RESEARCH ARTICLE

Spacing Pattern of the Crested Serpent-Eagle (*Spilornis cheela hoya*) in Southern Taiwan

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(Manuscript received 6 May 2011; accepted 15 July 2011)

ABSTRACT: We studied the home ranges and core areas of a native population of Crested Serpent-eagles in southern Taiwan by radio-tracking from November 2005 to May 2007. Mean home range areas for eight male and six female individuals were 16.65 km^2 and 6.93 km^2 based on the estimation by the minimum convex polygon (MCP) method and 4.52 km^2 and 1.46 km^2 based on the 95% fixed kernel (FK) method, respectively. Mean core areas for males and females were 1.16 km^2 and 0.36 km^2 based on the estimation by the Area Independent Method (AIM) and 0.64 km^2 and 0.20 km^2 based on the 50% FK method, respectively. Mean fixed kernel home ranges of males were 3.1 times greater than those of females, and AIM core areas of males were 3.2 times greater than those of females. All of the individuals exhibited core area overlap, especially in the case of male to male core areas. Male to male, male to female and female to female average AIM core area overlap was 37.0%, 14.9% and 1.9%, respectively with these differences all being statistically significant. Therefore, at the level of AIM core area overlap, core areas of females were smaller, and female to female relationships showed considerably more range exclusivity than those of male to female and male to male. In contrast, male core areas were more regularly shared with other male or female individuals. Since radio-tracked females were 18% heavier than radio-tracked males, we discuss how the differences in spacing pattern may be caused by female dominance.

KEY WORDS: Core area, home range, radio-tracking, space use, *Spilornis cheela hoya*

INTRODUCTION

Home ranges of animals are determined by a variety of abiotic and biotic factors. Abiotic factors known to influence home range sizes are climatic variables, but also geological variables, e.g. soil type which may influence the distribution of food plants. Biotic factors include the distribution of other species as well as the distributions of conspecific individuals. These biotic factors determine the distribution of resources such as food or nesting places, but also the distribution of predation pressures and intra- and inter-specific competition (Burt, 1943; Wywialowski, 1987; Block and Brennan, 1993; Tufto et al., 1996; Peery, 2000).

Most animal species do not use their entire home range evenly, but instead concentrate their use in some areas (Hayne, 1949), partly due to the uneven distribution of habitat resources but also to minimize travel times (Dixon and Chapman 1980; Springer, 1982). The core area is defined as an area of concentrated utilization with a relatively high proportion of residence; it usually contains numerous hiding or resting places, key food resources and other essential features for survival and reproduction (Hayne, 1949; Kaufman, 1962; Powell et al., 1997). Therefore, the distribution of utilized resources can have effects on the area and the boundaries of the core area (Samuel and Fuller, 1994; Fieberg and Kochanny, 2005). By determining core areas, we can differentiate concentrated versus peripheral areas of use within the home range. From this utilization distribution, we may then deduce the animal's ecological interactions that are important in shaping this distribution (Harris et al., 1990; Seaman and Powell, 1990; McGrath, 2005; Karubian and Carrasco, 2008).

A systematic study of the association between population density and body weight of the family Accipitridae, demonstrated that some regional raptor species are much better researched than others, and that knowledge for most tropical species is poor (Krüger, 2000). One of the reasons for this may be that many tropical species are elusive, secretive and forest-dwelling (Thiollay and Meyburg, 1988; Thiollay, 1993; Thiollay, 1994; Van Balen, 1994; Thiollay, 1998;

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Watson, 1998). Therefore, many conservation biologists have strongly encouraged more field work on tropical raptors (Burnham et al., 1994; Bildstein et al., 1998). The Crested Serpent-eagle *Spilornis cheela* is distributed across tropical Asia from India to Malaysia where it is mostly described as common, although some subspecies are locally uncommon (del Hoyo et al., 1994). It uses almost exclusively forests and woodlands for breeding but also explores open environments such as farmlands, scrublands and grasslands for foraging. While their overall density and requirements of habitat types are well known (Naoroji and Monga, 1983; Thiollay and Meyburg, 1988), quantitative information on their home ranges and core areas within the Asian region is limited. Thiollay and Meyburg (1988) first estimated the overall home range for the Crested Serpent-eagle to be 5-10 km^2 using roadside counts on the island of Java.

The subspecies *hoya* of the Crested Serpent-eagle is endemic to Taiwan (Brown and Amadon, 1968; Weick and Brown, 1980; Stepanyan, 1993). Research on nesting site selections in southern Taiwan has shown that the nearest nest distance for the species was closer than ever described with an average distance of 517.0 ± 261.2 m (Chou, 2006). High density means high probability of interactions between individuals. The degree of space-use overlap in home ranges and also in core areas is an applicable descriptor of social tolerance (Gorman et al., 2006). Although its regional population density is relatively high (Chou, 2005), historical population decreases in southern Taiwan have been attributed to habitat destruction. Recently, forests in this region have gradually recovered after the establishment of the Kenting National Park in 1983, but other disturbances persist, such as recreation, sporadic illegal hunting, illegal grazing, and the reintroduction of the Formosan Sika Deer (*Cervus nippon taiouanus*), to the detriment of forest recovery.

Basic information on the behavior, home range and core area of the Crested Serpent-eagle is lacking in Taiwan, even though it is critical for conservation and management efforts. Since sex-related behavioral dominance may lead to different spacing pattern for the subordinate sex (Ardia and Bildstein, 1997), we tracked 14 individuals of both sexes and varying ages using radio-telemetry to determine their home ranges and core areas, and examined their correlation to the individual's body mass. We also quantified the overlap of their home ranges and core areas.

MATERIALS AND METHODS

Study area

Our study area was located on the Eluanbi peninsula (centered on 21°58'N, 120°48'E) near the southernmost tip of Taiwan, with most of the study area inside Kenting National Park (Fig. 1). This peninsula originates from uplifted coral reef terrain and its elevation is below 300 m. The terrain is rugged, and most roads and developments are found along the outer coastline. The central region of the peninsula is mainly uninhabited, and development of the forest is prohibited. However, many paths and trails crisscross the area. There are also sporadic farmland and grazing areas in the border regions between the forest and the coastline. We set up our study center in Sheding which is the only settlement with more than 300 people.

Kenting has a tropical climate with little variation in temperature. The monthly average temperature is above 20°C (meteorological data from 2003-2007 provided by the Taiwan Central Weather Bureau) with the lowest average in January (21.2°C) and the highest in July (28.2°C). Annual rainfall is about 2,080 mm with distinct wet and dry seasons. The dry season lasts from November to April while the wet season lasts from May to October during which about 92% of the annual total precipitation falls. Each year, several typhoons hit the area and are the main source of rainfall; they are also the primary cause of death among first-year Crested Serpent-eagle chicks (Chou, 2005). Strong northeasterly winds occur between September and April with wind speed averaging 2.9-5.8 m/s. Strong gusts reaching up to 12-15 m/s are also common. During the dry season, most surface waters and small ravines dry up.

For the past 100 years, the forest in this area has experienced frequent and severe reclamation burn offs, logging for charcoal production and grazing, leaving the forest in a heterogeneous condition. At present, the natural vegetation of this area can be roughly divided into littoral plant communities and foothill plant communities. Foothill plant communities can be further divided into grassland, scrub and forest communities. The formation of grassland communities was due to the cutting, burning, grazing and trampling of the original forest or bushes (Chen et al., 1991). Forest trees do not grow easily on mountain peaks and coral rocks where strong winds blow, whereby *Aglaia formosana*, *Drypetes littoralis*, *Gordonia axillaries* and *Myrica adenophora* form the dominant scrub communities. High coral vegetation grows and flourishes in areas that accumulated weathered soil where the main plants include *Diospyros philippensis*, *Diospyros maritima*, *Ficus microcarpa*, *Heritiera littoralis* and *Dendrocnide meyeniana* (Wang et al., 2004). Due to the strong winds, forest growth is only found in the rift valley and coral reef crevices along the southwestern slope of the peninsula while wind resistant *Casuarina equisetfolia* is mainly distributed on the open ridges along the

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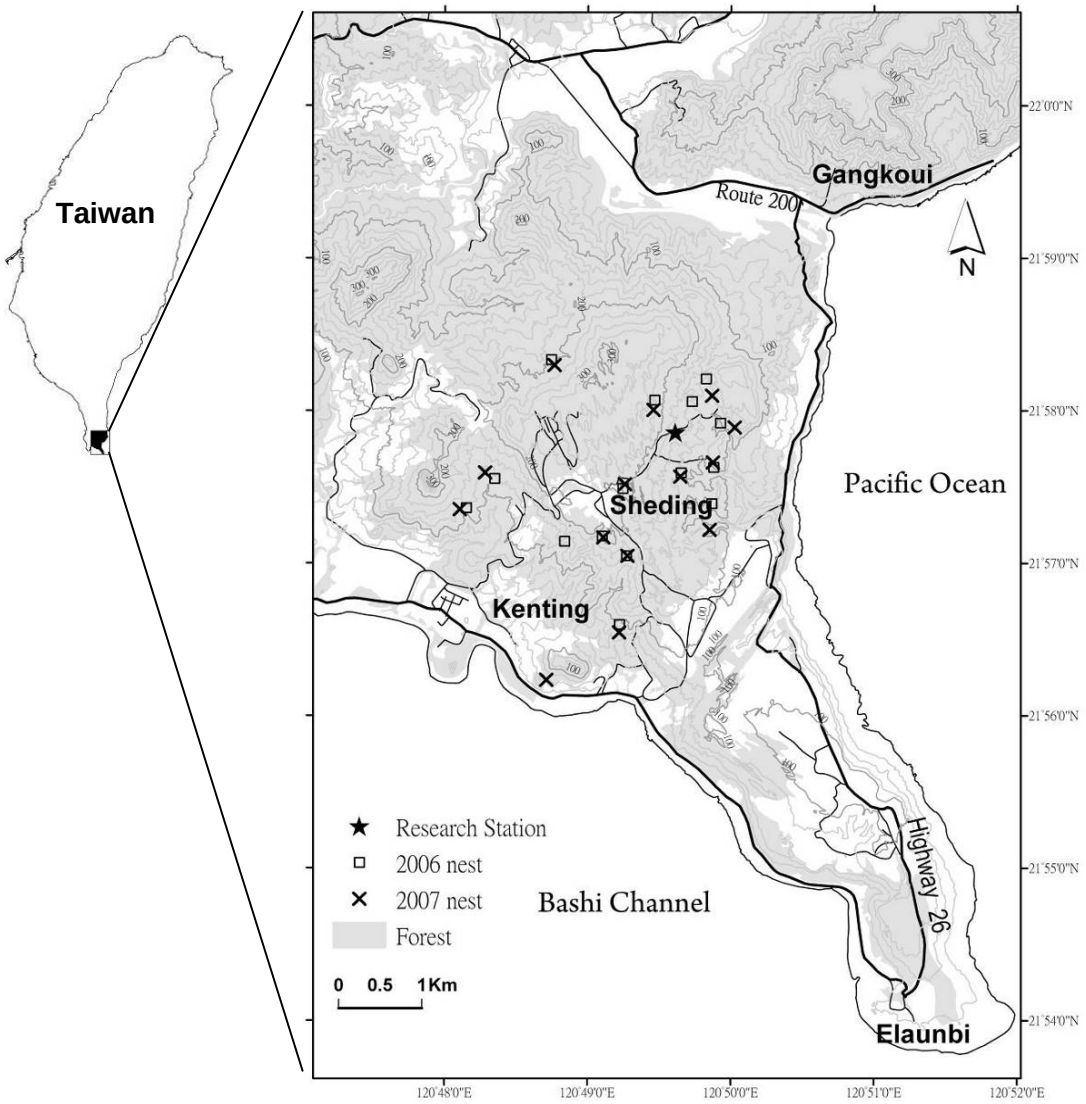


Fig. 1. Location of the study areas on Eluanbi peninsula of southern Taiwan where Crested Serpent-eagles were radio-tracked between November 2005 and May 2007. The shaded areas are potential forest habitats for the eagles. Paved roads (thin lines) and numerous trails (not shown here) protruded into these forests from towns and villages such as Kenting, Sheding, Gangkoui and Elaunbi, as well as from Provincial Highway 26 and County Route 200 (thick lines). The research station (star) became a base for checking traps, tracking of individual birds, and nest survey.

northeastern slope (Liu, 2000).

In recent years, a population of Crested Serpent-eagles has flourished in the study area. By 2005, 15 territorial pairs had been surveyed, with the locations of all nests identified (Chou et al., 2004; Chou, 2005). The Formosan Crested Goshawk (*Accipiter trivirgatus formosae*) is the only sympatric raptor (Chen, 1997). Because we did not observe any behavioral interactions during our study between these two species, or between Crested Serpent-eagles and migrating raptors (T. C. Chou, unpublished data), we did not study the possible impact of interspecific habitat competition.

Trapping and radiomarking

To facilitate the identification and tracking of individuals, we put transmitters on individual eagles. In order to capture subadult and adult birds beginning in November 2005, we set up bow net traps (Tordoff, 1954) below rest perches identified by the amount and freshness of their droppings. Although previous studies from this area indicated that individuals mainly preyed on snakes, we used large earthworms (*Metaphire posthuma*) and eel (*Conger cinereus*) as bait to fulfill legal restrictions. Traps were laid near the side of several gravel roads in the center of the study area that are used by park rangers for patrols. At least 500 meters

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separated each of these traps. In order to reduce disturbance of breeding sites, we did not place traps within 100 meters of the nearest nesting site. Once an individual bird was captured, we measured its body weight and wing span. After taking pictures of the features of various body parts, we put a wing tag, a leg band, and a back-pack style radio transmitter with an action sensing module (AVM Instrument, Colfax, CA, USA) on the individual. The transmitter had a frequency of 230 MHz, a weight of 25 g, and a battery life of about 350 days. Depending on terrain obstacles and the bird's posture, signals could be received from a distance of approximately 5-10 km. The total weight of all the attachments was 35-40 g, which is less than 3% of the average weight of an eagle. We also collected 0.1 ml of blood for sex identification which was determined using the methods developed by Chang et al. (2008). Each bird was released in situ. All birds resumed normal activities soon after release, and we observed no subsequent transmitter installation-related problems.

Radio-telemetry and tracking

Radio tracking was carried out by two to three persons starting at sunrise. Each tracker would be positioned at the vantage point of a predetermined location to perform signal triangulation using a set of AVM receivers (model LA12-Q), a 3-element yagi antenna and a compass to determine the approximate perch location of each tracked individual. The trackers discussed their respective tracking target and route using two-way radios. Afterwards, the researchers would use the 'homing' method (White and Garrott, 1990) to locate individuals which involves a careful approach until the perch coordinates and habitat features of individuals are confirmed. Coordinates were obtained from landmarks on aerial photo maps and a GPS device. If other banded individuals were witnessed to be perching nearby, they would also be recorded. During the transmitting period, the position of each individual was tracked 3-5 times a week. The amount of location data varied for each individual depending on its movements, weather conditions and the actual number of tracking days.

Data collection and processing

Since the fixed kernel method requires a minimum sample size of 30 sites to estimate an individual's home range (Kenward, 1992; Seaman et al., 1999), we only selected data from individuals which had been tracked at least three months of the dry season and three months of the wet season during one year of tracking. Tracking data from each dry and wet season had to have at least 30 location points. For individuals whose tracking period exceeded 12 months, we only used the set of 12-month data that contained the highest number of individual home range overlaps in order to adopt a maximally concentrated time period to explore the use of space by individuals. However, due to the lack of sufficient seasonal positioning data points from some individuals, the total data acquisition period stretched over 14 months.

The Crested Serpent-eagle is not an active species. Foraging activity is done mostly by means of perching, waiting and shifting of perch position in a leap-frog fashion (Liu, 2011). In order to avoid problems arising from temporal autocorrelation of locational data, we divided the tracking time into three periods: sunrise to 10:00, 10:00 to 14:00, and 14:00 to sundown. These three time periods were used for non-seasonal breeding activities that the birds living in the study area would undertake (i.e., mornings for trips from roosts to feeding points, around noon is the peak period for feedings, and afternoons are for perching and loafing). From each time period, we only picked one locational datum using a random selection procedure. Therefore, the hour at which the first item of tracking information was recorded was not necessarily in the same time period each day.

We used new and old feather features and moulting status to identify young (within first year of leaving the nest), subadult and adult individuals. First year individuals are mostly still at the dispersal stage or have not established a stable home range yet (Chou, 2005). Therefore, we did not use ranging data information from young individuals that had left the nest for less than one year. Moreover, if participating female individuals were breeding, we did not use the locational information of the individual females during their breeding period (March to June) to avoid impact on home range estimation of possible incubating and hatching behavior of female individuals. However, if ranging behavior was resumed after breeding was interrupted for any reason, we resumed the locational data collection of individuals. In fact, we often randomly, but not deliberately, recorded and tracked the return of the male bird to the nest's vicinity. Since the male bird spends most of his time away from the nest during the breeding season to provide food for the female and chicks, the locational data of the male was not concentrated near the nest.

In each of the years from 1995 to 2007 except for 1997 and 1998, we carried out two or more systematic searches of Crested Serpent-eagle nesting sites in the study area at the start of the breeding season (late February; Chou et al., 2004; Chou, 2005; Chou 2006; Chou and Shiu, 2007). Therefore, we were able to record the change and occupancy of nesting sites in various areas which allowed us to monitor the relationship between tracked individuals and their nesting sites.

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Raptors may make excursions from their ordinary range area (Hodder et al., 1998) and the distances covered during such brief excursions are far beyond the typical use of their home ranges. Therefore, these excursions should be excluded in the analysis of core areas (Burt, 1943), and areas within an outer home-range boundary should be avoided (White and Garrott, 1990). We observed that Crested Serpent-eagles wandered out of their ordinary home ranges a few times during their tracking period, and these excursions made up less than 1% of their total locational data. When we analyzed the data of individual home ranges, we removed the locations from these excursions (Hodder et al., 1998). We used ESRI ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA) GIS software and its extension module Animal Movement (AM) SA v2.04 beta extension (Hooge and Eichenlaub, 1997) to calculate minimum convex polygon (MCP) and fixed kernel area. To define the home range, we used the 100% MCP area and 95% fixed kernel area (from hereupon referred to as the 95% FK area). The fixed kernel area estimation process used least squares cross validation (LSCV) (Seaman et al., 1998) to determine the smoothing factor (Worton, 1987). Other parameters were set to default settings.

We used a univariate general linear model to compare differences in home ranges and core areas between sexes and ages (in this case, subadults and adults). Given that parametric assumptions of general linear models were evaluated with a Lilliefor's test for normality, and equality of variance was assessed with Levene's test, home ranges of different sexes and ages were compared using the Mann-Whitney *U*-test. We also used Spearman rank correlations to test whether the body weights of individuals were correlated with the maintenance of home ranges (100% MCP area and 95% FK area).

We used the Area Independent Method (AIM) by Seaman and Powell (1990) to verify for each bird whether any difference existed in their use of the internal versus the surrounding areas. Based on the raster layer of kernel home range output from the AM module, we calculated the size of the kernel area for each probability of use increment from 5% to 95% and then divided the area value by the home range area (95% FK area) to obtain the percentage of the kernel area within a specific probability of use. We then plotted the relationship curve between the percent of the home range (Y-axis) against a given relative probability of use (X-axis). Seaman and Powell (1990) defined the dividing point between high and low use as the point where the plot is cut (touched) from a straight line with a slope of -1. The dividing point is also the turning point where the percent of home range begin to drop slower. Only a concave curve shows the drop in area of use from periphery to core becoming more shallow (from up to down, left to right). If the curve was concave, it demonstrated that the bird was using the home range non-randomly; thus the cutting point of the curve and a straight line with slope of -1 was found. The point derived is the turning point between a high utilization area and a low utilization area and is also the dividing point as the usage intensity of home range slowly moves down from the core to the periphery. We used the probability of use at such a point to identify areas of concentrated use. We called such an 'objective' core area the AIM core area and compared it to the generally defined 50% fixed kernel core area.

In addition, we applied the method of Kernohan et al. (2001) to calculate the overlap coefficient of the AIM core area between individuals using the following equation: $C_{i,j} = A_{i,j} / A_i$ where $C_{i,j}$ is the area percentage of overlap between core area of individual i and core area of individual j over the core area of individual i; $A_{i,j}$ is the area of overlap between core areas of individual i and individual j; A_i is the area of the core area of individual i. Therefore, $C_{i,j}$ and $C_{j,i}$ are not the same. It rarely happens that there is no overlap in the use of space under the home range scale when birds are neighbors. In addition, the degree to which core areas overlap may provide a more profound and appropriate description of the level of interaction between neighboring birds than those provided by their home ranges. Therefore, we only quantified the level of core area overlap for those birds with 95% FK home range overlapped. The area of overlap was calculated using ArcView 3.2. We divided the interaction between overlaps into three groups based on sex (i.e., male-male, female-male, or female-female) or age (i.e., adult-adult, adult-subadult, or subadult-subadult). We used randomization tests with 1000 replicates (Manly, 1997) to check for differences between the various groups.

RESULTS

Radio-telemetry

From 1 November 2005 to 15 May 2007, we captured 17 Crested Serpent-eagles. We recorded the proportion of banded individuals within aerial flocks during 30 counts on different mornings. From these counts, we estimated that the 17 captured Crested Serpent-eagles made up about 40% of the total population (unpublished data). The 17 individuals were captured by six out of the nine traps we set up, with one trap catching nine individuals and the rest separately catching 1, 1, 1, 2, and 3 individuals. This distribution indicates that some locations had a higher degree of

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Table 1. Summary (mean ± SD and range) of radio-tracking information for 14 Crested Serpent-eagles (*Spilornis cheela hoya*) tracked on Eluanbi peninsula of southern Taiwan between November 2005 and May 2007 (see Methods and Results for details).

Class	Adult		Subadult	
	Male	Female	Male	Female
n	5	3	3	3
Location points	164.3 ± 72.7 (76-248)	204.3 ± 64.7 (135-263)	185.0 ± 123.8 (70-316)	264.7 ± 50.2 (207-299)
Tracking days	115.6 ± 54.4 (63-195)	161.3 ± 86.2 (64-228)	116.3 ± 54.5 (61-170)	152.0 ± 39.0 (107-176)
Tracking months	11.3 ± 3.6 (6.5-12.6)	12.4 ± 3.9 (10.0-14.1)	9.7 ± 2.0 (6.9-11.9)	10.7 ± 2.6 (8.4-12.0)

Table 2. Home range areas and core areas of 14 Crested Serpent-eagles (*Spilornis cheela hoya*) tracked in southern Taiwan between November 2005 and May 2007 (see Methods and Results for details).

		Home range area (km^2)				Core area (km^2)			
		100% MCP		95% FK		AIM[a]		50% FK	
Group	n	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Age class									
Adult	8	13.76	12.19	3.50	2.77	0.97	0.86	0.54	0.57
Subadult	6	10.78	5.01	2.82	1.73	0.60	0.30	0.33	0.17
Sex									
Male	8	16.65	10.98	4.52	2.30	1.16	0.73	0.64	0.50
Female	6	6.93	2.38	1.46	0.44	0.36	0.20	0.20	0.15
Total	14	12.48	9.59	3.20	2.32	0.81	0.68	0.45	0.44

[a] Probability of differential space use of fixed kernel area determined by AIM.

overlap in space usage. Of these 17 individuals, only 14 provided tracking data covering dry and wet seasons for at least three months thus meeting our minimum requirement of the number of locations of at least 30 points for each season (Table 1). To avoid autocorrelation, 3,479 location points were sieved after which 2,779 points remained. The numbers of location points for individuals ranged from 70 to 316 (Table 1). The 14 Crested Serpent-eagles can be divided into 8 adults (5 males, 3 females) and 6 subadults (all after second year) (3 males, 3 females). Among these breeding individuals, only two mating pairs (M258 and F138, F400 and M536) were comprised.

Home range and core area

The 100% MCP areas ($\overline{X}$ ± SD) of individual males (16.65 ± 10.98 km^2) were significant larger (U = 5.0, P = 0.014) than those of individual females (6.93 ± 2.38 km^2) while there was no significant difference between those of the adults (13.76 ± 12.19 km^2) and the subadults (10.78 ± 5.01 km^2) (U = 20.0, P = 0.61) (Table 2). The 100% MCP areas of five individuals covered a low proportion of sea waters (M258 - 4.4%, M277 - 5.9%, F417 - 1.8%, M459 - 0.9%, M475 - 4.3%). Since inclusion or exclusion of sea waters had no evident effect on our results, we removed sea waters in the following analyses.

The overall 95% FK areas of the 14 Crested Serpent-eagles ranged from 0.94 to 7.85 km^2, with an average of 3.20 km^2 ± 2.32 km^2 (Table 2, Fig. 2). No significant difference in 95% FK areas of adults (3.50 ± 2.77 km^2) and subadults (2.82 ± 1.73 km^2) was found (U = 28.0, P = 0.61). However, the 95% FK areas of males (4.52 ± 2.30 km^2) were significantly larger than those of females (1.46 ± 0.44 km^2) (U = 0.0, P = 0.002). Only one individual (M258) had a 95% FK area covering 0.4% of the sea area. We again removed sea waters from subsequent analyses.

The patterns for the AIM and 50% FK core areas were consistent with the overall result for the 95% FK areas (Table 2). AIM core areas showed that males used larger areas than females (U = 6.0, P =0.02), but with no significant difference between the ages (P =0.90). Similarly, analysis for the 50% FK core areas also showed differences between the sexes (U = 8.0, P = 0.04) but not between the ages (P = 1.00).

The area–probability of use curve of the Crested Serpent-eagles showed a concave trend (Fig. 3). All 14 individual plots showed perfect concave curves, indicating all eagles established cores. Fig. 3 is a combined version of these plots and indicated that the 14 Crested Serpent-eagles tended to use the internal space of their home ranges in a centralized way rather than randomly or uniformly. All of the core areas of individuals that were assessed by AIM had a demarcation point for the relative probability of use

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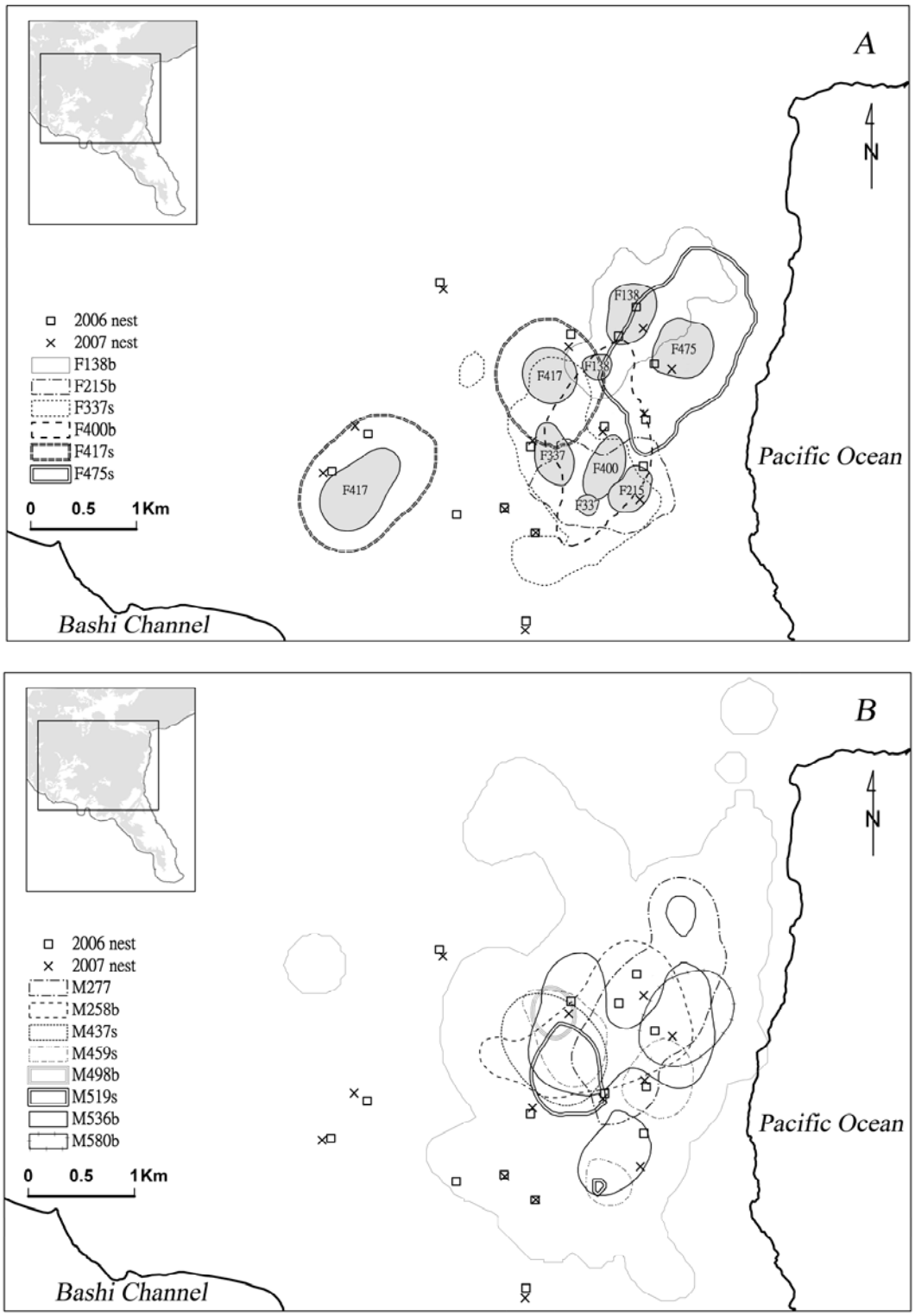


Fig. 2. Maps of (A) 95% fixed kernel areas (differently styled lines) and Area Independent Method areas (shaded polygons) for female and (B) Area Independent Method areas (differently styled lines) for male Crested Serpent-eagles (see Tables 1 and 2 and Results for details). Because the 95% fixed kernel areas of individual males highly overlapped, only the outer border (light grey line) which demarcates the merged 95% fixed kernel areas of all the individual males is shown. The letters attached to the female and male identification numbers correspond to (b) breeding individual and (s) subadult.

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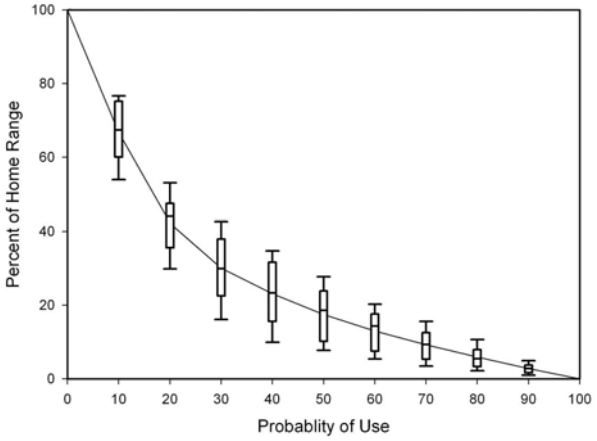


Fig. 3. Relationships between the probability of use and percentage of the home range within specific probability of use of 14 Crested Serpent-eagles (*Spilornis cheela hoya*) in Eluanbi peninsula of southern Taiwan, 2005-2007. The curve represents the average percentage value of utilization area relative to home range area under various probabilities of use by the 14 eagles. The box plots show the maximum and minimum as well as upper and lower quartiles under various probabilities.

which ranged between 23 and 42%. The percentage of the AIM core area that was accounted for in the 95% FK area was 24.7 ± 6.6% (12.8% - 34.7%, n = 14) indicating that the eagles primarily used only a small part of their home ranges. Moreover, the AIM areas (0.81 ± 0.68 km^2, range 0.17 – 2.08 km^2, n = 14) of individuals were always greater than their 50% FK areas (0.45 ± 0.44 km^2, range 0.10-1.70 km^2, n = 14). However, this difference was not significant (P = 0.11).

Females (1824.0 ± 285.7 g, n = 6) were slightly heavier than males (1538.9 ± 184.0 g, n = 8) (P = 0.045). Although adults within the male and female groups were slightly heavier than the subadults, the age difference was not significant (P = 0.35). No correlation between pooled body weights and home ranges was found (MCP, R^2 = 0.02, P = 0.61 and 95% FK area, R^2 = 0.01, P = 0.81). However, male body weights and 95% FK areas were positively correlated (R^2 = 0.81, P = 0.02) while no such correlation was found for the females (R^2 = 0.04, P = 0.95).

Any of our radio-tracked individuals overlapped with at least another 11 individuals using the 95% FK home range scale, and at least another three individuals at the core area scale. Considering only individuals with some extent of 95% FK home range overlap with another radio-tagged eagle (n = 87 combinations), overlap of AIM core areas occurred in 67.8% (n = 59 combinations) of the interactions. Of the eagles with overlap at the 50% core area, female–male (54.2%, n = 24) interactions occurred most frequently, followed by male–male interactions (40.7%, n = 32) and female–female interactions (5.1%, n = 3) (Fig. 4).

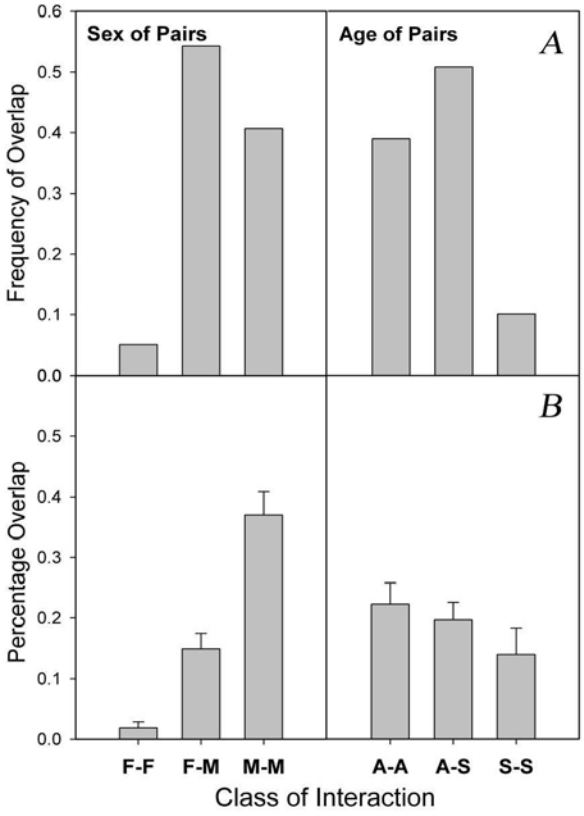


Fig. 4. (A) Frequency and (B) percentage of AIM core area overlap for pairs (mean ± SE) of individuals (see Results for details). The frequency refers to the percentage of the total number of individuals which overlap in the core area. Type of interactions was categorized as: F-F = female-female, F-M = female-male, M-M = male-male, A-A = adult-adult, A-S = adult-subadult, S-S = subadult-subadult.

Among individuals with 95% home-range interactions, males had an average of 37.0% of their core areas overlapping with another male and 14.9% of their core areas overlapping with a female (Fig. 4). On average, 1.9% of a female eagle's core area overlapped with another female (Fig. 4). Sex differences in percentage of core-area overlap were statistically significant (P < 0.001), with pairwise comparisons indicating that the amount of overlap was significantly different between male–male pairs and female–male pairs (P < 0.001), male–male pairs and female–female pairs (P < 0.001), and female–female pairs and female–male pairs (P = 0.003).

As for the overlap of core-area which occurred among age-class pairs, adult–subadult interactions (50.9% of pairs, n = 30) were the most frequent (Fig. 4), followed by adult–adult (39.0%, n = 23) and subadult–subadult interactions (10.2%, n = 6). Mean proportions of core-area overlap calculated for adult–adult, adult–subadult, and subadult–subadult were 22.3%, 19.6%, and 13.9%, respectively (Fig. 4). No age

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differences among these three percentages of core-area overlap was detected ($P = 0.40$).

DISCUSSION

In this study, the locational data of radio-tracked Crested Serpent-eagles showed that all individuals stayed in the study area during the research period and did not engage in any dispersal or regular long-distance movements, thereby meeting the required assumptions for home range studies (Spencer and Barrett, 1984; Hooge, 1995). Therefore, by monitoring the number of breeding pairs and nesting sites, we also learned that the majority of the individuals caught were almost entirely concentrated in the central study area where the traps were set, allowing us to understand the interactions of ranging behavior among these individuals, as well as the connection they have to their nesting sites.

In our study, sex-related area requirements and interactions of home range areas and core areas differed between male and female Crested Serpent-eagles. The annual home range areas and core areas of males were approximately three times larger than those of females. Male core areas were considerably shared with the male and the female individuals. On the contrary, the core areas of female eagles were not only smaller, but showed a much lower level of sharing with other females as well as males. Sex-related differences in the size of home range areas are well documented in many raptors. Two major reasons for these sex-related differences may be attributed to the sexes' respective reproductive roles and dominance (Newton, 1979; Ardia and Bildstein, 1997). First, home ranges of birds of prey may differ between sexes because of the sexes' different lifestyles (Kennedy et al., 1994; Ardia and Bildstein, 2001). The usually larger size of the males' home ranges is partially due to their responsibility of providing food during the breeding period (Newton, 1979). The expansion of the home range allows for the potential consumption of more food items either by breeding males or inexperienced subadult males (Fernández et al., 2009; Willey and van Riper, 2007). Second, reversed sexual size dimorphism (where females are larger than males) is found in most birds of prey (Newton, 1979; Paton et al., 1994; Massemin et al., 2000; Krüger, 2005) and confers female dominance over males in competing for better food resources, perches, roosts or territories (Newton, 1979; Mueller and Meyer, 1985). Some studies showed that a difference of 10-15% in body mass between sexes, e.g., in kestrels, may contribute to ecological and energetic differences such as different habitat use (Smallwood, 1988), habitat selection (Ardia and Bildstein, 1997) and habitat segregation (Ardia, 2002).

In this study, radio-tracked females were 18% heavier than radio-tracked males, which is presumably large enough for females to actively exclude males from their preferred areas. Therefore, we found support for the hypothesis proposed by Ardia and Bildstein (1997) that sex-related behavioral dominance can lead to different habitat use for the subordinate sex. The supposed dominance of females would explain the differential use of core areas. The female core areas were arranged in a manner of compactness (see Fig. 2A), from which other females but not males were excluded. On the other hand, male core areas were larger and much more overlapping with those of other females and males. Therefore, among males the core area overlap was highest and territoriality was nearly absent.

The lowest core area overlap occurred between the adjacent female Crested Serpent-eagles, indicating territorial boundaries existed. Female raptors may more aggressively and conspicuously defend the territories around their nests against other females but not males because females pose a larger threat. Such a threat could be the loss of the valuable nesting site, the deposition of another female's eggs, the predation of its own young or the appropriation of valuable food items near the nesting site. Territorial defense behaviours, such as calling or chasing intruders, were much more commonly observed for the females than the males in our study; e.g., 19 out of 22 chases of intruding individuals were performed by females (T. C. Chou, unpublished observations). Therefore, females appear to have higher levels of territorial aggression than males. Because food resources and suitable nesting sites are among the most critical components of habitat quality for raptors (Newton, 1979; Kostrzewa, 1996), the females of our study may have been more prone to territorial aggression and the resulting exclusivity than the males. As in most carnivores, limiting intrasexual access to foraging or nesting sites by other females is a better strategy (Macdonald, 1983; Katnik et al., 1994; Yamaguchi and Macdonald, 2003). Moreover, burning, logging, and charcoaling as well as grazing activity in this forest area over the past one hundred years have likely contributed to the eradication of historical nesting trees which need to be concealed and wind-resistant (Chen, 1997; Chou, 2006), making their defense even more urgent. In previous studies, the Crested Serpent-eagles showed high fidelity to its nesting trees (Chou, 2005; Chou, 2006). Furthermore, the majority of nesting trees (92.5%) were located in small, sheltered humid valley terrains which had high prey abundance (Chou, 2005). Because of the need to defend the nesting site and core foraging area from potential intruders, breeding females may have decided not to stray far away from their nesting sites and foraging grounds to

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avoid having their resources appropriated. All the above reasons probably caused females to have more compact core areas.

No significant age differences for the size of home ranges and core areas or for the proportions of core area overlap were apparent among the three different age-class comparisons. This may be because individuals after the second year begin to adopt similar ranging behaviors or pursue similar resources as the adults. For instance, Griffin and Baskett (1985) found that the mean winter range sizes did not differ between immature and adult bald eagles which used similar foraging areas.

In general, the size of the home range areas of predators is not only related to factors such as sex and age, but also to body weight (Harestad and Bunnell, 1979), trophic status (Schoener, 1968; Newton, 1979) and food availability (Krüger, 2000; Zabel et al., 1995). We found a positive correlation between male body mass and home range area which may be explained by the increase in daily energy demand with increasing body weight, resulting in an increased food gathering range (Peery, 2000). However, no such correlation was found for the females; a possible reason for the absence of this correlation may be that females occupied much more productive foraging areas so that any difference in home range area due to body weight differences was not apparent statistically, even if it existed.

Since the nesting sites of Crested Serpent-eagles may not necessarily be centered in the home ranges (Fig. 3), and because the home ranges of female and male individuals of mating pairs may not overlap completely, nest locations are not a useful standard to define valuable areas for conservation purposes. Therefore, conservation plans should consider the home range and core areas of both sexes. Moreover, we recommend that the larger home range areas are used as a reference for management decisions in order to successfully conserve this species. The compact core areas within the home range areas of all individuals were heavily used by various individuals for food and roosting throughout the year. Therefore, conservation management should try to maintain the crucial forest ecosystems by curtailing potentially harmful recreational activities. Furthermore, access to sections necessary for foraging and breeding should be regulated or prohibited at least during the breeding season.

ACKNOWLEDGEMENTS

We thank Kenting National Park Headquarters of Taiwan for financial support and two anonymous reviewers for comments and suggestions. We thank M. S.-Pan, K.-F. Chen, J.-C. Hu, B.-R. Huang, and T.-W. Jang for field assistance and H.-S. Chen and C.-S. Ho for providing valuable advice and technical assistance.

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臺灣南部大冠鷲（*Spilornis cheela hoya*）空間利用型態

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(收稿日期：2011 年 5 月 6 日；接受日期：2011 年 7 月 15 日)

摘要：本研究於 2005 年至 2007 年間利用無線電追蹤技術，針對臺灣南部不同性別與年齡的大冠鷲，進行活動範圍與核心區域的空間利用研究。採用最小多邊形（minimum convex polygon）法，計算 8 隻雄鳥和 6 隻雌鳥的平均活動範圍分別為 16.65 km^2 和 6.93 km^2；採用固定核區域法（95% fixed kernel method）則分別為 4.52 km^2 和 1.46 km^2。所有個體的活動範圍經獨立區域法（Area Independent Method）驗證空間利用機率差異，證實存在客觀密集利用的核心區域，雄鳥和雌鳥此客觀利用的核心區域平均面積分別為 1.16 km^2 和 0.36 km^2，大於主觀以 50% fixed kernel area 定義的 0.64 km^2 和 0.20 km^2。以固定核區域法計算的雄鳥平均活動範圍是雌鳥的 3.1 倍大，以獨立區域法獲得的雄鳥核心區域是雌鳥的 3.2 倍大。所有個體的活動範圍呈現高度相互重疊，甚至核心活動區域也與其他個體呈現不同程度分享。雌性個體間、雌性與雄性個體間、以及雄性個體間三個組合的核心區域面積重疊比例的平均分別為 1.9%、14.9% 和 37.0%，相互呈現顯著差異。相較於雄鳥對雄鳥和雄鳥對雌鳥，雌鳥對雌鳥的核心區域的空間分布與利用呈現明顯的排他性。此種雄鳥的核心區域相對較大且重疊度高以及雌鳥的核心區域相對較小且共享程度低的情形，我們認為由於雌鳥的平均體重高於雄鳥約 18%，此種空間利用型態的差異與雌鳥的強勢有關。

關鍵詞：核心區域、活動範圍、無線電追蹤、空間利用、大冠鷲。

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