited an arrhythmic activity pattern of 58% activity. A marbled cat was tracked for 1 month, ranged 5.3 km^2, and was primarily nocturnal in its habits. Examination of limited data indicated diverse prey use by clouded leopards. Illegal hunting and collecting of aloewood (*Aquilaria crassna*) threaten the felid community in Phu Khieo Wildlife Sanctuary.

Key words: Asiatic golden cat, *Catopuma temminckii*, clouded leopard, conservation, ecology, marbled cat, *Neofelis nebulosa*, *Pardofelis marmorata*, Thailand

Felids of Southeast Asia are poorly represented in field studies. Thailand contains 9 felid species, of which only the leopard (*Panthera pardus*) and leopard cat (*Prionailurus bengalensis*) have been investigated more than once (Austin 2002; Grassman 1999, 2000; Rabinowitz 1989, 1990). The natural histories of the clouded leopard (*Neofelis nebulosa*), Asiatic golden cat (*Catopuma temminckii*), and marbled cat (*Pardofelis marmorata*) remain virtually unknown. Most of the ecological information on these felids in this region comes from status reports (Datta 1998; Jorio 2000; Rabinowitz et al. 1987; Santiapillai 1989), anecdotes, and accounts of captive felids (Barnes 1976; Gee 1961; Louwman and Van Oyen 1968; Müller and Müller 1989; Selous and Banks 1935; Yamada and Durrant 1989). No field studies of these felids have been published. It is important to understand the ecological requirements of rare carnivores for implementation of effective management and conservation strategies.

The clouded leopard is medium-sized (11–20 kg), with short legs, long body, an exceptionally long tail, and a distinctive cloudlike pelage pattern (Nowell and Jackson 1996; Sunquist and Sunquist 2002). The arboreal talents of this cat are considerable, rivaling those of the margay (*Leopardus wiedii*) of South America (Nowell and Jackson 1996). Clouded leopards have the longest canines proportional to body size of any felid (Nowell and Jackson 1996; Sunquist and Sunquist 2002). The Asiatic golden cat is medium-sized with a uniform but highly polymorphic pelage ranging from black to golden red (Sunquist and Sunquist 2002). The marbled cat is the size of a large domestic cat and resembles the clouded leopard morphologically, with a long tail, cloudlike pelage pattern, and elongated canines (Pocock 1932; Sunquist and Sunquist 2002).

Wildlife conservation is often based on habitat and species protection (Duckworth et al. 1999; Nowell and Jackson 1996; Seidensticker et al. 1980; Sunquist et al. 1999), and by maintaining ecological processes (Balmford et al. 1998; Weddell 2002). The conservation of felids in Thailand is no different. The main threats affecting the future of felid populations in Thailand are habitat loss and illegal hunting of the cats and their prey (Grassman 1999; Rabinowitz 1989, 1991).

Since the 1960s, forest cover in Thailand has decreased from 53% to 22% (Elliott 2001; Ma 1999), with only 12% remaining
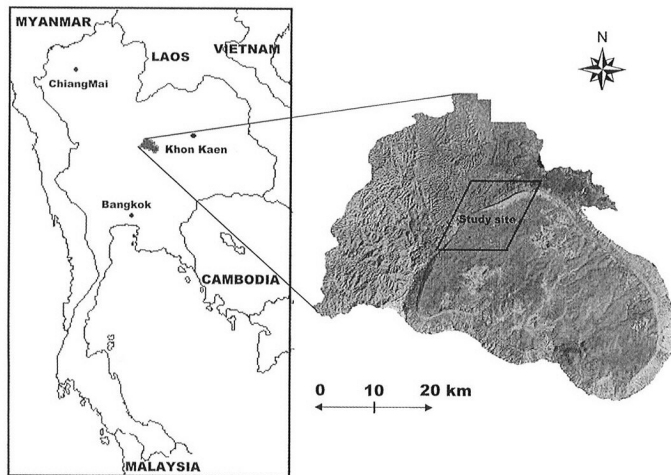
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Fig. 1.—Phu Khieo Wildlife Sanctuary and the study site in north-central Thailand.

in the northeast (Elliott 2001). The Western Issan Forest Complex, Khao Yai National Park, and Pang Sida National Park are the only large forest blocks remaining in the region. These areas represent critical habitat for clouded leopards and other rare felids in Thailand. We report the results of a field study of clouded leopards, Asiatic golden cats, and a marbled cat in north-central Thailand. The goal of this study was to investigate natural history of the clouded leopard, Asiatic golden cat, and marbled cat. Specific objectives included estimating annual and seasonal range size, intraspecific overlap, daily movements, activity patterns, and diet of these cats.

MATERIALS AND METHODS

Study site.—This study was conducted in Phu Khieo Wildlife Sanctuary, Thailand (16°5′–16°35′N, 101°20′–101°55′E; Fig. 1). Phu Khieo encompassed 1,560 km² of forests within the larger 4,550-km² Western Issan Forest Complex (Kumsuk et al. 1999), thus representing the largest protected area within the north-central region.

Phu Khieo was dominated by a mixed evergreen forest on an 800- to 1,100-m-elevation plateau. Topography consisted primarily of forested hills rising westward into mountains. Vegetation classified from a 1999 Landsat Thematic Mapper satellite image comprised dry and hill evergreen forest (75%), mixed deciduous forest (13%), dry dipterocarp forest (4%), bamboo (4%), grassland (3%), and a forest plantation (1%—Anonymous 2000). Grassland communities were patchy and dominated by the 3-km² Thung Kha Mang grassland near the sanctuary headquarters.

The climate of Phu Khieo was strongly influenced by seasonal monsoons. There were 2 distinct seasons, a wet season (April–October) and a dry season (November–March). Mean annual precipitation was 140 cm, with 90% occurring during June–October (Kumsuk et al. 1999). Annual mean temperature was 21°C (range −3 to 37°C). The 200-km² study area was located in the north-central portion of the sanctuary (Fig. 1). This area included the main park road, Thung Kha Mang Headquarters, smaller trails, the Phrom River, and several perennial streams. Site selection was based on its central location within the sanctuary, abundant carnivore sign, and low tourism use.

Phu Khieo was 1 of 3 protected areas in Thailand that did not contain a permanent human settlement (Kekule 1999). Before establishment of Phu Khieo as a sanctuary in 1979, parts of the area were under agricultural cultivation from 3 small villages and various logging camps (Natural Resources Management Section 2000). The Thung Kha Mang grassland was a remnant of an abandoned agriculture area vacated by farmers when Phu Khieo was established as a wildlife sanctuary.

The carnivore community of Phu Khieo is diverse, numbering 30 species. Eight sympatric felid species have been recorded: tiger (*Panthera tigris*), leopard, clouded leopard, Asiatic golden cat, fishing cat (*Prionailurus viverrinus*), jungle cat (*Felis chaus*), marbled cat, and leopard cat (Kumsuk et al. 1999). Tiger and leopard sign were observed least often (Lynam et al. 2001; L. I. Grassman, in litt.), whereas leopard cat presence was more commonly noted (Grassman 2004).

Hunting by local people in the study site was opportunistic and typically included birds, primates, small mammals, and deer (L. I. Grassman and K. Kreetiyutanont, in litt.). Illegal collection of aloewood (*Aquilaria crassna*) coupled with hunting often entailed large numbers of people in the forest for extended periods and was of particular conservation concern during the study period.

Trapping.—Felid trapping was conducted intermittently from 18 September 1998 to 28 November 2002. Animal handling protocol followed Texas A&M University–Kingsville and American Society of Mammalogists guidelines (Animal Care and Use Committee 1998). Five locally constructed wooden log box traps (250 × 90 × 100 cm) and 45 steel mesh box traps (150 × 40 × 50 cm) were used to capture felids. Traps consisted of a single door opening tripped by a foot treadle. Live domestic chickens were used as bait and placed in a separate, protective compartment attached to the end of the trap.

Traps were set along the main road, trails, and riverbanks where felid sign occurred in the form of tracks, feces, or scrapes. Camera-trap photographs of felids were used to identify sites for box-trap placement. Traps were visited daily to feed and water the bait chickens and check for captured carnivores. Traps were moved to a new location if no captures occurred after 1–2 months.

Captured felids were anesthetized with an intramuscular injection of tiletamine hydrochloride (Zoletil, Virbac, Ltd., Carros, France) at 10–15 mg/kg, or with a mixture of ketamine hydrochloride (Calypso, Gideon Richter, Ltd., Budapest, Hungary) and xylazine hydrochloride (Tranquivid®, Ben Venue Laboratory, Inc., Bedford, Ohio) at 10–25 mg/kg and 1–2 mg/kg, respectively (Grassman et al. 2004a). Sedated felids were aged, measured, weighed, radiocollared, and photographed. We also collected ectoparasites, and hair and blood samples for genetic analysis for a concurrent study (Grassman et al. 2004b). If abrasive injuries were present, a topical antiseptic was applied (Duphacycline, Fort Dodge Animal Health, Ltd., Southampton, United Kingdom). Felids received a multivitamin injection (Biocatalin, Fatro, Ltd., Bologna, Italy) to mitigate capture stress.

Individuals were aged by using tooth wear, body size, evidence of sexual development and previous births, and overall body condition. Four age classifications were assigned: juvenile, subadult, adult, and old adult. After data collection and collaring, felids were returned to the trap for recovery and released when reflexes and natural behavior returned (about 2–4 h later).

Radiotelemetry.—Clouded leopards and Asiatic golden cats were fitted with a 120-g radiocollar and a marbled cat was fitted with a 55-g radiocollar (Advanced Telemetry Systems, Inc., Isanti, Minnesota). Radiocollar frequency was 148–149 MHz, and each transmitter contained an activity switch activated by animal movements. An internal lithium battery provided a constant pulse signal for 9–18 months.

Radiotracking occurred primarily on the ground with either a handheld 3-element antenna or a large, vehicle-mounted null

antenna (Kenward 2001). Triangulation bearings (≥3 bearings) were taken from receiver locations determined by a handheld global positioning system (GPS—Garmin International, Inc., Kansas City, Kansas). Hilltop stations frequently were used for establishing initial bearings when a radiosignal could not be received at lower elevations. Radiotracking by helicopter was occasionally used for determining the general location of missing animals. Signal range varied from 1 to 15 km depending upon elevation and obstruction of the terrain.

We attempted close approaches of radiocollared felids for visual observation of the individual to determine if it was feeding on a kill and to record the habitat used by the cat. Because of the difficulty of walking through dense vegetation on a straight-line bearing, close approaches were only attempted when triangulation indicated that the cat was <1 km from the road or trail.

Radiotelemetry error was assessed with a GPS by identifying the location of 20 radiotransmitters placed by another person within the forest (Blankenship 2000; Kenward 2001). Distances between the hidden transmitter and receiver were >1 km. Mean distance between triangulated locations and GPS locations indicated a mean triangulation error of 68 m ($n = 20$, ± 62 m *SD*, range 12–225 m).

Spatial patterns.—Independence of locations was assumed by using only 1 location during each 24-h period. Animal locations were determined from triangulation of bearings by using the LOAS software program (Ecological Software Solutions, Inc., Sacramento, California). Ranges were analyzed by using the 95% and 100% minimum convex polygon estimators (Mohr 1947), and the 95% fixed-kernel estimator with the Animal Movement Extension (Hooge and Eichenlaub 2000) of Arc View (version 3.2, Environmental Systems Research Institute, Inc., Redlands, California). Several range estimators enabled comparisons with other studies. Core areas were generated by using 50% of locations after outlier removal (Hooge and Eichenlaub 2000). Overlap comparisons were calculated by averaging percentage overlap between intra- and intersexual pairs of 95% minimum convex polygon annual ranges. Daily movements were calculated by measuring the linear distance between consecutive daily locations (Bailey 1993; Rabinowitz 1989). Because of varying topography and a nonlinear route followed by felids, the distances covered between consecutive days were greater than expressed (Bailey 1974).

Vegetation types were delineated on a Royal Thai Survey Department 1:50,000-scale topographic map from Satéllite Probatoire d'Observation de la Terre (SPOT) satellite imagery obtained March 1992. Three vegetation types were delineated within the study site: closed forest, open forest–grassland, and abandoned orchard. Habitat use was compared to availability with a chi-square goodness-of-fit test to compare the observed number of telemetry locations in each vegetation type to the expected number. If the chi-square test indicated significant vegetation selection, a Bonferroni Z-test 95% confidence interval was calculated to determine which type was selected or avoided (Byers et al. 1984; Neu et al. 1974). This method was used because of its widespread use in ecological studies and because the recommended number (≥50) of observations per animal required to adequately test the model was met (Alldredge and Ratti 1986). We recognize that we violate the assumption of independence of observation because we use multiple observations per animal, but the small samples of individual cats precluded the use of individuals as the experimental unit.

Activity patterns and temporal segregation.—Activity for each radiocollared cat was determined by variation in pulse volume and cadence of the transmitter. We assumed that 15 min satisfied independence of observation between activity readings (Crawshaw and Quigley 1989; Rabinowitz and Nottingham 1986). Activity was sampled intermittently up to a 24-h duration.
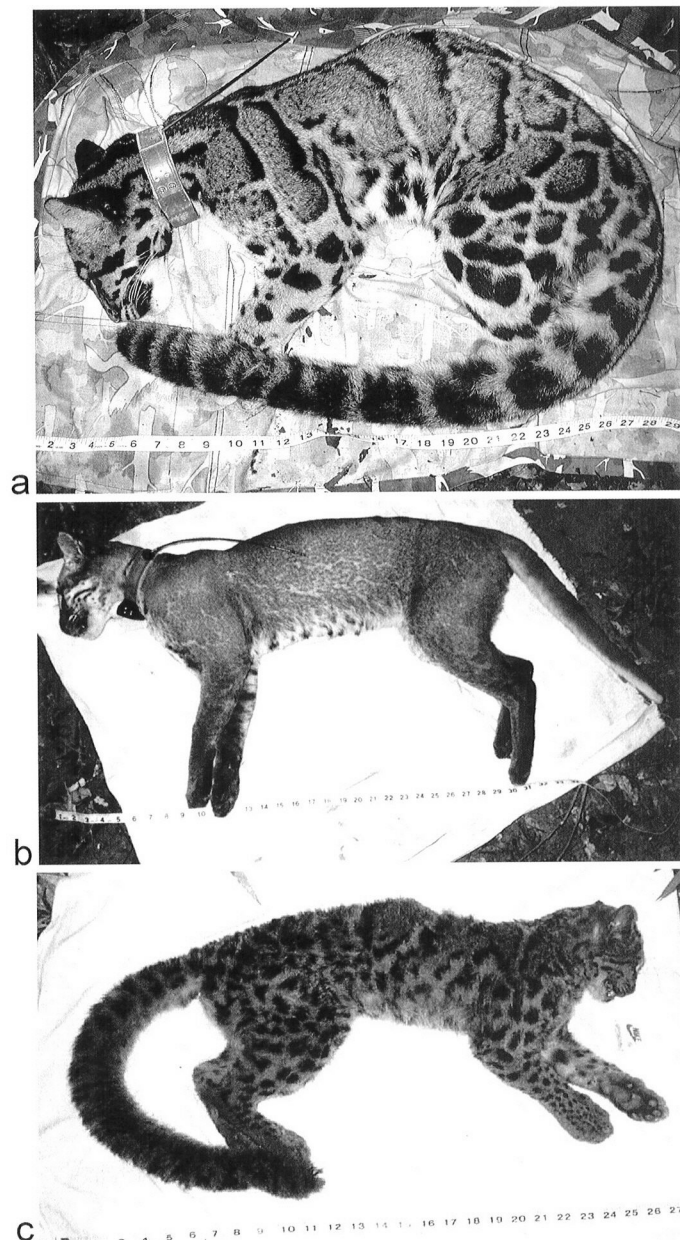

FIG. 2.—Anesthetized felids used in the study. a) Clouded leopard female CF2, b) Asiatic golden cat male GM1, and c) marbled cat female MF1. Scale in inches (1 inch = 2.54 cm).

Temporal segregation among clouded leopards was examined by sex and season. Comparisons were made by using the average percentage of time spent active by individual clouded leopards per season. We included ± 1 *SD* and range with the means.

Data were checked for normality and tested with an independent *t*-test if normal or a Mann–Whitney *U*-test if not normal (SPSS for Windows, version 11.0, SPSS, Inc., Chicago, Illinois). Statistical significance was determined at $P \leq 0.05$.

Food habits.—Felid diet was determined by scat analysis and identification of prey carcasses. Scats in the field were identified and matched to cat species by the presence of tracks, scrapes, and scat diameters. Mean fecal diameter for small- to medium-sized felids was used to classify scat in the field (Grassman 1997). Because of the

TABLE 1.—Physical parameters of study clouded leopards, Asiatic golden cats, and a marbled cat in Phu Khieo Wildlife Sanctuary, Thailand.

Species	Identification number	Sex	Age class		Body measurements				
				Weight (kg)	Head and body length (cm)	Tail length (cm)	Right hind-foot length (cm)	Ear length (cm)	Upper right canine length (mm)
Clouded leopard	CM1	Male	Subadult	12	99	72	18	6	30
	CM2	Male	Adult	16	98	67	18.5	6	32
	CF1	Female	Adult	13.5	82	74	15.5	5	25
	CF2	Female	Subadult	10.5	86	71	15.5	6	23
Asiatic golden cat	GM1	Male	Adult	13.5	91	41	18	5.5	16
	GF1	Female	Adult	7.9	77	39.5	15.5	—	13
Marbled cat	MF1	Female	Adult	3.7	62	53	12.5	5	10

potential for confusing scats of small cats with those of other nonfelid species, only those samples accompanied by felid tracks were used. Most scats of clouded leopards and Asiatic golden cats were pooled as being from "medium-sized cats" because of size similarities, whereas scats from trapped individuals and observation of cat kills were attributed to the specific felid.

Scats were washed over 1-mm wire mesh with tap water to separate hair, bone, and other contents. Hair samples were mounted on microscopic slides to compare the cuticular and medullar characteristics with known specimens in a reference collection (Baker et al. 1993; Reynolds and Aebischer 1991). Number of prey species found in a scat was based upon body parts or hairs found, and it represented a minimum estimate. Prey use was recorded as frequency of occurrence and live weight (Emmons 1988; Rabinowitz 1989). Live weight was averaged from values reported by Lekagul and McNeely (1977) and measurements of intact carcasses.

RESULTS

Trapping.—We accumulated 27,928 trap-nights, with 456 captures of 31 vertebrate species (Appendix I). Seventeen carnivore species were captured, including 4 species of cats.

Clouded leopard.—Between April 2000 and February 2003, 2 adult male and 2 adult female clouded leopards were captured, radiocollared, and tracked for 7–17 months (Fig. 2). Clouded leopard female CF1 was pregnant when captured and classified as late term (>2 months into pregnancy). Clouded

leopards exhibited complete dentition and excellent physical condition (Table 1).

We used 330 radiolocations to calculate range size for the 4 clouded leopards. Overall, range sizes (95–100%) varied from 22.9 to 51.0 km^2, with no obvious difference between sexes (Table 2). Ranges encompassed small core areas ($\bar{X} = 6.0$ km^2 $\pm$ 2.1 SD, range 3.6–8.8 km^2). Each clouded leopard range overlapped a conspecific with the greatest range of overlap occurring between males and females ($\bar{X} = 31\%$ $\pm$ 28 SD, range 11–83%; Fig. 3). However, intramale overlap also was considerable (31% and 47%). Radiocollared clouded leopards were located 110 times on consecutive days, with only 1 location showing no movement. Distances between consecutive-day locations averaged 1,932 m ($\pm$ 1,497 m, range 122–7,724 m; Table 3).

Clouded leopard ranges encompassed 3 vegetation types: closed forest (83.9% coverage), open forest–grassland (15.7% coverage), and abandoned orchard (0.4% coverage), in addition to major streams and the main paved road. Distributions of clouded leopard locations were relatively uniform, with the exception of clouded leopard female CF1, whose locations were clumped around a likely den area in the closed forest. Female clouded leopards used vegetation types in proportion to occurrence ($\chi^2 = 2.1$, $d.f. = 2$, $P > 0.10$); however, male clouded leopards did not use habitat proportionally ($\chi^2 = 18.4$, $d.f. = 2$, $P < 0.001$). Clouded leopard male CM1 used closed

TABLE 2.—Mean annual ranges (km^2) of felids by using the 100%, 95%, and 50% minimum convex polygon and 95% and 50% fixed-kernel estimators in Phu Khieo Wildlife Sanctuary, Thailand, from February 1999 to February 2003.

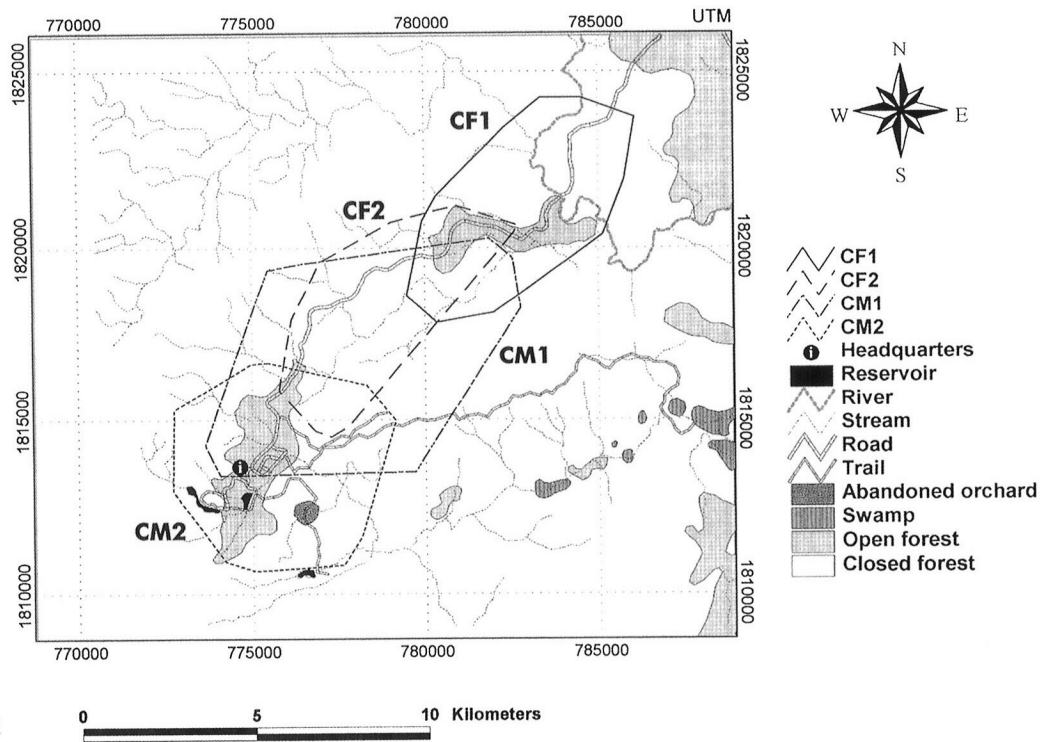| Species	Identification number	Sex	Locations (n)	Home range estimator (km^2)				
				Minimum convex polygon			Fixed-kernel	
				100%	95%	50%	95%	50%
Clouded leopard	CM1	Male	62	51	45.1	3.6	35.5	3.1
	CM2	Male	70	34.4	29.7	8.8	43.5	4.3
	CF1	Female	133	31	25.7	5.2	33.6	5.9
	CF2	Female	65	31.1	22.9	6.4	39.7	7.5
Asiatic golden cat	GM1	Male	85	82.5	47.7	12.3	73.3	11.1
	GF1	Female	69	33.4	32.6	10	58.4	16.2
Marbled cat	MF1	Female	23	5.9	5.3	1	11.9	1.5

FIG. 3.—Clouded leopard annual ranges (95% minimum convex polygon estimator) in Phu Khieo Wildlife Sanctuary, Thailand (April 2000 to February 2003). CF = females, CM = males, as described in Table 1.

forest proportionally more ($\chi^2 = 6.0$, $d.f. = 1$, $P < 0.02$; Bonferroni Z-test 95% confidence interval $0.945 < p_1 < 1.000$, expected: 0.881) than open forest–grassland. Clouded leopard male CM2 was located in open forest–grassland habitat more than expected ($\chi^2 = 12.4$, $d.f. = 2$, $P < 0.01$; Bonferroni Z-test 95% confidence interval $0.290 < p_2 < 0.544$, expected: 0.238). All recorded locations of clouded leopard male CM2 ($n = 24$) in open forest–grasslands occurred at night. It used the grasslands at night for hunting hog deer (*Axis porcinus*) and muntjak (*Muntiacus muntjak*), which were observed to bed down en masse after sunset. This clouded leopard was located on 8 occasions resting along the forest edge before venturing into the grasslands at night.

Clouded leopards were active during 1,421 (58%) of 2,433 activity readings. No significant ($P > 0.05$) differences were found in activity between male (57%) and female (59%) clouded leopards. Also, no significant seasonal variation was found in activity between the wet (60%) and dry (57%) seasons

($P > 0.05$). Highest average monthly activity (71%) was recorded during October and lowest activity (50%) was recorded during January. Diel activity patterns indicated that clouded leopards exhibited arrhythmic activity, with peak activity occurring between 0801–1200 h ($\bar{X} = 70\%$) and 1801–2000 h ($\bar{X} = 69\%$; Fig. 5). Nocturnal activity peaks were observed between 2001–2200 h and 0001–0200 h ($\bar{X} = 66\%$).

Close approach for a direct observation of a clouded leopard by using radiosignals was successful only once. Clouded leopard female CF2 was approached at 1115 h until it jumped from a large, low (about 3.0 m) evergreen tree branch in which it was resting. Directly under this position were the remains of a recently killed Malayan pangolin (*Manis javanica*). From the beginning of the close approach until the observation, the radiosignal pulse indicated that this individual was resting in the tree before our disturbance and was not driven up the tree.

Examination of a dead male hog deer found in grasslands near the previous night location of clouded leopard male CM2

TABLE 3.—Mean daily distances (m) traveled by felids in Phu Khieo Wildlife Sanctuary, Thailand, from February 1999 to February 2003.

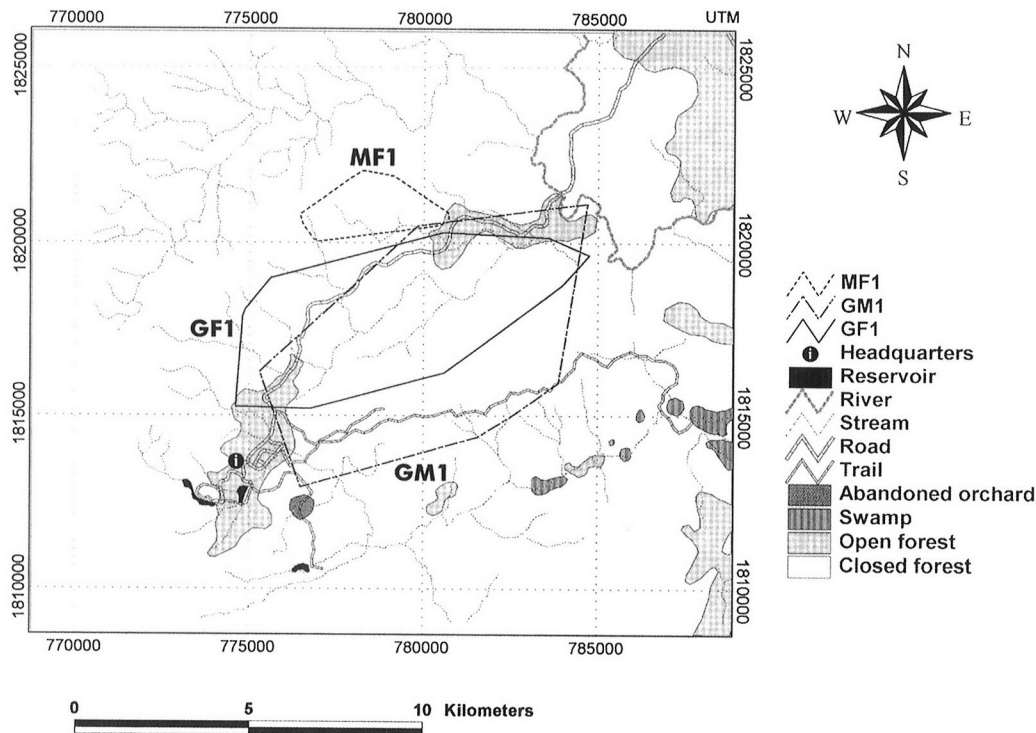| Species	Sex	No. animals	Dry season			Wet season		
			Mean ± *SD*	No. locations	Range	Mean ± *SD*	No. locations	Range
Clouded leopard	Male	2	2,577 ± 160	2	2,463–2,691	2,232 ± 1,715	26	122–7,724
	Female	2	3,380 ± 1,970	13	455–7,178	1,554 ± 1,139	70	1,250–4,254
Asiatic golden cat	Male	1	2,984 ± 1,649	7	1,608–6,082	2,072 ± 2,473	17	638–9,276
	Female	1	894 ± 603	14	55–2,350	1,257 ± 965	21	90–3,006
Marbled cat	Female	1				477 ± 180	18	200–726

FIG. 4.—Marbled cat and Asiatic golden cat annual ranges (95% minimum convex polygon estimator) in Phu Khieo Wildlife Sanctuary, Thailand (February 1999 to June 2001). MF = marbled cat female, GM = Asiatic golden cat male, GF = Asiatic golden cat female, as described in Table 1.

indicated a clouded leopard attack. Examination revealed 2 narrow canine punctures through the spine above the shoulder. The canine punctures were deep (about 3 cm) and separated by 3 cm. In addition, the shoulder and flank of the deer showed several claw scrapes typical of felid attacks. The puncture depth and spacing closely matched the canines of clouded leopard male CM2 (Table 1), or perhaps another clouded leopard.
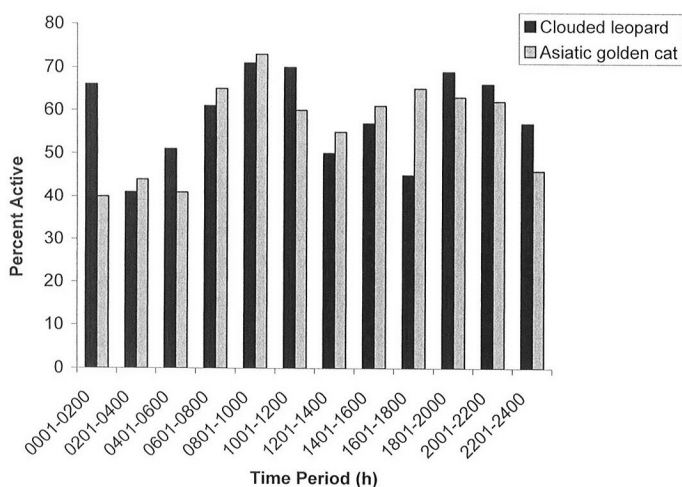

FIG. 5.—Clouded leopard ($n = 4$) and Asiatic golden cat ($n = 2$) cumulative diel activity patterns in Phu Khieo Wildlife Sanctuary, Thailand (February 1999 to February 2003).

Asiatic golden cat.—Between February 1999 and November 2000, 1 adult male and 1 adult female Asiatic golden cat were captured, radiocollared, and tracked for 12 and 16 months, respectively (Fig. 2). The female exhibited a high degree of melanism, with dark brown pelage, whereas the male was light brown. Except for the female being blind in 1 eye from a previous trauma, both cats appeared healthy (Table 1).

We collected 154 radiolocations for these cats to calculate range size. Fifty-three percent of the range of Asiatic golden cat male GM1 encompassed 78% of the range of Asiatic golden cat female GF1 (Fig. 4). Asiatic golden cats were located 55 times on consecutive days and traveled a daily mean of 1,597 m ($\pm$ 1,674 m, range 55–9,276 m; Table 3). They used habitat (closed forest 95% and open forest–grassland 5%) in proportion to occurrence ($\chi^2 = 0.3$, $d.f. = 2$, $P > 0.10$), and locations were uniformly distributed.

Asiatic golden cats were active during 569 (56%) of 1,015 activity readings. Daily activity levels indicated that they exhibited arrhythmic activity dominated by crepuscular and diurnal patterns, with activity peaks occurring between 0801–1000 h and 1601–1800 h ($\bar{X} = 69\%$; Fig. 5). The greatest numbers of inactive periods were scattered throughout late night (0001–0200 h and 0401–0600 h, $\bar{X} = 40\%$ activity) time periods. Highest mean monthly activity (79%) was recorded during July, whereas the lowest activity (46%) was recorded during March.

Marbled cat.—One female marbled cat was captured, radiocollared, and tracked for 1 month (May–June 2001; Tables 2 and

3; Figs. 2 and 4). This individual was an old adult that appeared healthy but underweight, as indicated by this cat's lean musculature and protruding hip and rib bones (Table 1). Physical examination indicated no evidence of previous births. This marbled cat moved consistently westward toward mountainous terrain until the radiosignal could not be received. Subsequent radiotracking from a helicopter failed to locate this individual again. The marbled cat was active during 84 (46%) of 181 activity readings. Data were insufficient to characterize activity patterns.

Diet.—Analysis of 21 scats and 2 observations indicated that medium-sized cats consumed at least 9 species (Table 4) that consisted of terrestrial and arboreal mammals. Confirmed prey for clouded leopards included hog deer, slow loris (*Nycticebus coucang*), bush-tailed porcupine (*Atherurus macrourus*), Malayan pangolin, and Indochinese ground squirrel (*Menetes berdmorei*). One confirmed scat of an Asiatic golden cat contained the remains of Indochinese ground squirrel. Small mammals ($\leq$ 2.5 kg) constituted 78% frequency of occurrence, with an important murid component (39%). No scats were attributed to marbled cats.

DISCUSSION

Range sizes of clouded leopards in our study were similar to those calculated (95% fixed-kernel) by Austin (2002) for a female (39.5 km^2) and a male (42.2 km^2) clouded leopard in Khao Yai National Park, Thailand. However, core areas (50% fixed-kernel) for clouded leopards in Phu Khieo were larger ($\bar{X} = 5.2$ km^2) than for clouded leopards in Khao Yai ($\bar{X} = 2.9$ km^2). Prey availability and foraging activity are considered major factors influencing range size in cats (Goszczynski 1986; Norton and Henley 1987; Seidensticker 1976). Clouded leopards in our study area traveled twice the daily distance ($\bar{X} = 2,039$ m) of clouded leopards in Khao Yai National Park (Austin 2002), although range sizes were similar.

We believe female clouded leopard CF1 gave birth soon after capture and its small core area was probably related to den use. Clouded leopard young are reported to den in tree hollows (Prater 1965), but nothing else is known about rearing habits in the wild (Sunquist and Sunquist 2002). We used telemetry and close approach to identify the area of the potential den site but failed to locate cubs. A search within a 200-m radius identified a large impenetrable thicket of dead branches from several fallen trees and vegetation that may have contained a den.

Asiatic golden cats had larger ranges than clouded leopards, although they were similar in body size. In contrast to clouded leopards, Asiatic golden cat movements were not clustered around small core areas and space use within the home range was relatively uniform. Mean daily-movement distances (1,717 m) and activity (56%) were similar to those of clouded leopards.

Low densities of tigers and leopards may have influenced clouded leopard and Asiatic golden cat movements and distributions. Seidensticker (1976) demonstrated how coexistence between tigers and leopards in Nepal was likely related to social dominance, a diverse prey base, and dense vegetation structure. These same criteria may have shaped spatial patterns

TABLE 4.—Prey species identified from scats of clouded leopards, Asiatic golden cats, and "medium-sized cats" ($n = 21$) and from confirmed kills ($n = 2$) in Phu Khieo Wildlife Sanctuary, Thailand, from February 1999 to February 2003.

Prey species	n	Live mass (kg)[a]	Frequency of occurrence	Source
Muntiacus muntjak	2	24.0	8.6	Field
Axis porcinus	1	40.0	4.3	Observation[b]
Trachypithecus	1	7.5	4.3	Field
Nycticebus coucang	2	1.5	8.7	Trap[b]
Tragulus javanicus	1	1.3	4.3	Field
Atherurus macrourus	3	2.5	13.0	Trap,[b] field
Manis javanica	1	6.0	4.3	Observation[b]
Menetes berdmorei	3	0.1	13.0	Field,[b] trap[c]
Muridae	9	0.1	39.1	Trap,[b] field
Total	23			

[a] Averaged from the work of Lekagul and McNeely (1977) and intact carcass measurements.
[b] Confirmed clouded leopard.
[c] Confirmed Asiatic golden cat.

of medium-sized felids and their coexistence with tigers and leopards in Phu Khieo. In Huai Kha Khaeng Wildlife Sanctuary, Thailand, where the largest population of tigers and leopards existed, clouded leopard presence was low (Rabinowitz 1991; N. Bhumpakphan, pers. comm.), indicating that the presence of other large cats may shape clouded leopard densities.

Intersexual overlap for clouded leopards and Asiatic golden cats was expected because most social systems of solitary felids include such overlap (Sandell 1989). Similar to our results, Austin (2002) observed overlapping ranges of >50% between a male and female clouded leopard. However, extensive overlap between 2 male clouded leopards ($X = 39\%$) was unexpected because both individuals were mature and had established ranges. This overlap between males suggests a high degree of social tolerance, possibly between 2 related individuals or because the complexity of the habitat made it disadvantageous to invest heavily in territorial defense (Crawshaw and Quigley 1991). Significant overlap between males in other large cats has been observed for jaguars (*Panthera onca*) and leopards (Crawshaw and Quigley 1991; Grassman 1999). However, our small sample size prevented clear patterns of habitat preferences for male clouded leopards.

Clouded leopards are generally believed to occur in primary evergreen forests (Nowell and Jackson 1996; Sunquist and Sunquist 2002), but they also have been reported in secondary, logged forests (Rabinowitz et al. 1987), coastal hardwood forests and coniferous forests (Rabinowitz 1988), and in grasslands (Santiapillai and Ashby 1988). We documented individual preferences of males for open- or closed-forest habitats. Austin (2002) recorded use of semievergreen forest (closed forest) by a female clouded leopard more than available in proportion to other habitat types.

A combination of terrestrial camera-trap photos (Lynam et al. 2001; Royal Forest Department, in litt.), personal observations, and livetrapping suggested that clouded leopards traveled on the ground more than previously reported in the literature.

Sunquist and Sunquist (2002) stated that clouded leopards are able to hunt on the ground, but large terrestrial predators may cause clouded leopards to hunt more arboreal prey. Tiger and leopard densities were low in Phu Khieo, whereas dholes (*Cuon alpinus*) were more common (Grassman et al., in press). Dholes were observed individually and in packs on numerous occasions. Clouded leopards and Asiatic golden cats would likely avoid confrontations with this dominant predator and their movements may have been influenced by dhole presence.

Results of scat analysis indicated a diverse prey selection for clouded leopards and "medium-sized cats." Clouded leopards in our study consumed diurnal and nocturnal prey, which is consistent with our data on clouded leopard activity patterns. A high proportion of large daily movements may have indicated that small prey were eaten more often than large prey, which would have resulted in more consecutive days with minimal movements. Scat analysis from 2 trapped clouded leopards contained the remains of slow loris, a nocturnal primate, whereas diurnal prey also were identified in scats of clouded leopards and "medium-sized cats." The diet of Asiatic golden cats has been described as mammals ranging in size from a rat to a muntjak (Lekagul and McNeely 1977; Nowell and Jackson 1996). Terrestrial prey were recorded for an Asiatic golden cat in Phu Khieo (Indochinese ground squirrel) and from south-central Thailand (grass snake [*Natrix* spp.]—Grassman 1998).

The marbled cat remains perhaps the most enigmatic small felid of mainland Southeast Asia. Capture of the marbled cat was unexpected because this species was not listed in the most recent mammal list for Phu Khieo (Kumsuk et al. 1999). In addition to the radiocollared individual, marbled cats were observed on 2 other occasions. An individual was observed for about 5 s on a trail in hill evergreen forest at 0900 h. On another occasion, a pair of adult marbled cats was observed for several minutes walking through a large salt lick (Grassman and Tewes 2002). A long-term camera-trapping effort failed to photograph this felid in Phu Khieo.

The climbing and balance of the marbled cat has been observed in captivity (Leyhausen 1979; F. Rocca, pers. comm.), suggesting a semiarboreal existence similar to that of the clouded leopard. Observations in the wild have indicated arboreal and terrestrial habits (Choudhury 1996; Conforti 1996; Grassman and Tewes 2002). Results from our study yielded only minimal information on the natural history of this species. Marbled cat density may have been low, as suggested by the failure to capture additional individuals in box traps and camera traps. Future surveys and field studies are vital to clarify the status of this cat in the wild.

This study contributed to an understanding of the natural history of 3 relatively unstudied Asian felids. Clouded leopard, Asiatic golden cat, and marbled cat populations in Phu Khieo are threatened by habitat loss, poaching, and illegal aloewood collection. Management and conservation planners should consider the results of this study for future conservation strategies. More research with a greater sample size of individuals is needed to clarify the ecology of and threats to these species regionwide.

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APPENDIX I

Livetrapping results from Phu Khieo Wildlife Sanctuary, Thailand, from September 1998 to November 2002 ($n = 27,928$ trap-nights).

Common name	Species	No. captures
Carnivores		
Dhole	*Cuon alpinus*	3
Asiatic jackal	*Canis aureus*	1
Asiatic black bear	*Ursus thibetanus*	2
Back-striped weasel	*Mustela strigidorsa*	2
Yellow-throated marten	*Martes flavigula*	40
Burmese ferret badger	*Melogale personata*	5
Large Indian civet	*Viverra zibetha*	68
Small Indian civet	*Viverricula indica*	10
Common palm civet	*Paradoxurus hermaphroditus*	24
Masked palm civet	*Paguma larvata*	5
Binturong	*Arctictis binturong*	31
Three-striped palm civet	*Arctogalidia trivirgata*	1
Javan mongoose	*Herpestes javanicus*	9
Leopard cat	*Prionailurus bengalensis*	69
Asiatic golden cat	*Catopuma temminckii*	6
Marbled cat	*Pardofelis marmorata*	1
Clouded leopard	*Neofelis nebulosa*	4
Other Mammals		
Pig-tailed macaque	*Macaca nemestrina*	1
Assamese macaque	*M. assamensis*	1
Hoary bamboo rat	*Rhizomys pruinosus*	5
Malayan porcupine	*Hystrix brachyura*	4
Birds		
Red junglefowl	*Gallus gallus*	42
Scaly-breasted partridge	*Arborophilia chloropus*	1
Spotted dove	*Streptopelia chinensis*	2
Besra	*Accipiter virgatus*	1
Blue pitta	*Pitta cyanea*	1
Reptiles		
Yellow tortoise	*Indotestudo elongata*	3
Leaf turtle	*Cyclemys dentata*	1
Red-eared terrapin	*Trachemys scripta*	1
Bengal monitor	*Varanus bengalensis*	31
Water monitor	*V. salvator*	81
Total		456