Population Density, Home Range, and Habitat Use of Crested Serpent-Eagles (Spilornis cheela hoya) in Southern Taiwan: Using Distance-Based Analysis and Compositional Analysis at Different Spatial Scales

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POPULATION DENSITY, HOME RANGE, AND HABITAT USE OF CRESTED SERPENT-EAGLES (*SPILORNIS CHEELA HOYA*) IN SOUTHERN TAIWAN: USING DISTANCE-BASED ANALYSIS AND COMPOSITIONAL ANALYSIS AT DIFFERENT SPATIAL SCALES

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ABSTRACT.—For many tropical raptors, studies of population density and habitat use are still lacking. We used radio-tracking to study population density, home-range size, and habitat use of the Formosan Crested Serpent-Eagle (*Spilornis cheela hoya*) in Kenting National Park, southern Taiwan, during 1995–1997 and 1998–2007. Over two years, we documented a minimum population density of 2.69 individuals/km^2, which is one of the highest ever reported. Home ranges calculated using minimum convex polygons and 95% fixed kernel areas averaged 12.34 km^2 and 2.86 km^2 ($n = 18$), respectively. Core areas represented by the 50% fixed kernel areas averaged 0.41 km^2. We used distance-based analysis and compositional analysis to compare habitat use within the entire study area and the home ranges. Both methods indicated the overwhelming use (>90%) of somewhat degraded and semi-open mixed forests, followed by the use of *Acacia confusa* forests and grasslands to a much lesser degree. Habitat use was nonrandom both within the study area and the home range, as mixed forests covered only 24.4% of the study area. Many perch sites were near the primary monsoon forest, which was, however, almost never used for hunting. As many other species of serpent-eagles are threatened by habitat loss and human persecution, our study provides valuable information for their future monitoring and management.

KEY WORDS: *Crested Serpent-Eagle*; Spilornis cheela hoya; *core area*; *habitat preference*; *habitat selection*; *home range*; *Taiwan.*

DENSIDAD POBLACIONAL, ÁMBITO DE HOGAR Y USO DE HÁBITAT DE *SPILORNIS CHEELA HOYA* EN EL SUR DE TAIWÁN: UTILIZANDO ANÁLISIS BASADOS EN DISTANCIAS Y ANÁLISIS DE COMPOSICIÓN A DIFERENTES ESCALAS ESPACIALES

RESUMEN.—Todavía faltan estudios de densidad poblacional y uso de hábitat para muchas rapaces tropicales. Utilizamos radio transmisores para estudiar la densidad poblacional, el tamaño del ámbito de hogar y el uso de hábitat de *Spilornis cheela hoya* en el Parque Nacional Kenting, sur de Taiwán, durante 1995–1997 y 1998–2007. A lo largo de dos años documentamos una densidad poblacional mínima de 2.69 individuos/km^2, la

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cual es una de las más altas jamás reportadas. Los ámbitos de hogar calculados utilizando polígonos convexos mínimos y las áreas de kernel fijo de 95% promediaron 12.34 km^2 y 2.86 km^2 (n = 18), respectivamente. Las áreas núcleo representadas por el 50% de las áreas de kernel fijo promediaron 0.41 km^2. Utilizamos análisis basados en las distancias y análisis composicionales para comparar el uso del hábitat dentro de toda el área de estudio y de los ámbitos de hogar. Ambos métodos indicaron el abrumador uso (>90%) de los bosques mixtos algo degradados y semi-abiertos, seguidos en un grado mucho menor por el uso de bosques de *Acacia confusa* y pastizales. El uso del hábitat no fue al azar tanto dentro del área de estudio como en el ámbito de hogar, a la vez que los bosques mixtos cubrieron sólo el 24.4% del área de estudio. Muchos sitios de percha se ubicaron cerca del bosque monzónico primario, el cual sin embargo, nunca fue utilizado para cazar. Debido a que muchas especies de *Spilornis* están amenazadas por pérdida de hábitat y persecución humana, nuestro estudio provee información valiosa para su futuro manejo y monitoreo.

[Traducción del equipo editorial]

Raptors of the genus *Spilornis* are found only in the Indo-Malay zoogeographical region (Thiollay 1994, Ferguson-Lees and Christie 2001). Among these, the Crested Serpent-Eagle (*Spilornis cheela*) is the most widely distributed (Amadon 1974, Stepanyan 1992). One of its subspecies, the Formosan Crested Serpent-Eagle (*Spilornis cheela hoya*), has the largest body size and is endemic to the island of Taiwan, where it is one of the most widespread and conspicuous raptors (Weick and Brown 1980, Lin 2005, Brazil 2009, Walther et al. 2011, Wu et al. 2014).

For many tropical raptors, habitat loss and fragmentation have contributed to population declines (Thiollay 1993, Bildstein et al. 1998). Although the global conservation status of the Crested Serpent-Eagle is of ''least concern'' according to the IUCN Red List (BirdLife International 2014), populations of some subspecies, such as those found on islands, are endangered because they are found in threatened habitats or have a small distribution or population size (Thiollay 1994, Bildstein et al. 1998, van Balen 1998). Due to past hunting pressure and current development pressure in Taiwan, the Formosan subspecies of the Crested Serpent-Eagle is listed as a ''rare and valuable'' species by the Taiwanese Council of Agriculture and is protected by the Wildlife Conservation Act (1989) of Taiwan.

Raptors generally require extensive areas (Thiollay 1989, Gjershaug et al. 2004, Kaneda et al. 2007), and protecting critical habitats of endemic populations should be a priority for conservation (Real and Mañosa 2001). Although the breeding behavior and habitat preferences of the Crested Serpent-Eagle have been documented for several subspecies across Asia, including those in China, India, Japan, and Taiwan (Morioka 1995, Ueta and Minton 1996, Lin et al. 1998, van Balen 1998, Zhang 2000, Sano 2003, Chou et al. 2004, Chou 2005, 2006, Lin 2005, Nijman 2007), little is known about population density, home-range size, and habitat preferences of the Formosan Crested Serpent-Eagle (but see Chou and Shiu 2007, Chou et al. 2012). Since this knowledge is important for animal ecology (Manly et al. 1993, Conner et al. 2003), population ecology (Newton 1979), and conservation (Bildstein et al. 1998, Thiollay 1998a, Sergio et al. 2008), we used observations and radio-tracking to estimate population density and home-range size and to investigate the habitat use of the Formosan Crested Serpent-Eagle.

METHODS

Study Area. Our study area, Kenting National Park on the Hengchun-Eluanbi peninsula, southern Taiwan (Fig. 1), covers 181 and 152 km^2 of land and sea, respectively. The land area is a moderately hilly (0–300 masl) area that extends from the town of Eluanbi in the south to the Gangkou River in the north. The region has a monsoon climate with 2200 mm annual precipitation (Chen and Chen 2003). The average annual temperature is 24.4°C, highest in July (27.2°C) and lowest in January (19.1°C; Lu et al. 2004).

Historically, the area's forests were disturbed by slash-and-burn farming of early inhabitants. Between 1940 and 1980, wood-cutting by local villagers became the primary cause of forest degradation. After the establishment in 1984 of Kenting National Park, the forests growing on the higher hilly areas regenerated well, and two mostly undisturbed forest communities are now found there: the tropical coastal forest and the tropical monsoon rainforest (Chang et al. 1985, Su 1985). However, Kenting National Park draws about 6 million tourists annually. To serve them, more and more tourist facilities have been built both legally and illegally along the coast and even within the adjacent lower-lying

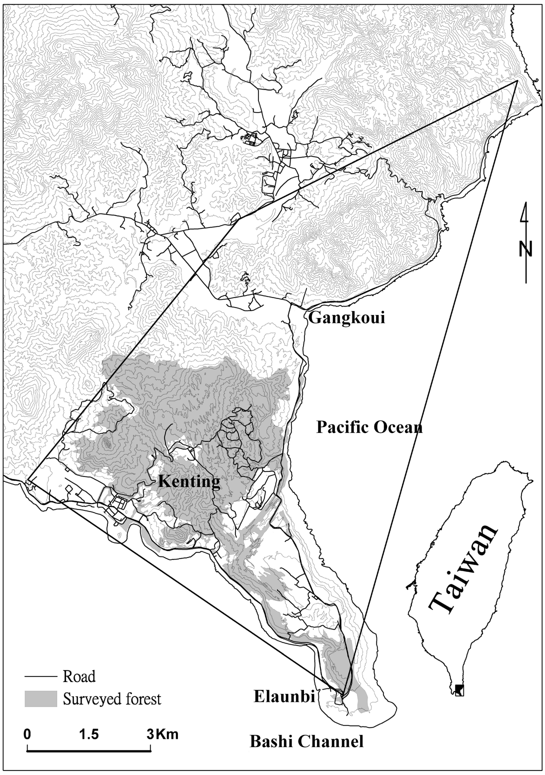

Figure 1. The study area in Eluanbi peninsula, southern Taiwan (the bottom right outline depicts the location of the telemetry study area within the outline of the main island of Taiwan). The area depicted in this figure was determined by surrounding the radio locations of the 18 radio-tracked Crested Serpent-Eagles with an MCP (depicted as a thick black line). The land area within this polygon (51.1 km^2) was used to calculate the available habitat (second-order selection, Table 1). The smaller dark grey area represents the forest study area (combining *Acacia*, dry, mixed, and monsoon forests, Fig. 2) covering 20.1 km^2 in total, which was intensively surveyed for nesting individuals and was also used to calculate population density (see details in Methods). Thin black lines represent streets and roads, and thin grey lines represent topographic lines. The boundaries of the national park are outside of the Figure.

forests, causing increased disturbance (Lee and Lin 2006). Grazing of cattle (e.g., water buffalo [*Bubalus bubalis*]) and Formosan sika deer (*Cervus nippon taiouanus*) have also disturbed the vegetation, creating a mosaic of habitats. As a result, much of the study site is now composed of a mixture of pastures, scrubland, tourist trails and facilities, and somewhat fragmented forest and secondary growth (Su 1985, Chen and Chung 2003).

The Formosan Crested Serpent-Eagle and the Formosan Crested Goshawk (*Accipiter trivirgatus formosae*) are the only nonmigratory diurnal raptor species within the study area. We assume that there was little interspecific competition because both species often nested less than 50 m from each other without any observed aggressive interactions (Chen 1997, Chou 2006). Furthermore, the Formosan Crested Goshawk targets different prey species using active-pursuit hunting, and the serpent-eagle is a typical sit-and-wait predator, usually using perches situated in or along semi-open or open ground to hunt for ground-foraging vertebrates and invertebrates (Chou 2005, Huang et al. 2006, Liu 2011).

Study Area for Determining Population Density. To calculate population density, we chose a small portion of the study area, which was known to have a very high abundance of the Formosan Crested Serpent-Eagle (Chou et al. 2004). This area was naturally bounded on three sides by the ocean, and, in the north, by a river with agricultural and residential areas on both sides (Fig. 1). We then chose interior forests (shown in dark grey in Fig. 1) as the breeding area to be intensively surveyed for nest sites for the following reasons: (1) the vegetation situated along the peninsula's coastline was not suitable because the forest was relatively low in height and also disturbed by various human activities, so that no nest sites were found there during any breeding season despite searches (see below), and (2) we arbitrarily restricted the extent along a trail in the north and west for logistical reasons, because our manpower did not allow for a larger survey area and because a sufficient number of birds for analysis were found within the smaller study area.

Within this smaller defined study area (20.1 km^2), we conducted a survey of territorial pairs and their nests during every breeding season from 1995 to 2007 except 1997 and 1998. During each breeding season (mid-January to late March), two to three researchers (including T.-C. Chou) walked approximately 9 hr per day through the study area to survey almost every individual tree for the presence of nests. Since every tree which could potentially hold a nest (many small trees were not surveyed) was visually examined at least once and usually several times, we consider our survey exhaustive. Furthermore, it is extremely unlikely that, given the observer intensity in the study area (approximately 900 human-hr per breeding season), any eagle flying to and from its nest would have escaped detection. During these 11 breeding seasons, the smaller study area contained 15–20 active territorial pairs (Chou et al. 2004, Chou 2005, Chou 2006, Chou and Shiu 2007, Chou et al. 2012).

To estimate total population density including the nonbreeding individuals, we intensively searched the smaller study area during 2006 and 2007, spending a total of 966 and 873 human-hr, respectively, which were divided evenly across the study area. Knowledge from previous breeding seasons was used to locate historical breeding sites. Nonbreeding individuals (including territorial pairs without nests and floaters) were also counted by monitoring individuals that were identified by molting patterns, uniquely numbered wing tags, metal rings, and/or radio-transmitter signals. As a result, every individual that was uniquely identifiable was observed several times (often almost daily), ensuring that our sampling of identifiable individuals was exhaustive. However, because some nonbreeding individuals could not be identified with certainty, our population estimates should be considered minimum estimates. We calculated the minimum population density by dividing the number of breeding and nonbreeding individuals by the surveyed forest area (20.1 km^2).

Trapping and Radio-tagging. In addition to the breeding survey, we also trapped 26 Crested Serpent-Eagles (8 adults, 6 subadults, and 12 nestlings) for radiotelemetry between 16 June 2004 and 15 May 2007. Methods and mean home-range sizes for 14 of these radio-tagged birds were published in Chou et al. (2012), but are included here because the objectives and analyses of the two studies differ. Sex was determined as described by Chang et al. (2008), and the age of subadults and adults was determined by molt characteristics (Ferguson-Lees and Christie 2001). We trapped the young birds before they fledged from the nests and the adult birds using a bow net or a bal-chatri trap (Berger and Mueller 1959) baited with conger eels (*Conger cinereus*). Every individual was fitted with a metal leg ring, patagial tags, and a backpack-mounted radio transmitter with a built-in action module (AVM Instrument Company Ltd., Colfax, California, U.S.A.). Uniquely numbered vinyl wing tags were fixed to the wings so that they could be read with binoculars. Transmitters, antenna, and harness mass was <40 g total (<3% of mean body mass). We released all birds within 1.5 hr after capture, and we did not observe any obvious differences in individual behavior before and after transmitter fitting. Following the radio-tagging and banding of nestlings, we observed from a blind for 3 d; in all cases, normal parental care continued.

Radio-tracking. We located the radio-tagged birds using a 3-element hand-held Yagi antenna and a portable LA12-Q receiver manufactured by AVM Instrument Company Ltd., Colfax, California, U.S.A. All locations were collected when birds were perched and when triangulation angles were between 45° and 135° to reduce telemetry error. In a pilot test, we found that precise locations of the birds could not be obtained when angles were above the standard triangulation range of between 45° and 135° (Kenward 2001) or when the observer-bird distance was >500 m, due to the often rugged terrain and dense forests.

To avoid erroneous habitat classifications (Samuel and Fuller 1994) due to such locational errors, we instead confirmed locations as follows: after the field researchers had detected the approximate position of each individual, we then decided on the optimal way of tracking the maximum number of individuals on that day. A location was recorded only after one of the researchers had observed the perched individual. The location was then recorded with a Garmin 60CSx GPS unit and on aerial photographic maps. If a perched bird was flushed, we stopped tracking that individual for the remainder of the day to avoid including locations biased by disturbance.

To avoid temporal autocorrelation of location data, we divided our tracking time into three periods: sunrise to 1000 H, 1000–1400 H, and 1400 H to sundown (sunrise varied from 0510 H in summer to 0640 H in winter, and sundown from 1710 H in summer to 1845 H in winter). As recommended by Otis and White (1999), these three time periods were selected based on a study of the Crested-Serpent Eagle's diurnal activity pattern (Liu 2011), which established that individuals usually use the morning period for trips from roosts to foraging locations, the midday period for feeding, and the afternoon period for perching and loafing (see also Chou et al. 2012). If possible, one location per individual per period was taken, but only rarely were three locations taken per day; typically, we took only one or two locations per day. Nevertheless, locations were relatively evenly divided among time periods.

Each individual was followed for 1–5 d per week and for a period of 6–12 mo. Eighteen individuals (five adult males, three adult females, three post-second-year subadult males, three post-second-year subadult female, two juvenile males, two juvenile females) of the total of 26 radio-tagged individuals were (1) tracked for at least three dry and three wet season months during the period from 2 November 2005 to 20 November 2007 and (2) produced ≥30 locations in each season (see also Chou et al. 2012). The remaining eight individuals did not qualify because of transmitter failures (n = 6) or mortality due to human hunting (n = 2). Juveniles had left the nest at least 1.5 months before we began tracking them, when the parents no longer fed them. For these 18 individuals, we obtained 70–316 locations, which was a sufficient sample size for the determination of each individual's home range. All 18 individuals were confirmed to be sedentary within the study area for the entire duration of this study based on their wing-tag identifiers or radio signals. Some of the female individuals also bred in the study area. However, we did not use the locations of the females during the incubation or early brood-rearing period because breeding females are more tied to their nests than males and would skew home-range sizes downward.

Delineation of Habitat Type. A digitized land cover map of the study area was supplied by the Administration Office of Kenting National Park (Fig. 2). This map was digitized using images from the Ikonos satellite and digital aerial orthophotos (40 × 40 cm resolution) which had been ground-truthed by Chen and Chung (2003) and further refined in this study. All researchers were trained before tracking began to ensure that they were able to consistently categorize the habitat types.

Estimation of Home Range. Location data were analyzed using ArcView GIS version 3.2 (ESRI 1996), and fixed kernel area and 100% minimum convex polygon (hereafter, MCP) home-range sizes were constructed using the Animal Movement 2.0 Extension in ArcView GIS version 3.2 (Hooge and Eichenlaub 1997). For each individual, we calculated three types of home ranges; specifically, the MCP, the 95% fixed kernel area and the 50% fixed kernel area (hereafter, 95% FKA and 50% FKA). The MCP and 95% FKA were used as representations of each individual's home range, and the 50% FKA represented core area. We used the default settings in the Animal Movement 2.0 Extension with the least squares cross validation for the smoothing factor to produce the 95% FKA and 50% FKA.

Habitat Selection. We generated an MCP as the polygon representing the combined study area by pooling the locational data of the 18 chosen individuals to create the study population's ''available habitat.'' We then excluded the oceanic areas from this study area. The study area polygon and each individual's 95% FKA and 50% FKA were transferred to ArcView 3.2 and overlaid with the land-cover map layer to determine the type and amount of habitats that were covered by each MCP and FKA. We then calculated the habitat compositions in the study area, and in each 95% FKD and 50% FKD, and the proportion of telemetry locations from each individual within each habitat type.

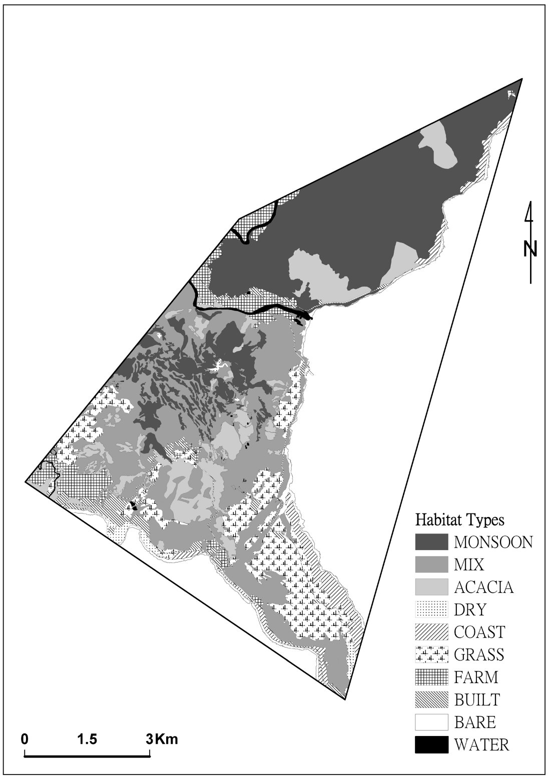

Figure 2. Habitat types available to Crested Serpent-Eagles within the study area. The ten different habitat types and their abbreviations are described in the Appendix.

Analysis of Habitat Use. Two commonly used procedures for the assessment of habitat selection via animal locations are distance-based analysis (Conner and Plowman 2001, Conner et al. 2003) and compositional analysis (Neu et al. 1974, Aebischer et al. 1993). Distance-based analysis (hereafter, DA) is a method based on measuring the Euclidean distance between individual locations and all of the nearest habitat features (Conner et al. 2003). Compositional analysis (hereafter CA) is a method used to categorize animal locations by habitat type and to calculate the proportional use of those habitats

Table 1. MCPs, 50% FKAs, and 95% FKAs (in km^2) of 18 Crested Serpent-Eagles radio-tracked in our study area in southern Taiwan, May 2005–November 2007. Dry season, wet season, and annual estimates are based on all data pooled for each respective time period. To test for significant differences between dry and wet season, we used pairwise Wilcoxon rank sum tests.

	DRY SEASON	WET SEASON			ANNUAL
	MEAN ± SD (RANGE)	MEAN ± SD (RANGE)	*Z*	*P*	MEAN ± SD (RANGE)
Number of locations	134.1 ± 57.1 (39–226)	83.0 ± 37.9 (30–158)			217.2 ± 80.3 (70–316)
Number of days monitored	84.8 ± 38.3 (31–139)	48 ± 18.5 (23–92)			132.8 ± 51.7 (61–228)
MCP home range	11.87 ± 8.78	9.26 ± 9.79	−1.198	0.231	12.34 ± 8.59
95% FKA	2.76 ± 2.49	2.85 ± 2.72	0.675	0.5	2.86 ± 2.15
50% FKA	0.40 ± 0.51	0.40 ± 0.33	1.198	0.231	0.41 ± 0.40

(Aebischer et al. 1993). DA and CA provide somewhat different interpretations of habitat selection; e.g., CA is not able to identify the importance of habitat edges (Conner et al. 2003). Because of the fragmented nature of the habitats used by our study species, we also used DA because its results are more robust when individuals use fragmented landscapes or point-like or linear habitats, such as ponds or forest edges (Aebischer et al. 1993, Conner et al. 2003).

To use DA, we generated 1000 random points with Hawth's tool in ArcView GIS 9.2 (ESRI 2009) within the entire study area, and then the same number of random points as each respective individual's locational points within each of the homes ranges of the 18 individuals. To determine habitat use within the study area (second-order selection; Johnson 1980), we considered random points within the home ranges as habitat use and random points within the study area as habitat availability. To determine habitat use within each individual's home range (third-order selection), we considered each individual's locational points as habitat use and the same number of random points within that individual's home range as habitat availability.

To test for non-random habitat use within the study area and within each individual's home range, we used ArcView GIS to calculate the distances between the 1000 random points and the nearest feature of each habitat type. When a point was situated within a habitat type, the distance to that habitat type was set to zero. These distances were averaged to create a vector (r) for each individual (i) (following the notation used by Xu et al. 2006). We then calculated and averaged the distances between the locations and habitat types for each individual (i) to create the vector u_i. The ratios for each individual (d_i) were calculated by dividing the u_i by r. A MANOVA test was used to ascertain whether the mean of the ratio vectors (ρ) derived from d_i was significantly different from a vector of 1. We based all tests on 999 data randomizations. If nonrandom habitat use occurred within the entire study area, univariate *t*-tests were used to test whether the individual ratio of each habitat type differed significantly from 1. High and low values of the elements in ρ correspond to the least and to the most used habitats relative to habitat availability. Pairwise Mann-Whitney *U*-tests were performed to evaluate relative habitat preferences, from which a ranking matrix of *t*-statistics was constructed.

CA is based on the log-ratio method of statistical analysis of compositional data developed by Aitchison (1986). Since the dataset of habitat components summed to 1 (or 100%), we used the improved log-ratio transformation method for those components to avoid the unit-sum constraint (Aebischer et al. 1993). We used the use-availability design by Aebischer et al. (1993) to test whether the observed habitat use differed from habitat availability (see also Xu et al. 2006). For the second-order selection, we compared the composition of available habitat within the total study area to the composition within each 95% FKD home range. For the third-order selection, we compared the composition of used habitat defined by the proportion of radio locations within each habitat type to the composition of each individual's respective home range. We therefore calculated log-ratio differences from the compositional data for both second- and third-order selection and used these differences as dependent variables in a multivariate analysis of variance (MANOVA). Since CA does not allow for zero values, zero values for nonused habitat types were replaced by a value of 0.001% (cf. Aebischer et al. 1993).

Table 2. Habitat use of 18 Crested Serpent-Eagles. Habitat abbreviations are defined in Appendix. The second and third rows show the means and standard deviations of each habitat type within the 95% FKAs and 50% FKAs. The top row shows the percent availability of each habitat type within the study area (*cf.* Fig. 1–2). Empty cells denote a habitat type which was not used.

	HABITAT TYPES									
	MIX	ACACIA	MONSOON	GRASS	BUILT	BARE	COASTAL	DRY	FARM	WATER
Total study area	24.42	11.25	34.68	7.23	2.97	4.53	3.56	2.59	6.88	1.93
95% FKA	90.10 ± 11.61	4.72 ± 5.53	0.35 ± 1.44	3.76 ± 5.77	0.43 ± 0.64	0.11 ± 0.42	0.11 ± 0.44	0.13 ± 0.56	0.28 ± 0.43	0.02 ± 0.06
50% FKA	99.02 ± 2.75	0.11 ± 0.39	-	0.84 ± 2.76	0.03 ± 0.12	-	-	-	-	-

Table 3. Pairwise Mann-Whitney *U*-tests of the habitat use of 18 Crested-Serpent Eagles using DA. The first and second number given in each cell are the *U*-value and the *P*-value, respectively. The lower-left triangle shows the results of the CA within the study area (second-order selection), and the upper-right triangle shows the results of the CA within the 95% FKA (third-order selection). *P*-values <0.05 are shown in bold letters (no Bonferroni corrections were made).

	MIX	ACACIA	MONSOON	GRASS	BUILT	BARE	COASTAL	DRY	FARM	WATER
MIX		**3.680 (<0.001)**	**3.680 (<0.001)**	**3.680 (<0.001)**	**3.680 (<0.001)**	**3.680 (<0.001)**	**3.680 (<0.001)**	**3.680 (<0.001)**	**3.593 (<0.001)**	**3.680 (<0.001)**
ACACIA	**3.724 (<0.001)**		1.154 (0.248)	0.457 (0.647)	0.980 (0.327)	1.111 (0.267)	0.893 (0.372)	0.196 (0.845)	0.022 (0.983)	0.762 (0.446)
MONSOON	**3.724 (<0.001)**	0.065 (0.948)		0.893 (0.372)	1.938 (0.053)	0.327 (0.744)	0.544 (0.586)	0.980 (0.327)	1.328 (0.184)	1.023 (0.306)
GRASS	**3.724 (<0.001)**	1.023 (0.306)	0.893 (0.372)		1.415 (0.157)	1.285 (0.199)	1.415 (0.157)	0.022 (0.983)	0.240 (0.811)	0.544 (0.586)
BUILT	**3.724 (<0.001)**	1.328 (0.184)	1.285 (0.199)	0.327 (0.744)		**2.548 (0.011)**	**2.591 (0.010)**	1.415 (0.157)	1.241 (0.215)	**2.069 (0.039)**
BARE	**3.724 (<0.001)**	0.980 (0.327)	1.328 (0.184)	0.196 (0.845)	0.283 (0.777)		0.065 (0.948)	1.590 (0.112)	1.372 (0.170)	1.372 (0.170)
COASTAL	**3.724 (<0.001)**	1.372 (0.170)	1.590 (0.112)	1.111 (0.267)	0.936 (0.349)	0.457 (0.647)		**2.112 (0.035)**	1.502 (0.133)	1.415 (0.157)
DRY	**3.724 (<0.001)**	**2.286 (0.022)**	1.590 (0.112)	0.762 (0.446)	1.154 (0.248)	0.327 (0.744)	0.240 (0.811)		0.457 (0.647)	0.196 (0.845)
FARM	**3.724 (<0.001)**	**2.853 (0.004)**	1.894 (0.058)	1.328 (0.184)	1.894 (0.058)	0.631 (0.528)	0.849 (0.396)	1.546 (0.122)		0.675 (0.500)
WATER	**3.724 (<0.001)**	**3.288 (0.001)**	**3.070 (0.002)**	**3.593 (<0.001)**	**3.593 (<0.001)**	**3.332 (0.001)**	**3.724 (<0.001)**	**3.549 (<0.001)**	**2.853 (0.004)**	

Table 4. Mean ± standard errors obtained by averaging log-ratio differences to determine the habitat use of 18 Crested-Serpent Eagles using CA showing the comparison of 95% FKA vs. total study area (second-order selection). All differences which were statistically significant at the $P < 0.05$ level using a MANOVA test are printed in bold.

	95% FKA vs. Total Study Area				
	Mix	Acacia	Grass	Built	Farm
MIX		**2.693 ± 0.549**	**4.11 ± 0.735**	**4.128 ± 0.505**	**5.651 ± 0.484**
ACACIA	**−2.693 ± 0.549**		1.417 ± 0.915	**1.435 ± 0.501**	**2.959 ± 0.661**
GRASS	**−4.11 ± 0.735**	**−1.417 ± 0.915**		0.018 ± 0.657	1.542 ± 0.799
BUILT	**−4.128 ± 0.505**	**−1.435 ± 0.501**	−0.018 ± 0.657		**1.524 ± 0.532**
FARM	**−5.651 ± 0.484**	**−2.959 ± 0.661**	−1.542 ± 0.799	**−1.524 ± 0.532**	
WATER	**−4.933 ± 0.214**	**−2.24 ± 0.56**	**−0.823 ± 0.681**	**−0.805 ± 0.492**	0.719 ± 0.423
BARE	**−5.715 ± 0.39**	**−3.022 ± 0.547**	**−1.605 ± 0.706**	**−1.587 ± 0.508**	−0.063 ± 0.644
DRY	**−5.479 ± 0.342**	**−2.787 ± 0.531**	**−1.369 ± 0.676**	**−1.351 ± 0.476**	0.172 ± 0.623
COAST	**−6.263 ± 0.381**	**−3.57 ± 0.559**	**−2.153 ± 0.702**	**−2.135 ± 0.484**	−0.611 ± 0.7
MONSOON	**−6.836 ± 0.519**	**−4.144 ± 0.915**	**−2.726 ± 0.882**	**−2.708 ± 0.745**	**−1.185 ± 0.684**

The mean and standard error of the log-ratio difference in the elements of the matrix were calculated for all 18 birds, and the significance of the mean ratio unequal to 0 was evaluated by 999 randomization univariate *t*-tests (df = 17) in accordance with the recommendations outlined by Aebischer et al. (1993) and Conner et al. (2003). To rank the habitat types in order of use, we used a ranking matrix of pair-wise habitat comparisons (Aebischer et al. 1993). To meet assumptions associated with parametric tests, we based all tests on 999 randomizations of the data (Aebischer et al. 1993). Because all hypothesis tests were based on 999 randomizations of the data, the minimum *P*-value which was attainable was 0.001. However, the level of rejection of a null hypothesis was set at $\alpha = 0.05$.

RESULTS

Population Density. During 2006 and 2007, we found 15 and 14 breeding pairs, 7 and 9 territorial nonbreeding pairs and 7 and 11 floaters, resulting in a minimum population estimate of 51 and 57 individuals, respectively. Thus, for the study area of 20.1 km^2, population densities were 2.54 and 2.84 individuals/km^2, respectively, or 2.69 individuals/km^2 for both years.

Estimates of Home-range Size and Core Area. Overall, the MCPs, 95% FKAs and 50% FKAs of Crested Serpent-Eagles were 12.34 km^2, 2.86 km^2, and 0.41 km^2, respectively (Table 1). There was no effect of sample size (i.e., the number of locations) on the size of MCPs (Pearson's correlation, $n = 18$, $r = 0.08$, $P = 0.76$), 95% FKAs ($r = 0.02$, $P = 0.96$) and 50% FKAs ($r = 0.10$, $P = 0.69$). There were no differences between any of these three measures between the wet season (May–September) and dry season (October–April) as defined by Chen and Chen (2003). Mean home-range size for 14 of these birds, along with differences due to sex and age, were published in Chou et al. (2012).

Habitat Use. The 18 radio-tracked individuals used every habitat type within the study area (Table 2). The study area of 51.1 km^2 (Fig. 1) comprised 70.4% forests, with the remaining seven habitat types covering the remainder (Table 2). Habitat types used varied among individuals, but the mixed-forests category was the main component of the 95% FKA of every individual, averaging about 90% (range 47.2–98.6%). All other habitat types covered on average <5% of the 95% FKA (Table 2). The mixed forest category was also the main component in the 50% FKAs of the birds at 99%, followed by grassland, *Acacia confusa* forest, and built-up (i.e., developed) land, with the remaining habitat types unused (Table 2).

DA Within the Study Area. The analysis of distance ratios indicated that random points in the Crested Serpent-Eagle home ranges differed from random points in the study area ($F_{10,8} = 7660.83$, $P < 0.001$). Crested Serpent-Eagles were associated with mixed forest ($\rho_{MIX} = 0.02 \pm 0.03$, $t_{17} = -131.7$, $P < 0.001$) and monsoon rainforest ($\rho_{MIX} = 0.88 \pm 0.19$, $t_{17} = -2.08$, $P = 0.02$), while areas with water were avoided more than expected ($\rho_{WATER} = 1.38 \pm 0.28$, $t_{17} = 6.70$, $P < 0.001$; Table 6).

DA Within the 95% FKA. Locations of eagles within the 95% FKAs with respect to different habitats differed from random points in the 95% FKAs ($F_{10,8} = 3.80$, $P < 0.04$). Eagles preferred mixed forest

Table 4. Extended.

95% FKA vs. Total Study Area					
Water	Bare	Dry	Coast	Monsoon	Rank
4.933 ± 0.214	**5.715 ± 0.39**	**5.479 ± 0.342**	**6.263 ± 0.381**	**6.836 ± 0.519**	9
2.24 ± 0.56	**3.022 ± 0.547**	**2.787 ± 0.531**	**3.57 ± 0.559**	**4.144 ± 0.915**	8
0.823 ± 0.681	**1.605 ± 0.706**	**1.369 ± 0.676**	**2.153 ± 0.702**	**2.726 ± 0.882**	7
0.805 ± 0.492	**1.587 ± 0.508**	**1.351 ± 0.476**	**2.135 ± 0.484**	**2.708 ± 0.745**	6
−0.719 ± 0.423	0.063 ± 0.644	−0.172 ± 0.623	0.611 ± 0.7	**1.185 ± 0.684**	5
	0.782 ± 0.465	0.547 ± 0.385	1.33 ± 0.459	**1.904 ± 0.59**	4
−0.782 ± 0.465		−0.236 ± 0.212	0.548 ± 0.232	1.122 ± 0.667	3
−0.547 ± 0.385	0.236 ± 0.212		0.784 ± 0.2	1.357 ± 0.63	2
−1.33 ± 0.459	−0.548 ± 0.232	−0.784 ± 0.2		0.574 ± 0.655	1
−1.904 ± 0.59	−1.122 ± 0.667	−1.357 ± 0.63	−0.574 ± 0.655		0

over all other habitats ($\rho_{MIX} = 0.43 \pm 0.30$, $t_{17} = -8.04$, $P < 0.001$) but avoided built-up land much more than expected ($\rho_{BUILT} = 1.05 \pm 0.09$, $t_{17} = 2.19$, $P = 0.04$; Table 6).

DA Using Pairwise Mann-Whitney *U*-tests. Pairwise comparisons of distance ratios associated with habitat types indicated that mixed forest was preferred to all other habitats ($P < 0.001$ in all possible comparisons within Table 3). For the remaining comparisons (lower-left triangle in Table 3), *Acacia confusa* forest was preferred over dry forest, farmland, and water, and water remained the least preferred habitat compared to all other habitats. All other comparisons were nonsignificant. For the remaining comparisons within the individual home ranges (upper-right triangle in Table 3), bare ground, coastal forests and open water were preferred over built areas, and coastal forests were preferred over dry forests. All other comparisons were nonsignificant.

CA Within the Study Area. When we compared the log-ratio differences of habitat use in the 95% FKAs with the habitat availability in the total study area, we found that its distribution was not multivariate normal (MANOVA test; $F = 87.81$, df = 9, $P < 0.001$). Therefore, the habitat use of the eagles was nonrandom within the study area (Tables 4–6).

CA Within the 95% FKA. Within the 95% FKAs, the habitats with the lowest rankings in the previous analysis (namely, WATER, BARE, DRY, COSTAL, and MONSOON) were absent from the FKAs of 61.1% of the individuals. Therefore, these habitats were excluded in subsequent analyses, and four individuals were also excluded because the remaining five habitat types did not occur in the 95% FKAs of these individuals. Analyzing this subset of individuals, habitat use within the 95% FKAs differed from random (MANOVA, $F = 74.83$, df = 3, $P < 0.001$ using 999 randomizations; Tables 4–6).

Table 5. Mean ± standard errors obtained by averaging log-ratio differences to determine the habitat use of 18 Crested-Serpent Eagles using CA showing the comparison of radio locations vs. 95% FKA (third-order selection). All differences which were statistically significant at the $P < 0.05$ level using a MANOVA test are printed in bold.

Radio Locations vs. 95% FKA						
	Mix	Acacia	Grass	Farm	Built	Rank
MIX		1.381 ± 0.585	0.804 ± 0.394	**0.983 ± 1.169**	2.388 ± 1.137	4
ACACIA	−1.381 ± 0.585		−0.738 ± 0.821	−0.174 ± 1.7	1.135 ± 1.043	3
GRASS	−0.804 ± 0.394	0.738 ± 0.821		0.19 ± 1.347	2.099 ± 1.469	2
FARM	−0.983 ± 1.169	0.174 ± 1.7	−0.19 ± 1.347		0.915 ± 2.51	1
BUILT	−2.388 ± 1.137	−1.135 ± 1.043	−2.099 ± 1.469	−0.915 ± 2.51		0

Table 6. Comparison of habitat rankings (most preferred [1] to least preferred [10]) resulting from DA (Table 3) and CA (Tables 4–5). Within each row, habitats with the same superscript letter did not differ at the significance level of $P < 0.05$.

		HABITAT RANKING									
METHOD	SCALE	1	2	3	4	5	6	7	8	9	10
DA	Within study area	MIX	ACACIA^{a}	MONSOON^{a}	GRASS^{a}	BUILT^{a}	BARE^{a}	COASTAL^{a}	DRY^{b}	FARM^{b}	WATER
DA	Within 95% FKA	MIX	ACACIA^{a}	MONSOON^{a}	GRASS^{a}	BUILT^{ab}	DRY^{b}	FARM^{bc}	BARE^{c}	COASTAL^{c}	WATER^{c}
CA	Within study area	MIX	ACACIA^{a}	GRASS^{ab}	BUILT^{b}	FARM^{bc}	WATER^{c}	BARE^{cd}	DRY^{cd}	COASTAL^{cd}	MONSOON^{d}
CA	Within 95% FKA	MIX^{a}	ACACIA^{ab}	GRASS^{ab}	FARM^{b}	BUILT^{b}					

Differences Between DA and CA. Habitat rankings differed between DA and CA (Table 6). Although all four analyses showed that mixed and *Acacia confusa* forests were the most and second-most used habitat, respectively, the subsequent rankings differed among analyses. The major difference in habitat ranking between the DA and CA analyses was the ranking of the monsoon rain forest. Although monsoon forests ranked third in both DA analyses, it ranked last in one CA analysis and did not even appear in the other CA analysis.

DISCUSSION

Our overall estimates of the size of the home ranges and core areas of Crested-Serpent Eagles were mostly within the range published for other forest species, although most of them have much larger home ranges, ranging from 4–120 km^2 (summarized in Gjershaug et al. 2004, Kaneda et al. 2007). Because of the relatively small mean home range at our study site, the estimated combined population density for 2006 and 2007 was 2.69 individuals/km^2; this is, to the best of our knowledge, one the highest population densities ever recorded for this species. One reason may be that we deliberately chose an area with one of the highest population densities in Taiwan and excluded coastal areas where we searched but found no nests. However, it may also be due to the insular syndrome (see below).

By comparison, Thiollay (1993) reported 0.42 individuals/km^2 of several species of raptors in southern India. Summarizing results for several South Asian raptor communities, Thiollay (1998b) reported in his Table 3 an average of 0.28 individuals/km^2 for open habitats, 0.92 individuals/km^2 for degraded forests, and 0.78 individuals/km^2 for selectively logged or primary forests.

In fact, our density estimate for just one species is higher than 6 of the 15 estimates of total density including all raptor species (Thiollay 1998a), and only slightly lower than the average of these 15 estimates given (namely, 2.82 individuals/km^2). We suggest that this high density of Crested Serpent-Eagles in southern Taiwan may be due to the so-called insular syndrome (Thiollay 1998a, 1998b, Thiollay and Meyburg 1988), whereby lower raptor species richness on islands is compensated by a higher raptor density and possibly broader habitat niches. In our study area, there is only one other sympatric raptor species, and that species does not compete for the same prey items. Therefore, the Crested Serpent-Eagle probably faces little interspecific competition, except perhaps during migratory seasons when hundreds of thousands of raptors migrate through the Kenting peninsula (Chen et al. 2007, Sun et al. 2010).

In a recently published description of Taiwan's avifauna (Severinghaus et al. 2010), the habitat of the Crested Serpent-Eagle was described as fragmented low-elevation and foothill forests, orchards, tea plantations, cemeteries, and even areas around abandoned residences. In our study area, 90.1% of the 95% FKAs and 99.0% of the 50% FKAs were covered by mixed forests, although mixed forests made up only 24.4% of the study area. Because mixed forests were in a process of successional recovery, they had a more open canopy, more open edge habitats and more open understory than the mature forests. One type of mature forest, namely monsoon forest, was rarely used although it made up the largest proportion of the study area. Instead, the Crested Serpent-Eagles almost exclusively used mixed forests, and, to a much lesser extent, *Acacia confusa* forests, both of which could be characterized as secondary forests.

Further support of this habitat preference comes from our behavioral observations, which confirmed that Crested Serpent-Eagles perched along the edges of forest patches within mixed and *Acacia confusa* forests, as well as the edges of monsoon rainforests, presumably hunting the adjacent semi-open and open habitats.

Despite the serpent-eagle's preference for mixed and *Acacia confusa* forests, other habitats may still play an important role in providing prey. Although an individual may spend most of its time perching in its preferred habitat, it may spend very little time actually striking prey on the open ground in adjacent habitats. Therefore, direct behavioral observations may show that habitat types containing open ground may be important for the species' survival, even if they appear to be rarely used when analyzed with habitat preference or time-budget studies. For example, we anecdotally observed Crested Serpent-Eagles scavenging carcasses killed on roads or trails, or searching above ditches for prey such as earthworms, crabs, amphibians, and reptiles in seasons when these prey species were abundant.

Furthermore, Liu (2011) studied the diurnal activity pattern of three nonbreeding radio-tracked Crested Serpent-Eagles from January to August 2008 in our study area. The individuals spent most of their time perching (98.6%) and very little time on inter-perch flights (0.2%), hunting (0.5%) and circling (0.9%). This apparent sit-and-wait foraging strategy further supports the notion that direct behavioral observations are a necessary complement to studies of habitat use such as this one, in order to understand all the habitat requirements of a species.

Studies of the habitat use of Crested-Serpent Eagles outside of Taiwan are also in general concurrence with our findings. In southern India, Crested Serpent-Eagles preferred higher levels of fragmentation than typical interior raptor species (Thiollay 1993). In Java, Crested Serpent-Eagles occupied mostly semi-open and open habitats and avoided primary rainforests (Thiollay and Meyburg 1988). In Sumatra, Crested Serpent-Eagles also occupied mostly open woodlands, degraded forests, and plantations (Thiollay 1998a, 1998b). Therefore, the Crested-Serpent Eagle should be considered an intermediate species (*sensu* Thiollay 1993) which favors edge areas of moderate fragmentation and a mixture of open woodlands and core forests.

Both DA and CA indicated that mixed and *Acacia confusa* forests are the most preferred habitats of Crested Serpent-Eagles. For the other habitats, habitat rankings differed between DA and CA. However, these habitat types were rarely used by Crested Serpent-Eagles anyway. The major difference in habitat ranking between DA and CA was the monsoon rain forest. DA indicated that locations were closer to the monsoon rain forest than expected. By contrast, the monsoon rain forest was the least preferred among habitats according to CA. From our observations, it was clear that the Crested Serpent-Eagles often used perches along the edges of, but not within, the monsoon rainforests. Such preference for habitats which run along habitat edges can only be identified by using DA and CA together and supplementing them with direct behavioral observations.

Furthermore, results for the second- and third-order selection differed for both DA and CA. Our results thus reiterate the importance of considering the spatial scale of habitat analysis (Johnson 1980). For example, Bald Eagles (*Haliaeetus leucocephalus*) displayed scale-dependent patterns of habitat use relative to many habitat features (Thompson and McGarigal 2002). Similarly, McGrath et al. (2003) found that different habitat features were important at different scales for the Northern Goshawks (*Accipiter gentilis*; see also Donner et al. 2013). Such a hierarchical process of habitat selection was also demonstrated for the Eurasian Eagle-Owl (*Bubo bubo*; Martínez et al. 2003).

Many species of serpent-eagles are threatened by habitat loss and human persecution, but knowledge of their life history and ecological requirements are still rudimentary (Sergio et al. 2008). Future research should determine whether the Crested Serpent-Eagle has a reproductive rate high enough to sustain the population outside of the protected areas such as Kenting National Park, or whether such areas are population sinks (Kauffman et al. 2004, Muñoz et al. 2005). If outside areas are population sinks, then protected areas such as Kenting National Park should be managed for a continued high density of eagles. However, if outside areas are sources, then the management of protected areas may focus on other conservation goals, e.g., letting mixed forest become mature monsoon rainforest, which is very rare in Taiwan.

If it is deemed necessary to manage Kenting National Park for a continued high density of Crested Serpent-Eagles, we suggest the following measures: both the land coverage of mixed forest as well as the population of eagles should be monitored; if too much mixed forest becomes mature forest, some open areas should be artificially created which should be interspersed or surrounded by large trees; the maintenance of open areas may also be achieved by large herbivores; e.g., the recently reintroduced Sika deer or feral water buffalo (Hsu and Agoramoorthy 1999); hunting and illegal trails used by hunters and hikers should be curtailed; illegal land conversions, such as building of new houses and hotels, must be arrested; and to curtail such illegal activities and reduce local opposition to conservation measures, community-based conservation programs that bring economic benefits to local people, such as paying for habitat management, ecotourism and birdwatching, should be initiated (Hsu and Agoramoorthy 1999). Based on recommendations generated by this research project, the park's management has cut down on illegal hunting, farming, logging, and pasture use in or around the forested areas, and ecotourism development in the forest kept away from all the known nest sites of the Crested Serpent-Eagle and Formosan Crested Goshawk discovered during this research project. Similar recommendations should also be applicable for other subspecies of the Crested Serpent-Eagle.

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APPENDIX

Ten habitat types within our study area were established by Chen and Chung (2003). They are: (1) MIX = mixed forests, 8–15 m tall, including various successional stages of areas which was formerly highly degraded natural forest, secondary forest, and mature tree plantations, and which will become either dry forest, *Acacia confusa* forest, or monsoon rainforest once fully regenerated; (2) ACACIA = *Acacia confusa* forests, 8–14 m tall, as well as fragmented patches of mature tree plantations dominated by *Acacia confusa*; (3) MONSOON = monsoon rainforests, 10–15 m tall, including large tracts of mostly original but in places moderately disturbed native evergreen forest, consisting mainly of *Aglaia formosana*, *Bischofia javanica*, *Diospyros discolor*, *Diospyros ferrea*, *Diospyros maritima*, *Diospyros philippensis*, *Drypetes littoralis*, *Ficus benjamina*, *Laportea pterostigma*, *Macaranga tanarius*, and *Palaquium formosanum*; (4) GRASS = grasslands, including pastures and small ranches; (5) BUILT

= built-up (developed) lands, including roads, trails, tourist facilities, and village areas; (6) BARE = nearly bare terrains with very little vegetation, including sandy beaches, badlands, and Karst topography; (7) COAST = coastal plant communities, 8–13 m tall, including patchily distributed degraded woodlands and bushes, consisting mainly of *Barringtonia asiatica*, *Bischofia javanica*, *Ficus caulocarpa*, *Hernandia nymphaeifolia*, *Terminalia catappa*, and *Palaquium formosanum*; (8) DRY = dry forests, 3–5 m tall, including low and dense woodlands, dominated by *Aglaia formosana*, *Leucaena leucocephala*, *Pandanus odoratissimus*, *Melanolepis multiglandulosa*, and *Vitex negundo*; (9) FARM = farmlands, including young tree plantations, areas of secondary growth, and agricultural land; and (10) WATER = water bodies, including open water bodies and large rivers, but excluding oceans.