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BREEDING ECOLOGY AND HABITAT USE OF THE DAITO SCOPS OWL (*OTUS ELEGANS INTERPOSITUS*) ON AN OCEANIC ISLAND

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ABSTRACT.—We studied the nest sites, diet, and habitat use of the endemic population of the Daito Scops Owl (*Otus elegans interpositus*), a subspecies of the Elegant Scops Owl (*O. elegans*), on a small oceanic island, Minami-daito, in the northwestern Pacific Ocean. We also investigated the relationships between habitat characteristics and breeding performance in the fragmented and developed habitats on the island. Most owls used nest cavities in introduced casuarina (*Casuarina* spp.) trees ($n = 30$), whereas a few owls used vertical hollows in broken native fan palm (*Livistona chinensis*; $n = 2$) as their nest sites. Owls fed on prey inhabiting both forests and open areas, including spiders (Heteropoda), cockroaches (Blattodea), grasshoppers (Orthoptera) and geckos (Gekkonidae). We tracked 17 territorial males and seven females using radiotelemetry in 2002–07. More than half of the owls selected *Ficus* forests during the breeding season. During the nonbreeding season, most owls selected edges between forests and open areas such as grasslands and sugar cane fields. Owls with more edge habitat within their home ranges laid eggs earlier ($n = 88$ breeding attempts) than those with smaller amounts of edge. Daito Scops Owls exhibited behavioral flexibility in their use of human-altered habitats on Minami-daito Island, which may have contributed to their avoidance of extinction.

KEY WORDS: *Daito Scops Owl*; *Otus elegans interpositus*; *Elegant Scops Owl*; *breeding*; *Casuarina*; *development*; *fragmented habitat*; *island*; *nest*.

ECOLOGÍA DE ANIDACIÓN Y USO DE HÁBITAT DE *OTUS ELEGANS INTERPOSITUS* EN UNA ISLA OCEÁNICA

RESUMEN.—Estudiamos los sitios de anidación, la dieta y el uso de hábitat de la población endémica *Otus elegans interpositus*, una subespecie de *O. elegans*, en una pequeña isla oceánica, Minami-daito, en el noroeste del Océano Pacífico. También investigamos las relaciones entre las características del hábitat y el rendimiento reproductivo en los hábitats fragmentados y desarrollados de la isla. La mayoría de las lechuzas usaron nidos en cavidades en árboles introducidos de *Casuarina* sp. ($n = 30$), mientras que unas pocas lechuzas usaron huecos verticales en la palma nativa *Livistona chinensis* ($n = 2$) como sus sitios de anidación. Las lechuzas se alimentaron de presas que habitan tanto bosques como áreas abiertas, incluyendo arañas (Heteropoda), cucarachas (Blattodea), saltamontes (Orthoptera) y geckos (Gekkonidae). Seguimos 17 machos territoriales y siete hembras usando radio telemetría entre 2002 y 2007. Más de la mitad de las lechuzas seleccionaron bosques de *Ficus* durante la estación reproductiva. Durante la estación no reproductiva, la mayoría de las lechuzas seleccionaron bordes entre bosques y áreas abiertas como las pasturas y los campos de caña de azúcar. Las lechuzas con más hábitat de borde dentro de sus rangos de hogar pusieron huevos más temprano ($n = 88$ intentos reproductivos) que aquellas con cantidades menores de borde. Los individuos de *O. e. interpositus* exhibieron una flexibilidad comportamental en el uso que hacen de los hábitats alterados por el hombre en la Isla Minami-daito, lo que puede haber contribuido a evitar su extinción.

[Traducción del equipo editorial]

Small, geographically restricted populations, such as insular endemic populations, are vulnerable to habitat loss (Thiollay 1997, Jones et al. 2001) and introduced species (Biber 2002). Of the 116 known

bird extinctions, 103 have occurred on islands (Gaston and Blackburn 1995). In contrast to those, some island species with wider niches are able to adapt or acclimate to habitat changes and introduced species (e.g., Vanderwerf 1994, Kato and Suzuki 2005, Velarde et al. 2007). Whether populations can survive

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following drastic or rapid habitat destruction often depends on their ecology, i.e., their habitat requirements, dietary specialization, body size, and geographic range (Redpath 1995, Sodhi et al. 2004, Hockey and Curtis 2008). To protect island populations from extirpation or extinction, we need to understand the detailed ecological aspects of each population in the community including native and introduced species.

Bird extinctions were recorded on the Daito Islands in the northwestern Pacific. After human settlement in about 1900 (Minami-daito Village 1990), four endemic avian subspecies became extinct (Ornithological Society of Japan 2000), perhaps because of deforestation for agriculture and/or phosphate mining.

Interestingly, the Daito Scops Owl (*Otus elegans interpositus*) inhabiting Minami-daito in the Daito Islands has avoided extinction, although it is dependent on tree cavities for nest sites (Takagi et al. 2005). In the fragmented and developed habitat currently available, this owl mainly inhabits the wooded shelterbelts and their margins (Takagi et al. 2007). The Daito Scops Owl is an endemic subspecies of the Elegant Scops Owl (*Otus elegans*). The Elegant Scops Owl is rated as a 'near threatened' species in the 2008 International Union for Conservation of Nature and Natural Resources (IUCN) Red List of threatened species (BirdLife International 2008). The number of territorial males of the Daito Scops Owl was estimated to be approximately 200 individuals on Minami-daito Island during 2005 to 2008 (Takagi et al. 2007, M. Takagi unpubl. data). Although Kita-daito Island is located approximately 12 km north of Minami-daito Island, Scops Owls are absent from Kita-daito Island (Anezaki et al. 2003), where less woodland remains. Minami-daito Island is currently the only island where the Daito Scops Owl lives.

We consider that the ecological flexibility of the scops owls has facilitated maintenance of the population on Minami-daito despite dramatic habitat alteration. We expect that these owls now depend on introduced species and developed or highly altered habitat for breeding and hunting because of reduction in native habitat. If so, conservation management, such as eradication of introduced species or restoration of native vegetation, should proceed carefully. Because a previous study showed that the owls only inhabit forested shelterbelts in the landscape (Takagi et al. 2007), we planned this study to further investigate habitat use in the home

ranges in these shelterbelts, as well as nest sites, prey use, and reproductive success.

METHODS

Study Area. Minami-daito Island (25°50'N, 131°14'E) is an oceanic island, 30.6 km² in area, with a 1-km-wide, 15-m-high band of small hills surrounding flatter land in the center. Agricultural land, mainly sugar cane fields, covers 60% of the island. Forested shelterbelt covers 13%, and the remaining areas comprise swamps, shoreline vegetation, and residential areas (Minami-daito Village 1990). The shelterbelts, 20–100 m (mean 62 m) wide, grow on the hills and are composed of a mixture of native species such as fan palm (*Livistona chinensis*) and Chinese banyan (*Ficus microcarpa*), and introduced casuarina (*Casuarina* spp.), mulberry (*Morus australis*), Ryukyu Island pine (*Pinus luchuensis*) and Alexandrian laurel (*Calophyllum inophyllum*). The island is located in the subtropics with a mean annual temperature of 23°C and a mean annual rainfall of 1627 mm (Japan Meteorological Agency 1961–2009).

Territory Estimates Using Call Playbacks. During the prebreeding periods (February–March from 2003 to 2009), we surveyed the shelterbelts for duetting pairs at night, and then searched for nest cavities where we had heard them during the day. We caught the nesting pairs using mist nets, and banded them with colored leg-bands covered with light-reflective tape.

We made an estimate of the males' territorial ranges using playbacks of male hoot-calls, broadcast with a portable mini-disk player. Territorial males followed us as we played the calls and walked away from the nest to the border with a neighboring male. We considered the point where a male stopped following us to be the edge of his defended area. In this way, we determined territory polygons with six points on the border for each male.

Reproductive Rates. We visited each nest at least once every 3 d from the prebreeding period to fledgling, and checked the nest contents with a miniature camera attached to the top of a pole. We considered any nest where eggs were laid to be a breeding attempt. We recorded breeding parameters such as laying date and clutch size per breeding attempt, and recorded the number of fledglings per successful nest, where a successful nest was defined as one where at least one nestling fledged.

Nest Characteristics and Availability. At natural cavity nests, we recorded the nest tree species and

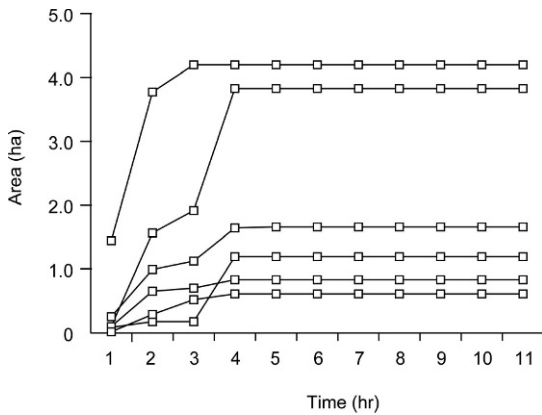


Figure 1. Relationship between time after sunset and cumulative 100% MCP home range size for each of the six Daito Scops Owls radio-tracked for one full night in the preliminary study from July to September in 2002.

diameter at breast height (DBH), nest height above ground, long and short axes of nest entrance, and depth of nest cavity. We measured the density of trees and available cavities (with larger entrance size and depth equal to or greater than the smallest natural nest cavity) in each tree species in 210 quadrates (10 m \times 10 m) randomly placed in the shelterbelts all over the island.

Diet. The diet of the owls was determined in two ways. We examined stomach contents of 11 owls accidentally killed by vehicles between 1999 and 2008. We also determined prey items brought to each nest by parents for nestlings by placing an infrared video-camera in front of nest entrances during the 4 hr after sunset. Each nest was filmed two or three times throughout the nestling period. Prey items were recorded to the order or family level.

Radio-tracking and Home-range Estimation. Territorial males and paired females were caught using mist-nets from 2002 to 2007. Radio transmitters were fitted to the owls using backpacks (Biotrack®, Wareham, Dorset, U.K.). The transmitters weighed 3.5 g including the Teflon harness, and averaged $4.2 \pm \text{SD } 0.2\%$ of the body mass in males, and $3.6 \pm \text{SD } 0.4\%$ in females. We tracked the owls on foot using a handheld 6-element Yagi antenna and receiver (Advanced Telemetry Systems®, Isanti, Minnesota, U.S.A.). A pilot study of six owls, tracked from sunset to sunrise in 2002, revealed that an owl would visit the entire extent of its home range during the first 4 hr after sunset (Fig. 1); in addition, parents fed nestlings most often in the first 4 hr after sunset (K. Akatani unpubl. data). Accordingly, we located

each tagged owl every 30 min during the 4 hr to determine home-range sizes and feeding sites. We tracked each tagged owl for one evening once per week. The location of an owl was estimated by triangulation with a mean horizontal error of $10.2 \pm \text{SD } 4.5$ m ($n = 20$) at a distance of <100 m from the owl (determined during the preliminary investigation). Home-range sizes were calculated using the 100% minimum convex polygon (MCP) method and 95% fixed kernel (FK) method using least-squares cross-validation (Seaman and Powell 1996). We used Home Ranger version 1.5 software (Hovey 1999) for calculating the kernel home ranges. Locations and home-range calculations were divided into the breeding season (May–August: nestling and fledgling periods) and nonbreeding season (September–December). We excluded location data in January–April (prebreeding and egg-laying period) from the analysis because few owls were tracked during this period.

Habitat Types. We constructed accurate hand-drawn maps of the habitat types in owl home ranges based on aerial photos. Where we could not determine habitat type from the photos, we visited sites and recorded habitat types directly. Six habitat categories were recognized within the home ranges: (1) Palm forests (fan palms, with few other tree species and understory mainly composed of native plants); (2) *Ficus* forests (stands on limestone outcrops, dominated by *Ficus* such as the Chinese banyan tree and other native plants); (3) Mixed forests (multilayered stands of casuarina, mulberry trees, Alexandrian laurel, and Ryukyu Island pine mainly consisting of introduced species); (4) Grass (open areas covered by grasses or shrubs with <100 cm height); (5) Cane (sugar cane fields); and (6) Others (bare soil, roads, and buildings). Habitat types from (1) to (3) were primarily in the shelterbelts, and types from (4) to (6) were in open areas. All six habitats were created or modified by human activity, including the forests composed of native plants (1, 2), which were replanted as shelterbelts in the 1920s (Minami-daito Village 1990). In particular, the habitat types from (3) to (6) did not exist before colonization (Minami-daito Village 1990).

Statistical Analysis. To examine whether owls selected edges between forests and open areas, we employed chi-square tests of differences between observed and expected number of locations for each individual. We only used locations in forests (habitats 1, 2, and 3) in this analysis because only 8.8% ($\pm \text{SD } 7.5\%$, $n = 24$) of locations were in open

habitats (4, 5, and 6), and owls used these habitats only for a few seconds if there were no perches. We considered that locations within 10 m from the edge were “edge,” and >10 m away were “within the forest,” based on the mean horizontal error of the preliminary telemetry study as noted above. We randomly chose 100 points from each 100% MCP home range (excluding open areas) to generate the distribution of the expected locations within the home range.

Second, we assessed the selection for each habitat type within the forests (i.e., >10 m within habitats 1, 2, and 3) using the resource selection ratio w_i (proportion of that habitat type used/proportion of that habitat type available) for each individual, following Manly et al. (2002). A value of $w_i = 1$ indicates no selection, a value >1 indicates greater use than expected based on availability, a value <1 indicates less use than expected. The w_i values were tested for significance using the chi-square test, based on the null hypothesis that owls used habitats in proportion to their availability. The proportion of each habitat type inside forests in the 100% MCP home range was taken as its availability. We excluded the locations at the nest sites from the analysis. Separate analyses were performed for breeding and nonbreeding seasons.

We examined the relationships of habitat to laying date, clutch size, and the number of fledglings from 2004 to 2009. As dependent variables, we used the area of the six habitat types and length of the edge between forests and open area in each territory, as determined in our playback investigation. The lengths of edge habitat within each territory were measured following the contours of the forests on aerial photos. We considered it appropriate to use the territories of all marked males, including tracked and non-tracked males, in this analysis because 100% MCP home ranges and the territories we estimated using playbacks were very similar (overlap of $92.0 \pm \text{SD } 9.6\%$, $n = 17$ tracked males). We used generalized linear mixed models (GLMM) with the year and individual owl as random factors, and the lme4 package (Bates et al. 2009) in R (R, version 2.8.1; R Foundation for Statistical Computing, Vienna, Austria). Laying date was analyzed with a normal error distribution and identity link; clutch size and number of fledglings were analyzed with Poisson error distribution and log link. There were no correlations among the seven dependent variables (Pearson's correlation analysis, $|r| < 0.7$, $P > 0.05$). The number of variables in the model was

progressively reduced using stepwise exclusion of the least significant terms.

RESULTS

Nest Characteristics and Availability. Of 32 natural nest cavities, 30 were in casuarinas, and the other two were in vertical hollows in snapped fan palms. The mean height of nests aboveground in casuarinas was 3.7 ± 1.6 (SD) m; the long axis of the entrance averaged 39.8 ± 25.9 cm; the short axis averaged 11.6 ± 4.5 cm; the depth of cavity was 52.4 ± 33.6 cm; and DBH was 57.0 ± 12.1 cm. The heights aboveground of the two fan palm nests were 1.1 m and 3.9 m; entrance diameters were 8.5 cm and 12.5 cm; depth of cavities were 100.0 cm and 108.0 cm; and tree DBHs were 8.5 cm and 23 cm, respectively.

The density of all tree species was $26.5 \pm 10.7/100 \text{ m}^2$. Only casuarina and fan palm species had available cavities. The density of casuarinas was $1.2 \pm 1.3/100 \text{ m}^2$ and cavity density was $0.05 \pm 0.22/100 \text{ m}^2$; however, fan palm density was $10.2 \pm 5.7/100 \text{ m}^2$ and cavity density was $0.014 \pm 0.12/100 \text{ m}^2$.

Diet. Grasshopper (Orthoptera) dominated in the food items found in the stomachs of the road-killed owls (Table 1). Although the samples were collected between January and August (three samples in January, two in March, two in April, one in May, two in July, and one in August), the small sample size prevented any analysis of seasonal changes in diet.

We obtained data on the diet of the nestlings from 25 nests (53 session totaling 106 hr of recording). Deliveries to the nestlings included spiders (Heteropoda), cockroaches (Blattodea), grasshoppers (Orthoptera), and geckos (Gekkonidae; Table 1).

Home Range and Habitat Selection. We tracked 17 territorial males and seven females of different owls over different years (Appendix). Twelve males and two females were tracked in both breeding and nonbreeding seasons. Median estimates of male 100% MCP and 95% FK home ranges in breeding season were 3.2 ha ($n = 15$, range 1.6–22.9) and 1.2 ha (range 0.5–6.2) respectively. Female home ranges in breeding season were 2.5 ha ($n = 6$, range 0.8–4.4) and 0.8 ha (range 0.3–2.8) respectively. In the nonbreeding season, male 100% MCP and 95% FK ranges were 2.3 ha ($n = 14$, range 0.9–9.9) and 1.0 ha (range 0.4–3.7). Female ranges were 3.1 ha ($n = 3$, range 3.0–3.9) and 0.9 ha (range 0.9–1.3).

Table 1. Diet of Daito Scops Owls determined from stomach contents of road-killed birds, and the food of nestlings determined by video-recording.

| TAXONOMIC GROUP | STOMACH CONTENTS (11 OWLS) | | FOOD OF NESTLINGS (53 NESTS) | |
|-------------------|----------------------------|------------|------------------------------|------------|
| | NO. OF PREY ITEMS | % | NO. OF PREY ITEMS | % |
| Reptilia | | | | |
| Squamata | | | | |
| Gekkonidae | 2 | 6.7 | 70 | 13.6 |
| Arachnids | | | | |
| Araneae | | | | |
| Heteropoda | 4 | 13.3 | 130 | 25.3 |
| Multipede | | | | |
| Scolopendormorpha | 0 | 0.0 | 15 | 2.9 |
| Insects | | | | |
| Blattodea | 1 | 3.3 | 130 | 25.3 |
| Orthoptera | 16 | 53.3 | 90 | 17.5 |
| Odonata | 3 | 10.0 | 23 | 4.4 |
| Lepidoptera | 1 | 3.3 | 48 | 9.3 |
| Unknown | 3 | 10.0 | 8 | 1.5 |
| Total | 30 | 100 | 513 | 100 |

The percentage of each habitat type within the 100% MCPs in breeding ($n = 21$) and nonbreeding seasons ($n = 17$), respectively, were Palm forest: $3.9 \pm SD 3.5\%$ and $4.0 \pm 3.5\%$; *Ficus* forest: $11.3 \pm 6.8\%$ and $11.4 \pm 7.0\%$; Mixed forest: $16.9 \pm 11.7\%$ and $17.1 \pm 11.7\%$; Grass: $13.2 \pm 14.4\%$ and $12.5 \pm 14.7\%$; Cane: $41.5 \pm 4.8\%$ and $41.8 \pm 4.8\%$; Others: $5.3 \pm 18.5\%$ and $5.3 \pm 18.6\%$.

More owls (both males and females) selected the edge habitat between forests and open area in the nonbreeding season than during the breeding season (Table 2, Appendix). More than half of the owls selected *Ficus* forests in breeding season, whereas

most owls used habitats according to their availability within forests during the nonbreeding season (Table 2, Appendix).

Breeding Ecology and Effect of Habitat. We monitored seven breeding attempts in 2004, 15 in 2005, 13 in 2006, 15 in 2007, 26 in 2008, and 19 in 2009. We found that these owls breed once a year and do not reneest after predation or make a second breeding attempt in the same season. Thirty-two nest sites were in natural cavities and four in nest boxes that we erected in 2002. Nests were often used over a number of years. Of 21 nests monitored >4 yr, 19 were used in >4 yr, one was used in 3 yr, and an-

Table 2. Selection of edge habitat between forests and open areas, and habitat types within forests for radio-tracked Daito Scops Owls. The symbols (+) and (-) indicate the habitat was used more and less than expected based on availability, respectively. No selection (ns) indicates the habitat was used in proportion to its availability. Additional details about statistics for each individual in Appendix.

| HABITAT | NO. OF OWLS SHOWING SELECTION, AVOIDANCE, AND NO SELECTION | | | | | |
|----------------------|--|---|----|---------------------------------|---|----|
| | BREEDING SEASON ($n = 21$) | | | NONBREEDING SEASON ($n = 17$) | | |
| | + | - | ns | + | - | ns |
| Edge | 4 | 0 | 17 | 13 | 0 | 4 |
| Forests | | | | | | |
| Palm forests | 0 | 2 | 19 | 1 | 1 | 15 |
| <i>Ficus</i> forests | 13 | 0 | 8 | 2 | 0 | 15 |
| Mixed forests | 0 | 9 | 12 | 0 | 1 | 16 |

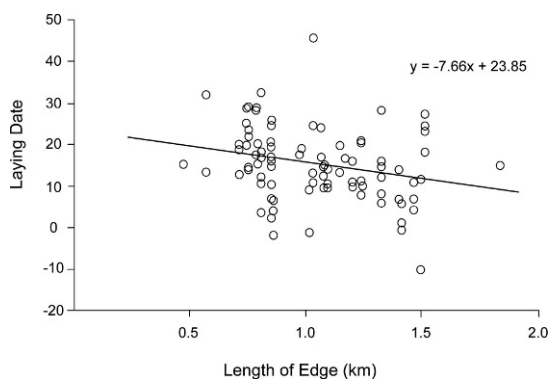


Figure 2. Relationship between length of edge between forests and open area and the egg-laying date of the Daito Scops Owl from 2004 to 2009 ($n = 88$ breeding attempts, 60 pairs). Day 0 = 1 April.

other was used in 2 yr. These nests were often used by same individuals on successive years (13 males used the same nest >4 yr, three used the same nest in 2 yr and eight used a nest for only 1 yr. Six females used a nest in >4 yr and eight used their nest in only 1 yr). The mean egg-laying date was 15 April ± 8.57 ($n = 88$ breeding attempts, 60 pairs), mean clutch size was 2.6 (range 1–3, $n = 93$ breeding attempts, 65 pairs). Mean number of fledglings per breeding attempt was 1.8 (range 0–3, $n = 95$ breeding attempts, 67 pairs) and mean number of fledglings per successful nest was 2.3 (range 1–3, $n = 75$ nests, 49 pairs).

Owls with a greater edge length in their home ranges laid eggs earlier (GLMM, $\chi^2 = 4.05$, $df = 1$, $P = 0.04$, $n = 88$, Fig. 2). The variables in best models for clutch size were “length of edge” and “area of grass,” and for the number of fledglings was “length of edge.” But these models did not differ significantly from null models (GLMM, clutch size: $\chi^2 = 0.53$, $df = 2$, $P > 0.05$, $n = 93$, the number of fledglings: $\chi^2 = 3.06$, $df = 1$, $P > 0.05$, $n = 79$).

DISCUSSION

Nest Characteristics and Availability. Of 32 natural cavity nests, 94% were in exotic casuarina trees, probably because this species tends to form a great number of cavities in their trunks. We speculate that the owls chiefly nested in snags of the native fan palms before introduction of casuarinas; logging of fan palms likely decreased the number of potential nest sites, because their cavities are scarce. Since the 1920s, planted casuarinas (Minami-daito Village 1990) have become the most important source of

nest sites for the owls. However, this alien tree poses a serious threat to native habitats (Wheeler et al. 2010), because accumulation of its litter suppresses the germination and initial growth of native species (Hata et al. 2010). Natural habitat restoration on the Ogasawara Islands has involved the removal of casuarina trees (Shimizu 2010). Although it is necessary that future natural habitat restoration on Minami-daito Island also includes this removal, the eradication of the alien casuarina and restoration of native vegetation in the present forests would likely harm the owl population by reducing the number of nest cavities. Therefore, increasing the area of forests sufficiently to maintain adequate supply of breeding sites in native trees is an important prerequisite to removal of the alien casuarinas, if the owl population is to be maintained. Installing additional nest boxes would also increase the supply of breeding sites, and would be a useful measure, as owls breeding in our boxes were successful. However, this would be a temporary solution, dependent on continual maintenance of the boxes. Ideally, this owl population should be preserved under natural nesting conditions.

Diet. Important prey species for this owl, cockroaches (Blattodea), appear in a wide range from open ground to forests (K. Akatani unpubl. data). However, other prey species are seen in particular habitats. Spiders (Heteropoda) inhabit mainly rocks, construction sites or their margins (Shinkai 2006, K. Akatani unpubl. data). This may be one reason owls select *Ficus* forests on limestone outcrops (see below). Grasshoppers (Orthoptera) are typical of open areas. Geckos (Gekkonidae) inhabit mainly construction sites or trees (Yamashiro et al. 2000). These were also common in the owls' diets. Owls apparently feed from a wide range of habitats from forests to open areas.

Habitat Selection. The edge between forests and open areas was selected by 19% of tracked owls in breeding season, and 76% in nonbreeding season. The edge provides useful perches from which the owls can search for prey in nearby open areas. Grasshoppers typical of open habitats were most likely spotted from such perches and then captured in hawking flights. Similar use of forest-edge perches by other raptors has been widely reported (Kenward 1982, Strøm and Sonnerud 2001).

More than half of owls selected *Ficus* forests during the breeding season. The *Ficus* tree is known to attract a wide range of frugivorous and herbivorous arthropods (Basset et al. 1997, Novotny and Missa

2000). Spiders and geckos, which are insect predators, may also be attracted to the *Ficus* in search of prey. *Ficus* forests are likely to contain abundant prey for owls.

During the nonbreeding season, the percent of owls selecting the edge habitat increased, and owls selecting *Ficus* decreased. Most of prey species were much less abundant in the nonbreeding season than in the breeding season; however grasshopper abundance did not differ (K. Akatani unpubl. data). It is possible that the seasonal change in habitat selection results from seasonal change of prey availability.

Breeding Ecology and the Influence of Habitat.

Owls with more edge habitat in their home ranges started egg-laying earlier in breeding season. Young hatched from earlier clutches will likely have a recruitment advantage on Minami-daito Island, as elsewhere. The available forested area is limited, so owl population density is consequently high, and competition for territories is intense. More than half of 34 young observed to survive to the spring following hatching did not find a breeding territory, and the male young fledged earliest established their territories closest to their natal nests (T. Matsuo unpubl. data). Early fledging favors successful territory establishment by offspring on an island where dispersal opportunities are limited. Edge habitats are important for parents in increasing their fitness through effective establishment of their offspring into the population.

In conclusion, we found that this owl has sufficient habitat flexibility to maintain its population despite habitat alteration. However, we recommend that conservation management, such as habitat restoration, should proceed gradually, if owl numbers are to be maintained.

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Appendix. Comparison of habitat used to habitat available for Daito Scops Owls in the breeding and nonbreeding seasons on Minami-daito Island. Proportion of used/available for edges between forests and open areas, selection ratio w_i of three forested habitat types, and the results of statistic analysis for each Daito Scops Owl.

| ID ^a | HABITAT USED/ HABITAT AVAILABLE | | χ^2 | P | SELECTION RATIO w_i^b | | | χ^2 | P | NO. OF LOCATIONS |
|---------------------------|------------------------------------|-------------------|----------|--------|-------------------------|--------------|---------|----------|--------|---------------------|
| | EDGE | WITHIN FORESTS | | | PALM | <i>Ficus</i> | MIXED | | | |
| Breeding season | | | | | | | | | | |
| M1 | 0.94 | 1.02 | 0.07 | 0.79 | 1.28 | 1.32(+) | 0.28(-) | 19.46 | <0.001 | 95 |
| M2 | 1.17 | 0.95 | 0.32 | 0.57 | 0.95 | 1.02 | 1.02 | 0.05 | 0.98 | 67 |
| M3 | 0.73 | 1.12 | 1.77 | 0.18 | 0.54 | 1.48(+) | 0.54(-) | 17.73 | <0.001 | 101 |
| M4 | 1.41 | 0.87 | 2.56 | 0.11 | 0.88 | 1.73(+) | 0.62(-) | 16.25 | <0.001 | 118 |
| M5 | 1.80 | 0.86 | 2.62 | 0.11 | 0.69 | 0.46 | 1.20 | 2.69 | 0.26 | 57 |
| M6 | 1.03 | 0.98 | 0.03 | 0.87 | 0.40 | 1.17(+) | 0.56 | 8.43 | <0.05 | 105 |
| M7 | 1.37 | 0.85 | 2.56 | 0.11 | 1.17 | 1.20 | 0.63 | 4.56 | 0.10 | 98 |
| M8 | 1.53 | 0.85 | 3.05 | 0.08 | 1.04 | 1.59(+) | 0.65(-) | 9.65 | <0.05 | 77 |
| M9 | 1.28 | 0.87 | 1.29 | 0.26 | 0.30 | 1.97(+) | 0.06(-) | 44.08 | <0.001 | 63 |
| M10 | 1.31 | 0.91 | 0.87 | 0.35 | 0.29 | 1.00 | 1.03 | 0.25 | 0.88 | 52 |
| M11 | 2.42 | 0.33 | 39.23 | <0.001 | 0.30 | 2.22(+) | 0.56 | 14.62 | <0.001 | 89 |
| M12 | 2.27 | 0.64 | 17.15 | <0.001 | 0.01(-) | 2.99(+) | 0.96 | 47.19 | <0.001 | 102 |
| M13 | 0.80 | 1.66 | 3.38 | 0.07 | 0.89 | 0.27 | 1.04 | 0.33 | 0.85 | 52 |
| M14 | 1.54 | 0.81 | 2.34 | 0.13 | 0.20 | 1.59(+) | 0.13(-) | 34.05 | <0.001 | 55 |
| M15 | 2.66 | 0.64 | 19.50 | <0.001 | 2.17 | 1.21 | 0.38(-) | 15.96 | <0.001 | 92 |
| F2 | 1.28 | 0.81 | 2.03 | 0.15 | 0.54 | 4.84(+) | 0.86 | 16.92 | <0.001 | 65 |
| F3 | 0.89 | 1.04 | 0.16 | 0.69 | 1.60 | 1.67(+) | 0.50(-) | 11.68 | <0.05 | 56 |
| F5 | 1.89 | 0.92 | 1.86 | 0.17 | 0.21 | 1.05 | 1.01 | 0.45 | 0.80 | 56 |
| F6 | 1.48 | 0.86 | 1.78 | 0.18 | 0.14 | 1.03 | 1.01 | 0.88 | 0.65 | 53 |
| F14 | 0.90 | 1.03 | 0.08 | 0.77 | 0.89 | 1.53(+) | 0.02(-) | 12.93 | <0.001 | 57 |
| F15 | 2.21 | 0.64 | 13.15 | <0.001 | 0.03(-) | 1.58(+) | 0.59 | 9.18 | <0.05 | 61 |
| Nonbreeding season | | | | | | | | | | |
| M1 | 1.35 | 0.86 | 1.39 | 0.24 | 1.37 | 0.79 | 1.18 | 1.52 | 0.47 | 55 |
| M3 | 1.83 | 0.64 | 12.81 | <0.001 | 3.74 | 1.16 | 0.71 | 5.29 | 0.07 | 102 |
| M4 | 2.02 | 0.68 | 12.48 | <0.001 | 0.77 | 1.29 | 0.93 | 1.83 | 0.40 | 93 |
| M6 | 1.89 | 0.50 | 23.50 | <0.001 | 0.06 | 0.99 | 1.19 | 2.65 | 0.27 | 134 |
| M7 | 1.27 | 0.89 | 1.59 | 0.21 | 3.37(+) | 0.82 | 1.02 | 13.96 | <0.001 | 130 |
| M8 | 2.40 | 0.61 | 11.91 | <0.001 | 0.15 | 0.65 | 1.26 | 2.20 | 0.33 | 56 |
| M9 | 2.03 | 0.54 | 22.18 | <0.001 | 0.02 | 0.90 | 1.34 | 5.34 | 0.07 | 121 |
| M11 | 2.33 | 0.37 | 32.17 | <0.001 | 1.01 | 1.75 | 0.56 | 5.41 | 0.07 | 79 |
| M12 | 2.80 | 0.49 | 33.31 | <0.001 | 0.09(-) | 1.90 | 1.21 | 21.58 | <0.001 | 107 |
| M13 | 0.94 | 1.19 | 0.18 | 0.67 | 3.52 | 0.70 | 0.59 | 4.30 | 0.12 | 52 |
| M14 | 2.95 | 0.31 | 29.21 | <0.001 | 0.10 | 1.64 | 0.03 | 5.66 | 0.06 | 53 |
| M15 | 3.94 | 0.36 | 48.64 | <0.001 | 1.65 | 0.48 | 1.49 | 5.09 | 0.08 | 72 |
| M16 | 11.86 | 0.31 | 71.59 | <0.001 | 0.25 | 1.09 | 1.54 | 4.43 | 0.11 | 52 |
| M17 | 4.20 | 0.60 | 35.42 | <0.001 | 1.10 | 2.45(+) | 0.85(-) | 24.87 | <0.001 | 253 |
| F2 | 1.14 | 0.91 | 0.53 | 0.46 | 0.43 | 1.71 | 1.20 | 4.82 | 0.09 | 73 |
| F6 | 3.03 | 0.43 | 43.76 | <0.001 | 0.09 | 1.30(+) | 0.58 | 7.54 | <0.05 | 120 |
| F17 | 4.86 | 0.52 | 33.89 | <0.001 | 0.59 | 1.80 | 0.95 | 2.22 | 0.33 | 58 |

^a M = male, F = female. Pairs share the same number.

^b (+) indicates the habitat was used significantly more than expected based on availability, and (-) indicates the habitat was used significantly less than expected.