

Habitat Selection of the Cooperative Breeding Taiwan Yuhina (*Yuhina brunneiceps*) in a Fragmented Forest Habitat

Pei-Fen Lee¹, Sheng-Feng Shen^{1,2}, Tzung-Su Ding³, Chyi-Rong Chiou³, and Hsiao-Wei Yuan^{3,*}

¹Institute of Ecology and Evolutionary Biology, and Department of Life Science, National Taiwan University, Taipei, Taiwan 106, R.O.C.
E-mail: leepf@ntu.edu.tw

²Present address: Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA
E-mail: ss456@cornell.edu

³School of Forestry and Resource Conservation, National Taiwan University, Taipei, Taiwan 106, R.O.C.
E-mail: ding@ntu.edu.tw (TSD), esclove@ntu.edu.tw (CRC), and hwyuan@ntu.edu.tw (HWY)

(Accepted July 22, 2005)

Pei-Fen Lee, Sheng-Feng Shen, Tzung-Su Ding, Chyi-Rong Chiou, and Hsiao-Wei Yuan (2005) Habitat selection of the cooperative breeding Taiwan Yuhina (*Yuhina brunneiceps*) in a fragmented forest habitat. *Zoological Studies* 44(4): 497-504. We used multilevel analyses (individual habitat selection and population structure) to study edge effects on the Taiwan Yuhina (*Yuhina brunneiceps*), an endemic subtropical species at Meifeng, central Taiwan. The 95% kernel home range area was used to study habitat preferences, and the source-sink threshold was calculated to determine whether this yuhina population is self-sustainable. Within the study site, woods, open spaces, orchards, buildings, and pond habitats were preferred in that order. Within the home ranges, orchard habitats were preferred to open spaces. Larger breeding groups had larger home ranges with more trees and open spaces. Nest sites were closer to forest edges than random points were. The density of Taiwan cherry trees was significantly higher within home ranges than available areas, especially near edges, suggesting the fruit's potential value to breeding yuhinas. Although the yuhinas suffered high rates of nest failure at Meifeng, this population still seemed to be self-sustaining due to the long breeding season with multiple broods and a cooperative breeding strategy. <http://zoolstud.sinica.edu.tw/Journals/44.4/497.pdf>

Key words: Edge, Fragmentation, Home range, Source-sink population dynamics.

Habitat fragmentation and habitat loss are considered major threats to biodiversity (Wilson 1992). One unavoidable consequence of habitat fragmentation is an increase in edge habitats, which in turn affects abiotic and biotic processes in the landscape (Murcia 1995). Nesting birds may disproportionately favor the edges of forest patches due to the availability of forest cover and abundant food, but may suffer high nest predation as a result. Therefore, edges may become "ecological traps" leading to severe population declines in edge-nesting species (Gates and Gysel 1978).

The effects of habitat fragmentation are not homogeneous. There are species-specific responses (e.g., Warkentin et al. 1995, Bourque

and Villard 2001, Flaspohler et al. 2001), guild-specific responses (e.g., Stouffer and Bierregaard 1995), and, theoretically, life history-specific responses (e.g., Donovan and Thompson 2001) to edge habitats. How individuals perceive patchiness and how they move among fragments influence how they are affected by fragmentation (Wiens 1994, Ims 1995, Andreassen et al. 1998). Therefore, understanding the pattern of habitat selection, together with the behavioral basis for the selection, can help explain variations in edge effects. Few studies have combined individual-level mechanisms with a population-level demographic structure. Even fewer, if any, multilevel studies have been conducted in tropical and sub-

*To whom correspondence and reprint requests should be addressed. Tel: 886-2-23660235. E-mail: hwyuan@ntu.edu.tw

tropical areas, where ecological contexts (e.g., higher predation risks and longer breeding seasons) and life histories (e.g., multiple broods) may widely differ from those of temperate species. These differences may have profound influences on a species' responses to edge habitats (Martin 1996, Russell 2000, Stutchbury and Morton 2001).

The Taiwan Yuhina (*Yuhina brunneiceps*), with monomorphic sexes, is a passerine bird endemic to Taiwan (Cibois et al. 2002). It is widely distributed in forests from 800 to 3000 m in elevation (Koh and Lee 2003). Yuhinas are the only known passerine species to consistently adopt a joint-nesting strategy in a large fraction of nests (Vehrencamp and Quinn 2004). Breeding groups include 2-7 individuals composed primarily of non-kin. Therefore juvenile delayed-dispersal is not observed (Yuan et al. 2004). Living in groups typically grants each individual increased protection from predators and increased chances of finding food (Krebs and Davies 1993). In White-throated Magpie-Jays (*Calocitta formosa*), a cooperatively breeding species, it has been shown that larger groups possess larger territories containing more food, which contributes to higher reproductive success (Langen and Vehrencamp 1998).

In this paper, we examined 1) the influence of fragmentation on yuhinas, at the individual level, with respect to (a) habitat selection and (b) the behavioral basis of habitat selection in terms of nest site and food resources; 2) this yuhina population's possible status as a source population (in terms of meta-population dynamics (Pulliam 1988); and 3) variations in home range qualities among breeding groups of different sizes.

MATERIALS AND METHODS

Behavioral observations

We conducted this study at Meifeng Highlands Experiment Farm of National Taiwan University in Nantou County, central Taiwan (24° 05'N, 121° 10'E, elevation 2150 m; Fig. 1). The study site, established for horticultural research purposes in 1961, a 50 ha area mixed with greenhouses, temperate-fruit orchards, meadows, Japanese Cryptomeria (*Cryptomeria japonica*) plantations, and various ornamental trees surrounded by natural forests composed mainly of Fagaceae and Lauraceae.

Since 1995, we have banded adult and juvenile yuhinas at Meifeng to study their breeding

ecology. By 2001, 97% of the adults in our study site were color-banded. We closely monitored the breeding success of 6, 11, and 13 groups in 1998, 2000, and 2001, respectively. Each morning of the 2001 breeding season (early Mar. to late Aug.), we walked along a fixed route that covered the entire study site, weather permitting. When we encountered a banded group, we followed the group and plotted each member's location on a fine-scale map every 5 min until contact was lost. To facilitate mapping, we established a grid system with reference points every 20 m at the study site.

In 2001, 91 nests were found from 20 breeding groups for nesting analyses. We searched for yuhina nests in both natural and man-made habitats and mapped the location of each nest. We were confident that most of the nests within the study site had been discovered, as yuhinas are an active and conspicuous species, and every breeding group was closely followed.



Fig. 1. Study area and land cover map at Meifeng, the Highlands Experiment Farm of National Taiwan Univ., Nantou County, central Taiwan.

Although the diet of yuhinas varies with the seasons, it consisted primarily of fruits, nectar, and insects within the study site. During the breeding season, yuhinas mainly foraged on 3 plant species: nectar (Jan.-Apr.) and fruits (May-June) of Taiwan cherry (*Prunus campanulata*), fruits (May-July) of Eastern debregeasia (*Debregeasia orientalis*), and nectar (Aug.-Sept.) of mistletoe (*Taxillus lonicerifolius*) (Liu 1999). We mapped the locations of these 3 species within the study site and used their abundances as food resource indexes for the yuhinas.

Habitat data analysis

A digitized habitat map of the study site was created by interpreting an aerial photo (1:5000, 0.5 x 0.5 m in spatial resolution, taken in 2000 by the Agricultural and Forestry Aerial Survey Institute of the Taiwan Forestry Bureau, Council of Agriculture, Executive Yuan) using ArcGIS 8.1 (ESRI 2001). Five major habitat types were identified by land cover and land use: woods, orchards, buildings, open spaces, and ponds (Fig. 1). Wooded habitat was defined as forest patches and hedgerow strips with trees more than 3 m in height and included primary forests and *Cryptomeria* plantations. Orchard habitats were plantations of temperate fruit trees, mostly apples, peaches, and pears. Building habitat included greenhouses, residences, and offices. Open space habitat included scattered open spaces with shrubs < 3 m in height, scattered individual trees, grass, bare ground, trails, concrete or asphalt roads, and nearby areas. Pond habitat consisted of human-constructed irrigation ponds. All patches of the 5 habitat types were confirmed by field verification.

Nest sites and all locations where banded group members were observed were mapped using ArcGIS 8.1. A fixed kernel density analysis was applied to delineate the home range of each breeding group. We used a 95% kernel area to avoid potential bias caused by extreme points (Silverman 1986, Powell 2000). To determine nest site preferences in wooded habitat, we generated random points in the wooded habitat within each group's home range using Animal Movement (ArcView) software (Hooge and Eichenlaub 2000), then calculated the distance from each nest site and random point to the nearest edge.

To determine habitat preferences of each group, we overlaid each home range with the habitat map and calculated the area composition of the habitat types. Food resource quality was indexed

by the density of the 3 major food plants within the home range. Those plants shared by home ranges of multiple breeding groups were equally divided by the number of groups and assigned to each home range.

Two levels of use-availability design (Johnson 1980), i.e., utilization vs. home range and home range vs. available area, were conducted to assess habitat selection by yuhinas. We determined the available area for each group separately by generating 100 m circular buffers around all group members' occurrence locations by ArcGIS (McClellan et al. 1998, Jones 2001). Because proportions of habitat types were not independent, we used compositional analyses to determine the habitat preferences of yuhinas (Aebischer et al. 1993).

Demographic data analysis

The source-sink threshold, as the number of juveniles per pair per year, was calculated according to the following equation (Trine 1998) for 1998, 2000, and 2001:

$$\text{Source-sink threshold} = \frac{2 * \text{adult mortality}}{1 - \text{juvenile mortality}}$$

The adult mortality rate was estimated by the overwintering return rate. Because juveniles commonly disappear from Meifeng (78%, Yuan et al. 2004) and we have observed banded juveniles which had dispersed as far as 7 km away, direct estimation of the juvenile mortality rate was extremely difficult. We used 50% of the adult survival rate to estimate yearling survival rate, as has been done in many migratory songbird studies (Greenberg 1980, May and Robinson 1985, Thompson 1993, Donovan et al. 1995). If the annual productivity of the population was higher than the calculated source-sink threshold, the population was considered to be a demographic source. Alternatively, the average number of fledglings and the adult mortality rate of a given year were applied to the source-sink threshold equation. We could thus obtain the maximum juvenile mortality rate for a self-sustainable population each year.

RESULTS

Nesting ecology

Most (84%) nests were found during the con-

struction stage. Seventy-six nests (84%) were built in wooded habitats (Fig. 2); among them, 63 nests (83%) were built in Japanese Cryptomeria. The Manly-Chesson indexes also strongly indicated that woods were the most-important habitat used by yuhinas (Table 1). The distance from



Fig. 2. Distribution of 91 yuhina nests found at Meifeng during the breeding season of 2001. Most (84%) of the nests were built in trees. The gray area indicates the wooded habitat as shown in figure 1.

each nest to the nearest wooded edge was significantly shorter than that from random points (Mann-Whitney U test = 1154.50, $p < 0.001$, $n = 74$; Fig. 3).

Home range preference

Of the 20 breeding groups followed, only 13 groups had home ranges completely within the study site, and the following analyses of home range preferences were limited to those groups. We recorded 99 ± 28 (mean \pm SD) occurrence locations (i.e., location of individual or group sightings) per group during the 2001 breeding season. The area of the 95% kernel home range of the breeding groups was 2.3 ± 2.0 ha (Fig. 4). Most of the breeding groups had home ranges which greatly overlapped those of other groups. The home range of each group, on average, overlapped with 2.5 other groups' home ranges. The

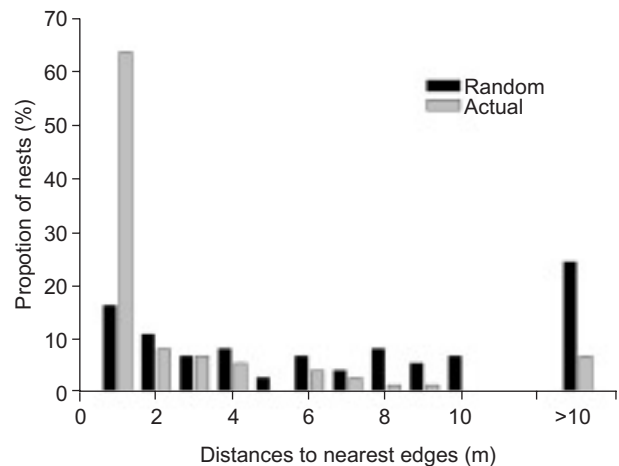


Fig. 3. Comparison of distances of nests and of randomly selected points within the wooded habitat to the nearest edge.

Table 1. Manly-Chesson selectivity indexes of nest site selection for yuhinas at Meifeng in 2001

	Habitat type				
	Buildings	Orchards	Open spaces	Woods	Ponds
Percentage available (%)	3.00	11.4	40.5	44.8	0.31
Percentage of all nests found (% , $n = 91$)	1.10	6.6	8.80	83.5	0.00
Manly-Chesson index ^a	0.37	0.58	0.22	1.86	0.00
Standardized Manly-Chesson index ^b	0.12	0.19	0.07	0.62	0.00

^aPercent used / percent available. ^bEach index was divided by the sum of all indexes.

average percent of overlap was about 35% (range, 0%-82%). The habitat composition of the 95% kernel home range significantly differed from that of the entire study site (Wilks' lambda = 0.087, $F_{5,20} = 44.0$, $p < 0.001$). The most frequently used habitats were woods, open spaces, orchards, buildings, and ponds, in that order. Similarly, within the home range of each breeding group, habitat composition of the occurrence locations of breeding groups significantly differed from the habitat composition of the home ranges (Wilks' lambda = 0.136, $F_{3,22} = 46.6$, $p < 0.0001$), indicating that yuhinas showed habitat preferences. Within the home ranges, woods, orchards, open spaces, buildings, and ponds were preferred, in that order.

Food plants were abundant within each groups' home ranges (Fig. 5). These plants were usually located within wooded patches, where they typically comprised the subordinate or shrub layers vertically. Only the density of Taiwan cherry was significantly higher within the home ranges than in other available areas (Mann-Whitney U test = 15.00, $p < 0.001$; Fig. 6). In addition, we found

that 85% of these trees were in wooded patches.

Group size effect of home range quality

Breeding groups did not choose home range areas and habitat types within home ranges at random (Wilks' lambda = 0.064, $F_{5,8} = 23.47$, $p < 0.001$). Larger groups used larger home range areas ($r_s = 0.684$, $p < 0.01$). However, the area per capita did not differ across groups (0.53 ± 0.27 ha, $r_s = 0.077$, $p = 0.234$). Two habitat types, wooded ($r_s = 0.712$, $p = 0.006$) and open spaces ($r_s = 0.712$, $p = 0.006$), made up larger proportions of the habitat within home ranges of larger breeding groups. Other habitat types did not vary from group to group ($p > 0.05$), and neither did food plants ($p > 0.05$).

Is the Meifeng yuhina population self-sustainable?

Adult mortality rates were estimated to be 28.6%, 18.8%, and 30.6% in 1998, 2000, and

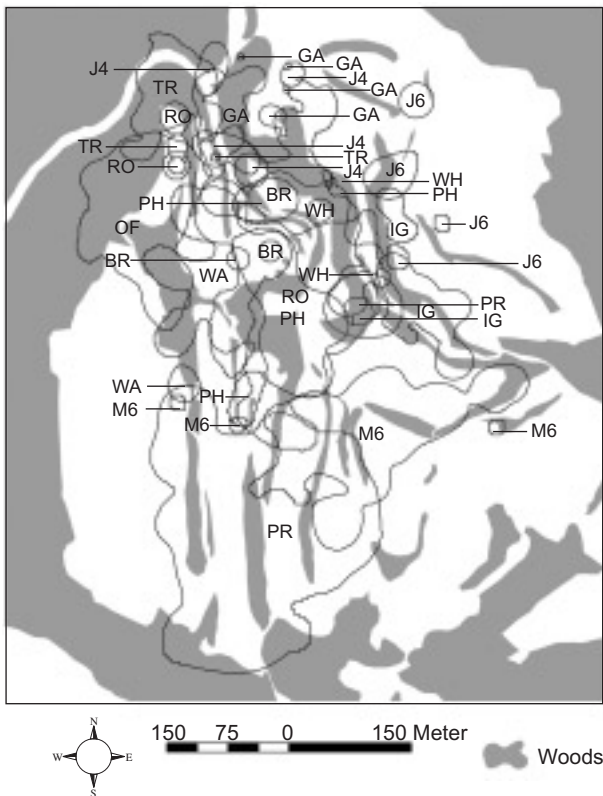


Fig. 4. Distribution of the 95% kernel home ranges of 13 yuhina breeding groups. Letters and numbers on the map refer to individual groups, and the gray area indicates the wooded habitat as shown in figure 1.

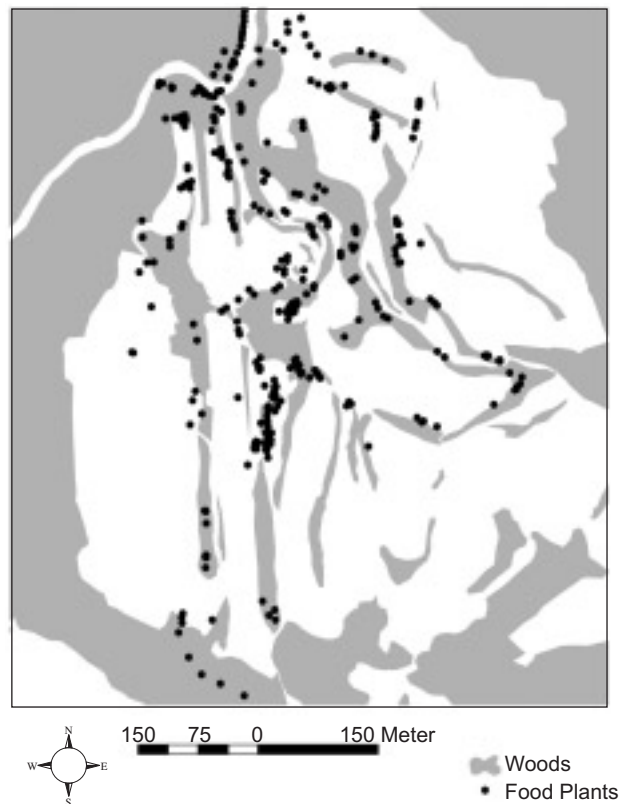


Fig. 5. Distribution of major food plants, Taiwan cherry (*Prunus campanulata*), Eastern debregeasia (*Debregeasia orientalis*), and mistletoe (*Taxillus Ionicerifolius*), at Meifeng. The gray area indicates the wooded habitat as shown in figure 1.

2001, respectively. The number of adults and fledglings of different groups were pooled for each year to calculate the annual productivity. There were 28, 48, and 49 breeders and 29, 30, and 40 fledglings in 1998, 2000, and 2001, respectively. The average numbers of fledglings per pair were 2.1 and 1.3 in 1998 and 2000, higher than the source-sink thresholds of 1.3 and 0.6, respectively. However, in 2001, the average number of fledglings per pair was 1.6, which equaled the source-sink threshold of 1.6.

We used the data given above to calculate the "maximum" juvenile overwintering mortality rates for the population to be self-sustainable (see "Methods" for details). These maximum juvenile mortality rates were 72.8%, 71.0%, and 61.8%, which were 2.5, 3.8, and 2.0 times higher than the adult mortality rates in 1998, 2000, and 2001, respectively.

DISCUSSION

The yuhina population within the fragmented habitats at Meifeng Farm seems to be a self-sustainable population based on our demographic analyses. We believe that the conventional assumption of a juvenile survival rate of 50% of the adult survival rate for migratory birds in our analyses is a conservative estimate, because yuhinas typically migrate short distances along local elevational gradients (Liu 1999). In addition, the maximum juvenile mortality rates for this population if it were self-sustainable were larger than those of most studies on migratory birds. As in Anders and Marshall's (2005) review of 7 species with detailed

estimations of fledgling survival rate, the average overwintering survival rate was 52% (range, 25%-72%), generating an average mortality rate of 48%. Therefore, even with such high estimated juvenile mortality rates in our study compared to others, this population is still (or very close to) self-sustainable.

Meifeng Farm is comprised of a mosaic of habitat types. One interesting question is the effect of such spatial heterogeneity on ecological processes for the yuhinas. We found that wooded patches were an important habitat type for providing nest sites and food supply at the individual habitat selection level. This might be "habitat compensation" which indicates that animals may compensate for the loss of their preferred habitat type (woods) by shifting to a less-preferred one (orchards) (Haila et al. 1989, Norton et al. 2000).

Yuhinas frequently selected wooded and orchard patches as nest sites, especially near the edge. Houbara Bustards (*Chlamydotis undulata*) were found to select edges as nesting sites to increase their ability to detect predators (Yang et al. 2003). Predation was the primary cause of nest failure at Meifeng in 2001 (55%, Yuan HW, unpubl. data). However, the major nest predators were Eurasian Jays (*Garrulus glandarius*) and Taiwan Sibilas (*Heterophasia auricularis*), which are abundant around forest edges. Evidently, nest security was not a factor in the yuhinas' choice of edge habitats. The higher density of Taiwan cherry trees within the home ranges, especially around edges, might be one of the advantages for using edges to breed. In fragmented landscapes, the food supply generally declines with decreasing fragment size (Zanette 2001). But this is not the case at Meifeng where many plants, such as Taiwan cherry, were deliberately planted to enhance the visual landscape and have incidentally become food resources for the yuhinas. Abiotic microclimatic factors may also play a role in the yuhinas' preference for habitat edges. The forest interior is usually damp and cool at Meifeng. Higher temperatures and lower humidities at the edges (reviewed in Murica 1995, Roadewald and Yahner 2001) may lower energetic costs for incubating adults (Wolf and Walsberg 1996, reviewed in Hansell 2000) and provide a more-suitable microenvironment for the survival of eggs and chicks.

However, with its cooperative breeding strategy, yuhinas have some advantages for coping with the high rates of nest failure by reducing the workload per breeder with each nest attempt. Yuhinas

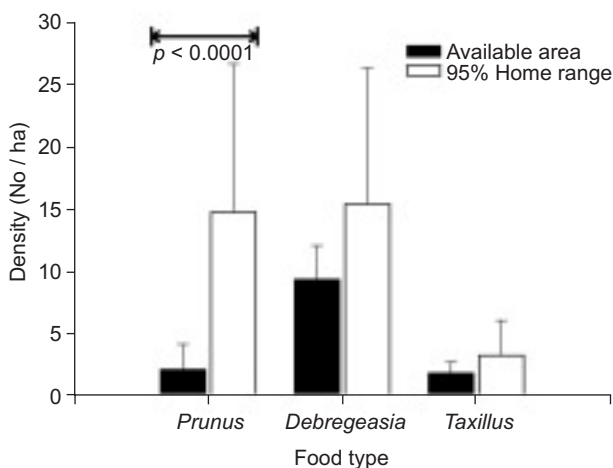


Fig. 6. Comparison of 3 food plant species densities within the 95% kernel home range areas with available areas.

exhibit multiple brooding in a single breeding season; greater numbers of breeders can accelerate the re-nesting process and therefore help spread out the risk of nest failure (Shen 2002). Thus, at the population level, the yuhinas at Meifeng served as the source populations in 1998 and 2000. In those years, the Mayfield nest survival rate was 27% and 25%, respectively (Yuan et al. 2004). In 2001, when predation and adverse weather condition caused an extraordinarily low nest survival rate (14%; Yuan et al. 2004), the population was static.

However, our study area is surrounded by natural forests, and our analyses were only carried at the habitat patch scale. Therefore, the landscape-scale effect of habitat fragmentation such as disruption of individual dispersal demonstrated by Cooper and Walters (2002) in the Brown Treecreeper (*Climacteris picumnus*) was not determined in our study. Further studies on multi-scale analyses will be valuable.

Larger groups using larger home ranges consisting primarily of wooded and nearby open habitat types is consistent with the overall home range habitat preferences of yuhinas, indicating a better home range quality for larger groups. White-throated Magpie-Jays (Langen and Vehrencamp 1998) and Groove-billed Anis (*Crotophaga sulcirostris*; Vehrencamp et al. 1988) show similar patterns. However, the area per capita is about the same. Also, there were no differences in the quantities of food plants in the home ranges of yuhina groups of different sizes, suggesting that larger groups using larger home ranges probably does not impact individual fitness in terms of food resource abundance. However, the greater proportion of wooded and open habitats within larger home ranges might provide nesting sites for larger groups.

While many studies on edge effects have been conducted in temperate zones, this study of a subtropical species with a unique life history has several implications for future work on edge effects. First, species life history characteristics (e.g., cooperative breeding and multiple broods) are important in understanding the edge effects on bird populations. Linking these mechanisms to larger-scale phenomenological explanations can further complete our understanding of edge effects and avoid misinterpretation of phenomena (like the high nest predation rate, in this case). Second, the ecological contexts of different regions can influence the edge effects (e.g., a long breeding season). Therefore, the study of edge ecologies of

tropical and subtropical regions and in the Southern Hemisphere will enhance our understanding and help delineate conservation policies (e.g., Schmiegelow and Mönkkönen 2002).

Acknowledgments: We thank LL Lee, SC Lee, the Chief Editor, and 3 anonymous reviewers for valuable comments on previous drafts of this manuscript; P Coulter and B Burt for English editing; and MC Tsai, KZ Lin, and other workers at the Meifeng Farm for logistical support. We greatly appreciate the volunteers from the NTU Nature Conservation Students' Club and School of Forestry and Resource Conservation, in particular HY Hung, IH Chang, and KD Zhong, for their help in the field. This study was partially supported by National Science Council and the Council of Agriculture, R.O.C.

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