Territoriality and the significance of calling in the Lanyu Scops Owl *Otus elegans botelensis*

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Territories of Lanyu Scops Owls *Otus elegans botelensis* overlap in both breeding and non-breeding seasons. Results of radiotelemetry showed that neighbouring owls do not use the shared areas of their territories at the same time. Frequent countersinging apparently permitted individuals to avoid potentially costly encounters with neighbours. Non-territorial owls can forage and rest in occupied territories. Experiments using decoys and playbacks showed that intruding owls were tolerated within either core or peripheral territories in all seasons if they remained silent, while calling intruders almost always incited threats or attacks even in autumn. Tolerating silent owls that are not competitors for mates or for nest sites appears to be an energy-saving territorial strategy.

Territoriality is a spacing system maintained by the behavioural patterns of a given species. The reward for territorial defence is frequently better survival or higher reproductive success. The territoriality of a species thus reflects important environmental and social constraints on the species. Models of the external conditions that favour territorial behaviour usually consider the quality, abundance and distribution of resources in space and time, as well as the density of competitors and their competitive abilities (e.g. Carpenter & MacMillen 1976, Myers et al. 1981, Davies & Houston 1984).

Economical defendability is a major determinant of territorial behaviour (Brown 1964), while the difference in resource value to the contestants may affect territorial strategies (Hammerstein 1981). Furthermore, the costs and benefits associated with territorial maintenance may affect the methods used in settling a contest (Harper 1991). Owls generally maintain all-purpose territories (Tawny Owl *Strix aluco*, Hirons 1985, Galeotti 1994; Little Owl *Athene noctua*, Finck 1990; Tengmalm’s Owl *Aegolius funereus*, Korpimäki 1987, 1988; Great-horned Owl *Bubo virginianus*; Spotted Owl *Strix occidentalis*, Hunter et al. 1995).

With radiotracking, which permits careful documentation of activity patterns within territories and determination of boundaries, the territories of neighbours in a number of species of owls have been found to overlap (Boreal Owls *Aegolius funereus*, Hayward et al. 1987; Eastern Screech Owls *Otus asio*, Belthoff et al. 1993; Barred Owls *Strix varia*, Nicholls & Fuller 1987). The overlapping areas are primarily used by one bird in Eastern Screech Owls (Belthoff et al. 1993), while in Barred Owls it is used only for short periods (Nicholls & Fuller 1987). No study has reported varying territory defence strategies of owls.

The territoriality of the insectivorous Lanyu Scops Owl *Otus elegans botelensis* is complex. They have overlapping activity areas so that they appeared non-territorial at first (Severinghaus 1986). However, border fights between neighbours suggest that activity areas may also be their territories. Territorial defence in this species is variable. Sometimes an intruder is tolerated while at other times it is expelled. This paper describes the unusual territoriality of this species, and reports the results of a series of experiments conducted to explore the following questions: (1) Does territorial aggression occur only at specific times? (2) Is aggression aimed at only specific individuals? (3) What stimulus may trigger aggressive responses from territory owners?

**METHODS AND MATERIAL**

**Study population**

The Lanyu Scops Owl is a small insectivorous owl (weight about 125 g) found throughout Lanyu Island southeast of Taiwan (longitude: 121°5'E, latitude: 22°N). I have been studying this population since 1985, and more than 80% of the birds in selected areas...
are colour-marked. The core habitat for this owl is mature woods with tall, broadleaf trees while the peripheral habitat contains small clusters of trees near villages, or next to agricultural fields where human disturbance is high (Severinghaus 1989). Habitat patches vary in size, in vegetation structure, in their number of known tree cavities, and in owl density.

The basic breeding biology of the Lanyu Scops Owl was reported by Severinghaus (1992). Young Lanyu Scops Owls enter the breeding population at two years or older and can live more than 13 years. The pair bond may be maintained for several years, but mate change is frequent between years. The tenure of good nest cavities is short (Severinghaus unpubl. data).

Male Lanyu Scops Owls make a hoo-hoo call, while females also make a yap call. Owls increase calling frequency in late December and early January when courtship and nest-cavity searching start. Countersinging by neighbours is common from January until early July. These calling bouts are interspersed with periods of silence. Males also utter a distinct copulation call, similar to that reported for Otus scops (Koenig 1973).

The work reported in this paper was conducted from 1989 to 1996 inclusive. In general, two field assistants and two to four summer students assisted with data gathering each year.

**Determination of activity areas**

The boundaries of owl activity areas were determined in two locations by the maximum area polygon method after mapping all the perch sites of each colour-ringed individual. The two locations were: (1) a 2.34-ha mature hardwood forest, and (2) a 3-ha coconut plantation with only dead trunks left. Many of the coconut trunks in the plantation had cavities in them which were used by breeding owls in 1990, but unfortunately the coconut trunks were levelled and the field converted to agriculture in spring 1991.

In the forest study area, perch sites were determined through intensive observations on three nights every month by three trained observers from July 1993 to June 1994. In the plantation, playback of owl calls were used in April 1990. The taped voice belonged to a deceased male recorded in 1989 from another location, so it was strange to all the owls present in 1990. Playback locations were regularly spaced at 20-m intervals in the plantation and the tape was played up to 20 minutes each time, depending on when any owl responded. The identity, sex, and type of response of each respondent were recorded.

Silent owls were not seen enough times to map out their activity areas and are considered non-territorial.

**Reaction to playback**

In the lowland areas around Lanyu Island, 60 playback stations were selected, each roughly 0.5 km apart. Every month from July 1990 to August 1991 taped male calls were played for 20 min at each station and all the responses and reactions of owls were recorded.

**Radiotracking**

We used AVM radio-transmitters to track Lanyu Scops Owls in 1990. Each transmitter weighed less than 5 g and was secured on the owl with a body harness (< 5% of bodyweight). Effective battery life was 2 months. The 24 owls we were tracking included one mated pair, two 2-neighbour (both one male one female), a 3-neighbour (one male and a pair) group, and isolated individuals. The four groups of birds listed above were respectively monitored simultaneously from two stations (White & Garrott 1990). Location readings were taken every 30 min throughout the night for three nights each in June and July 1989. Locations of these owls were marked on topographic maps. The maximum area polygon method was again used to determine territory sizes.

**Decoy and playback experiments**

I made life-size decoys with papier maché. In April 1995, I selected nine known nest trees and did the following experiments. (1) A decoy or a stuffed Lanyu Scops Owl specimen was placed on a perch or a rock directly below the nest cavity or as close to that point as possible, and about 3–5 m from it. The reactions of any owl to the decoy or the specimen were recorded for 25 min. (2) A tape of mixed female and male calls was played for 25 min from a tape recorder placed next to the decoy or the specimen, and the reactions of the owl were recorded. In January and October 1996, the same test was rerun in the same territories using only decoys.

The decoy experiments were conducted in April 1995, January and October 1996, because Lanyu Scops Owls’ reactions to playback were the most intense in April, weakest in autumn months (Fig. 1), while January is the very beginning of the breeding season. Test results were analysed by comparing proportions in paired samples (Snedecor & Cochran 1967).
RESULTS

Territory boundaries and radiotelemetry

In core habitat, territories of marked individuals overlapped greatly both in the breeding and in the non-breeding seasons in 1993–94 (Figs 2, 3). In peripheral areas, the degree of territory overlap varied from zero (April 1990 in the coconut plantation, Fig. 4) to a narrow strip (March–April 1990 along the highway, Fig 5). This latter overlap was discovered during monthly tape playback. Some owls were seen fighting and chasing each other during the spring. Yet, non-territorial owls were seen resting and foraging in a number of core and peripheral territories (as can be seen in Figs 2–4). No efforts by territory owners to exclude these owls were observed.

Results of radiotracking in 1989–90 also showed that during the breeding season neighbouring owls had overlapping territories (Table 1). Judging from the pattern shown between the pair and their male neighbour (Fig. 6), the female overlapped more with the neighbour than did her mate. The male neighbour was within the female's activity area 23.1% of the time that he was located by radiotracking, but he was never there when either the male or the female was there. In 13 tracking records taken 30 min apart, the male neighbour was in the overlapping area on the eighth, ninth and eleventh time, while one or both members of the pair was there on the second and ninth time. Within the overlapping area, the locations of the neighbouring male were only 17.6 ± 5.6 m from the previous locations of the pair, but the time they were there was at least 30 min apart. The mean distance between neighbours at any moment was significantly longer than that between the paired birds (Table 1, t-test, \( P < 0.0001 \)).

I used the activity pattern of these three owls to analyse further the interactions between neighbours. If an owl's utilization of its entire territory is 1, the probability that the overlapping area is used by this
individual should be equal to its proportion of the entire territory. The probability that two owls appear simultaneously in the overlapping area would be equal to the product of the two individual probabilities. These probabilities are used to calculate the expected frequencies for the four possible situations: both owls in the overlapping area, owl A in/owl B out, owl A out/owl B in, and both out. This is used to test the observed frequencies with a chi-squared test (Table 2).

Although the female and her male neighbour never used the overlapping area at the same time, the frequency with which they used the overlapping area did not differ from that expected. However, the male and his neighbour each used the overlapping area significantly more times than expected, but never at the same time. The two males apparently actively avoided each other in their frequent visits to the overlapping area.

**Decoy tests**

Test results showed that a silent decoy or stuffed specimen aroused no aggressive response from either paired owls in spring or resident owls in winter

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**Table 1.** Distances between neighbour owls obtained from radiotracking.

<table>
<thead>
<tr>
<th>Between</th>
<th>Case</th>
<th>Min (m)</th>
<th>Max (m)</th>
<th>Mean ± sd(m)</th>
<th>Overlap (ha)</th>
<th>Overlap (%)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mates</td>
<td>1</td>
<td>1.7</td>
<td>110.1</td>
<td>35.9 ± 34.8</td>
<td>0.69</td>
<td>90.7</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>15.0</td>
<td>75.0</td>
<td>33.2 ± 18.4</td>
<td>0.40</td>
<td>62.6</td>
</tr>
<tr>
<td>Males</td>
<td>1</td>
<td>34.5</td>
<td>198.8</td>
<td>149.1 ± 53.1</td>
<td>0.08</td>
<td>32.7</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>15.0</td>
<td>-</td>
<td>-</td>
<td>0.31</td>
<td>39.1</td>
</tr>
<tr>
<td>Female + male</td>
<td>1</td>
<td>36.3</td>
<td>191.0</td>
<td>132.4 ± 42.9</td>
<td>0.21</td>
<td>13.7</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>62.5</td>
<td>336.3</td>
<td>194.0 ± 83.0</td>
<td>1.40</td>
<td>37.1</td>
</tr>
</tbody>
</table>

*Overlap as a percentage of the male’s territory. When two males are involved, this number is the mean of the two percentages.

In the second case of ‘between males’ category, the two owls appeared simultaneously in the area only once. Thus only one distance measurement was obtained.
Figure 5. Narrow territory overlap of Lanyu Scops Owls in peripheral habitat in April 1990. Boundaries were determined by playback of taped calls. Fighting occurred when both males arrived at the same location.

(5.3) Table 3. When taped owl calls accompanied either a decoy or a stuffed specimen, most resident owls reacted vigorously, either by repeatedly flying over the 'intruder' while calling, or by physically attacking the intruder (Table 3). In April, some pairs mated after trying to expel the intruder. The owls did not react differently to the decoy or the stuffed specimen; thus results of decoy and specimen tests were pooled in making analyses for April. In each season, territorial owners' reactions to silent or vocal intruders differed significantly (Table 4, comparison of proportions in paired samples, $P < 0.025$).

**DISCUSSION**

Lanyu Scops Owls are territorial, but not exclusively so. It is believed that less than 50% of the adult Lanyu Scops Owls breed, because of a shortage of nest cavities (Severinghaus, unpubl. data). Although it is possible that some of these owls are actually breeders and we fail to find their nests, the large number of owls...

Table 2. Comparison of the frequency a pair of owls and their male neighbour used the overlapping area.

<table>
<thead>
<tr>
<th></th>
<th>Only female in</th>
<th>Only neighbour in</th>
<th>Both out</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed</td>
<td>0</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td>Expected</td>
<td>1.1</td>
<td>5.8</td>
<td>7.9</td>
</tr>
<tr>
<td>Chi-square</td>
<td>1.927</td>
<td>df = 3</td>
<td></td>
</tr>
</tbody>
</table>

The probability that the overlapping area is used by an owl equals its proportion of the entire territory. The probability that two owls simultaneously appear in the overlapping area would equal the product of the two individual probabilities. Expected frequency is calculated using these probabilities against the total number of observations.

Table 3. Summary of territory owner's reactions to decoy and tape playback experiments.

<table>
<thead>
<tr>
<th>Date</th>
<th>Type</th>
<th>$N$</th>
<th>Aggression</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr 1995</td>
<td>Decoy only</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Specimen only</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Decoy + tape</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Specimen + tape</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Jan 1996</td>
<td>Decoy only</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Decoy + tape</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Oct 1996</td>
<td>Decoy only</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Decoy + tape</td>
<td>8</td>
<td>8</td>
</tr>
</tbody>
</table>

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contesting for territories each spring is a strong indication that many owls have no breeding opportunities. They are prevented from breeding because suitable habitats are saturated with dominant individuals, as found in a number of species (e.g. Brown 1969, Eckert & Weatherhead 1987, Arcese 1989).

The population density of Lanyu Scops Owl appears to be correlated with the number of nest cavities available in an area (Severinghaus unpubl. data). Where owl population density is high, breeding territories overlap greatly; where owl density is low, territories do not overlap. Floaters have been seen foraging and resting in a number of territories. The overlap in Lanyu Scops Owl territories is most likely a result of high competition pressure for nest sites, rather than of food supply as in the Dunnock *Prunella modularis* (Davies & Hartley 1996). This is because in populations where members are food-limited, floaters probably cannot forage regularly in territories (Smith 1978). Furthermore, contests for food are unlikely to escalate into fatal fighting in animals (Enquist & Leimar 1990). Lanyu Scops Owls fight for nest cavities while tolerating the presence of silent foraging owls.

Radiotracking has shown that although territories overlapped, neighbouring Lanyu Scops Owls do not use the shared areas at the same time. Furthermore, the frequent countersinging of neighbouring males probably allows them to monitor each other’s positions, and to avoid potentially costly aggressive encounters, such as seen twice during tape playback when two male owls showed up to expel the calling stranger and ended up in a vigorous fight with each other. We have seen owls fight without tape playback. Chivers (1969) suggested that Mantled Howler Monkeys *Alouatta palliata* used dawn calls as a spacing mechanism in the overlapping part of their home ranges. Although Sekulic (1982) questioned the wisdom of Howler Monkeys informing neighbours of their position, it should be an adaptive strategy if frequent encounters lead to aggression each time.

Diverse species of birds can identify the calls of their mates and their neighbours (e.g. Wooller 1978, Weary et al. 1987, Speirs & Davis 1991). Many owls appear to recognize their mates by their calls, as do Tawny Owls (Galeotti & Pavan 1991), and Screech Owls (Cavanagh & Ritchison 1987). Tawny Owls can differentiate neighbours from strangers and gauge their responses appropriately to save agonistic energy (Galeotti & Pavan 1991, 1993). The calls of Great-horned Owls (Rohner 1997) have individually identifiable characteristics. Lanyu Scops Owls probably can differentiate the calls of their neighbours and mates from those of strangers, since the calls of individuals appear different on sonograms (Severinghaus 1986). Results of decoy tests indicate that the calling of an unfamiliar Lanyu Scops Owl is taken as an act of challenge to which they react aggressively. Yet the same ‘owl’ can be tolerated when resting silently. The non-territorial owls tolerated by territory owners were always foraging or resting silently.

Contests are costly to territory owners even when owners and floaters show what Maynard Smith (1982) calls payoff asymmetry, uncorrelated asymmetry, or competitive asymmetry. When floaters are many and persistent, it may be unprofitable for owners to try to evict them from their territories (Brown 1982). The following example testifies to this. One female owl established a territory around two adjacent cavities in early spring of 1993 and 1994. Each year she fought off intruding females for more than three months, only to be supplanted from both cavities just prior to egg-laying. Her energy reserves had perhaps been reduced after repeated contests.

Signalling can reduce the costs of territorial maintenance (Ydenberg et al. 1988). An opponent’s strength or abilities may be determined by assessing the information contained within the signals (Harper 1991). Vocalizations are particularly efficient signals for nocturnal animals. Lanyu Scops Owls do not have complex vocal repertoires. Their calls thus function both as a territorial proclamation and an advertisement of their availability to potential mates. Silent owls are not overtly advertising their presence as mating candidates, thus are not treated as competitors.

Temeles (1990) found that in Northern Harrier *Circus cyaneus* differences in potential payoffs lead to
differences in territorial defence against neighbours and floaters. Lanyu Scops Owls live in rich tropical forests with few food competitors and apparently are under no food shortage pressure. Defending territories against foraging owls would be of no benefit. If silence also denotes weakness, and weak owls stand no chance of winning a nest cavity, silent owls are not worth the effort of expulsion. Since the purpose of aggression is to expel the competitor, tolerating silent owls should be an energy-saving territorial strategy.

The fact that silent owls are ignored is not because they only lurk around in the periphery of defended territories, which is the case with the Great-horned Owl (Rohner 1997). Non-territorial Lanyu Scops Owls also use areas close to nest cavities. Some of them have been seen repeatedly in the same locations, similar to what Smith (1978) found with Rufous-collared Sparrow Zonotrichia capensis floaters.

Arcese (1989) suggests that the degree of habitat saturation should influence the tactics of floaters because it affects the probability of settling without engaging in conflicts. Lanyu Scops Owls live under very high population density. Floaters have adopted the behavioural strategy of being quiet in territories, which makes them tolerable to territory owners, permits them to wait for opportunities to replace the owners, and perhaps cuckold the owners in the meantime (Morton et al. 1990). One observation suggests the last situation may exist in Lanyu Scops Owl. One female territory owner disappeared before her young hatched. A floater female that frequently perched quietly near this nest took over incubation and the rearing of young. Whether the second female actually laid some of the eggs in that nest is unknown.

In conclusion, this study shows that vocalization plays an important role in the territoriality of Lanyu Scops Owls. Whether territorial aggression is displayed does not depend on variation in the food resource base, nor the number of owls present, but rather whether a competitor is displaying vocally.

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