Brown Shrikes *Lanius cristatus* are both transients and winter residents in Taiwan. Large numbers of birds crowd into the available habitat during the transient period, and the cost of maintaining territories changes greatly, depending on the number of shrikes present. This study examined how wintering Brown Shrikes adapt to the changing level of competition in territory establishment. About 24% of autumn transients arrived before any wintering birds, while 73% of wintering birds arrived during autumn transient time. The frequency of aggression recorded was significantly related to the number of birds seen along the transect line that day. Among ringed birds that returned during transient time, 80% returned directly to their previous territories, but some waited for the departure of transient birds before establishing territories. Territory compression occurred at high population densities. Departure from and arrival at the study area were frequent during the winter, but no birds moved territories within the study area. On average, 25% of ringed wintering shrikes returned to the study site in the subsequent years, while no transients returned. This low site tenacity may be, in part, a result of a high persecution rate along the migration route.

The intensity of competition and the economics of resource defence determine the expression of territoriality for a given species in its habitat. Researchers have examined many aspects of territoriality, including aggressive advantages over newcomers (Krebs 1982, Waage 1988), the costs and benefits of territory maintenance (Brown 1964, Carpenter & MacMillen 1976, Verner 1977), the effect of visibility on territoriality (Reid & Weatherhead 1988, Eason & Stamps 1991), habitat quality and territory size (Verner 1977), the sequence of territory settlement (Brooke 1979, Möller 1983, Matthysen 1990), environmental familiarity and territory acquisition (Stamps 1987) and the movement of territories (Beletsky & Orians 1987, Petersen & Best 1987).

In some migratory species, the timing of arrival may affect whether an individual obtains a territory. Furthermore, in regions where a migratory species is both transient and a winter resident, the intensity of competition and the economics of resource defence may fluctuate rapidly for wintering birds when transients pass through the area every year. Migratory behaviour in birds has a genetic basis, and its expression is subject to natural selection (Sutherland 1988, Berthold 1990, Berthold et al. 1992). The timing of migration and territorial strategy of winter residents in these regions should reflect effects of changing competition pressures.

The Brown Shrike *Lanius cristatus* is a common migratory species in eastern Asia (Mayr & Greenway 1960, Medway 1970, McClure 1974). It is a strongly territorial predator which occurs in Taiwan both as an autumn and spring migrant and as a winter resident (Severinghaus 1991). Thus, this species is suitable for the examination of whether different territorial strategies are used by wintering birds during transient and wintering periods and how territorial individuals adapt to changes in population density. This study analyses the timing of arrival of wintering birds in relation to the transient birds and the timing of territory establishment by wintering birds and documents if and how wintering territories are maintained under the high cost of extensive intrusion pressure during the transient period.

**METHODS AND MATERIAL**

The study area was 81 ha within the Tunghai University campus, in Taichung, central Taiwan (120°36'00"E, 24°10'30"N, elevation 220 m). The study area contained woods with both thick and sparse undergrowth, grassland, areas along irrigation ditches with mixed trees and shrubs, buildings and gardens.

This 3-year study was conducted during August–May 1987–1990 with the help of three assistants. We captured and colour-ringed 25 wintering Brown Shrikes in 1987 and 22 in 1989. Because there was much plumage variation between individuals, we also recorded the head and body colour patterns of all the individuals caught or seen as a means of individual identification. The plumage of ringed wintering birds remained the same at least until the spring. Thus, during autumn and winter, for unringed birds in any given locality, if any had the same plumage pattern as one previously seen in the same general area, it was considered
to be the same bird. If a bird of different plumage pattern
occupied a territory, it was counted as a new bird. This
method errs on the conservative side, in cases where a new
bird happened to possess the same plumage pattern as the
previous one.

A 5.6-km line transect was established in 1989 and
passed through all the habitat types in the study area. Daily
from August to October at 1.5 h after sunrise, we walked
the transect at 1.8 km per h. For each shrike seen within
50 m of the line, we recorded its location, habitat type,
aggressive behaviour and plumage pattern. In addition to
the transect, between November 1989 and mid-May 1990,
the entire study area was searched every 2 weeks for shrike
area was monitored.

During September 1987–May 1988, August 1988–May
1989 and November 1989–May 1990, we surveyed shrikes
over the entire study area on 12 days in each month,
mapped their flight paths (scale 1:300) and recorded the
type, location and habitat where aggression took place.

The boundary of each territory was determined by con-
necting the outermost points where an individual bird was
seen perching, showing aggression or flying over.

Wintering Brown Shrikes were sexed in 1990 by plumage
patterns, just prior to the spring migration, when they had
assumed breeding plumage (see Massey et al. 1985 for sex-
ual differences during the breeding season).

RESULTS

Transient v wintering birds

Brown Shrikes were present in the study area between late
August and mid-May (17 August 1987–16 May 1988 and
26 August 1989–14 May 1990). There was no clear sepa-
ration between the autumn migration and wintering period,
or between winter and spring migration (Fig. 1). Because
more than 90% of the autumn migrants remained in the
study area for less than 12 days (Fig. 2), this duration was
used to separate transient birds from wintering birds.

In the 1989–1990 season, 817 autumn transients passed
through the area covered by the line transect, 96% of them
before 20 October (Fig. 1). Because the transect covered only
half of the study area, the number of autumn transients
was estimated to be 1634 birds. In total, 154 Brown Shrikes
wintered in the study area, but only six shrikes passed
through the transect during the spring.

Wintering birds arrived in the study area later than tran-
sients in the autumn. The first wintering bird appeared on
10 September, while 196 (24%) of the transients occurred
on the transect before that date. Between 10 September and
20 October, 48 wintering birds were found along the tran-
sect, which eventually contained 66 territories, thus 73% of
the wintering birds were estimated to have arrived during
this time period.

Winter movements

New wintering shrikes appeared in, and old ones disap-
ppeared from, the study area in every month between Sep-
tember 1989 and April 1990 (Table 1). Although none of
the ringed shrikes was known to move territories within the
study area during a winter season, all these moves probably
reflected territory change within the wintering area. On 2
October 1989, a ringed bird marked in the 1987–1988 win-
ter was seen foraging about 200 m away from its original
territory. This individual disappeared 3 days later. One bird
ringed in 1987 in the study area moved in 1989 to a ter-
ritory about 500 m away.

Figure 1. The arrival of Brown Shrikes at the study area from 27 August 1989 to 3 May 1990. Five-day periods were used as a time unit. The mean number of new arrivals was calculated by summing the total number of new arrivals seen divided by the number of days surveyed within each time unit.
Intraspecific aggression

Brown Shrikes were seen fighting, chasing and making aggressive calls towards each other in 1987 and along the transect in the autumn of 1989. (Aggressive behaviour was not monitored in 1988.) During fighting, two birds would grapple with each other, separating only when they had tumbled to the ground. In one case, two birds even faced each other on the ground for about 10 s before flying away. The frequency of aggressive calling and fighting observed in 1989 had a significant relationship with the number of shrikes seen on the transect on that day (no. calling = 0.57 birds seen - 3.7, r = 0.67; no. fighting = 0.05 birds seen - 0.8, r = 0.33). Winter aggression peaked in late October and early November 1987-1988 and again in December. The types of aggressive behaviour seen did not change between the transient and the wintering period. Little winter aggression was seen in 1989-1990.

Territoriality

The entire study area was used by wintering Brown Shrikes, but the number of territories found differed every year. Generally, territory boundaries did not remain the same between years. The locations of territories of the early arrivals were scattered throughout the study area, while late arrivals gradually filled in the space between.

Among the 25 territories for which we have detailed boundary data in 1989-1990, 13 were established in September or October, 12 were established between November and February. Territory sizes varied greatly among birds but did not differ significantly between periods (autumn = 1734 ± 1079 m², n = 13; winter = 2440 ± 1188 m², n = 12; t-test). When a territory owner disappeared, neighbouring territories were expanded to take up the unoccupied space (Fig. 3).

Among the 48 wintering birds that were found on the

Table 1. Movements of Brown Shrikes in the winter of 1989-1990

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Figure 3. Change in territories of Brown Shrikes on Tunghai University campus, Taichung, Taiwan. At the departure of a territory owner, neighbours' territories expanded to occupy the empty space. This took place in January and May.

transect before 20 October in 1989, ten had been previously colour-ringed, eight of which were territory holders. The previous territory of a shrike wintering for the third time was occupied by other shrikes when it arrived on 10 September 1989. This bird used an area east of its previous territory until after the migration period, then it returned to its original territory in October and maintained an area of approximately the same size as in the two previous years (Fig. 4). Eight of 26 wintering shrikes ringed in 1987 and 4 of 22 ringed in 1989 returned in subsequent years. Among the eight from 1987, four males and three females used the same locality as before, while one female moved to another site within the study area.

Among wintering birds that could be sexed, 66 were males and 75 were females, a sex ratio not significantly different from equality ($\chi^2 = 0.57$).

DISCUSSION

The majority of wintering Brown Shrikes arrived during the transient period although somewhat later than most of the transient birds. Wintering Brown Shrikes establish territories upon arrival at a cost of frequent territorial defence, as shown by eight of the ten ringed wintering birds. Alerstam and Lindstroem (1990) suggested that optimal bird migration strategy may be to arrive earlier at the destination than competitors. Wintering Brown Shrikes arrived during and after the peak transient period and set up territories immediately.

One ringed shrike waited for the departure of a temporary occupant in its traditional territory before claiming it. The other occupant appeared to have gained prior-residence advantage (Cristol et al. 1990, Stamps & Krishnan 1990), which made its expulsion difficult. Nevertheless, this case demonstrates an alternative to fighting against high intrusion pressure.

The greatest amount of movement of Brown Shrikes from the study area took place in October, mostly by birds that arrived in September. The high frequency of fighting and aggressive calling observed then and evidence of territory compression suggest high levels of competition. Apparently, dominant individuals moved a minimal distance, while subordinates were forced to move much farther (Gauthreaux 1982). Taiwan is located near the northern limit of the wintering range of Brown Shrikes, and the great majority of the migrating shrikes go farther south to winter.

These movements could reflect a widespread effort by individuals to search for good quality territories in autumn. If the environmental conditions of a wintering site are favourable, birds are likely to return to it in subsequent years. If not, they may move on to different locations (Terrill
Figure 4. The territory boundaries of a ringed Brown Shrike in the winters of 1987, 1988 and 1989. The temporary activity area of this bird in the autumn of 1989 is also shown. The boundaries did not remain the same in different years, although they were in practically the same location.

1990). The presence of unfilled territories after the departure of occupants in midwinter suggests uneven habitat quality within my study area.

The return rate of ringed shrikes to the study site in the following year was 25% for wintering birds, but no transient birds returned. Almost certainly, some of the surviving wintering birds moved elsewhere, but those that returned tended to return to old territories, demonstrating site tenacity, even though their territory boundaries did not always remain the same. The overall low return rate of Brown Shrikes is similar to that found for Loggerhead Shrikes Lanius ludovicianus (Kridelbaugh 1983, Haas & Sloane 1989), where it was suggested that the return rate was lower in females than in males. This does not seem to apply to Brown Shrikes on my study site, for the sex ratio of ringed shrikes that returned was 1:1, and the low site tenacity here could not be attributed to the low return of females alone. Brown Shrikes have been heavily harvested by local people along its migratory route in Ryukyus, Taiwan and the Philippines (Severinghaus 1991). High mortality rates in this species during migration and in winter would affect the proportion of birds that return to the same wintering ground.

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REFERENCES


