

# Winter flocking behaviour of speckled warblers and the Allee effect

Janet L. Gardner

*School of Botany and Zoology, Australian National University, Australia*

Received 25 May 2003; received in revised form 8 August 2003; accepted 11 August 2003

## Abstract

The aggregation of individuals into foraging flocks is one behavioural trait that, if disrupted, can cause the Allee effect, which is a slowing in population growth at low density or small population size, and this can greatly increase the risk of extinction. Here, I describe intraspecific flocking behaviour of a colour-banded population of speckled warblers, *Chthonicola sagittata*, a species that has declined across a large part of its range in the fragmented temperate woodlands of Australia. I make predictions about the context in which the Allee effect might be expressed and the consequences for the viability of populations living in small habitat remnants. Speckled warblers lived in discrete, stable social groups throughout winter, the nucleus of which was the residents from one or more adjacent breeding territories. The timing and mode of flock formation and the size of flocks varied between two winters, apparently in response to the severity of conditions; thus flocking probably facilitates increased foraging efficiency and predator detection, potentially leading to increased survival in harsh conditions. Because flock territories were up to 30 ha each, and larger territories are likely, birds living in remnants smaller than 40 ha may suffer increased mortality if there are too few birds available to form flocks of an appropriate size to facilitate the benefits of grouping when conditions are most extreme. Further, in small remnants where survival is reduced, dominance behaviour and male–male competition may act to compound the Allee effect by reducing reproductive success. Regardless of these predictions, speckled warbler populations may only be viable in remnants that are large enough to support multiple flocks, to enable rapid recruitment to breeding vacancies and thus provide adequate numbers of birds for flocking.

© 2003 Elsevier Ltd. All rights reserved.

**Keywords:** Habitat fragmentation; Allee effect; Flocking; Behaviour and conservation; Birds

## 1. Introduction

A variety of behavioural traits, subject to particular conditions, can cause the Allee effect, which is a slowing in population growth at low density or small population size (Allee, 1931; Sæther et al., 1996; Courchamp et al., 1999; Stephens and Sutherland, 1999). One of the best-known examples of such behaviour is the aggregation of individuals into foraging groups (Sæther et al., 1996; Courchamp et al., 1999; Reed, 1999; Stephens and Sutherland, 1999; Stephens et al., 1999). Grouping is thought to facilitate increased foraging efficiency and predator detection and therefore acts to increase survival in harsh conditions (Pulliam, 1973; Ekman, 1987; Hogstad, 1988; Lima and Dill, 1990; Bednekoff and Lima, 1998). The benefits of grouping increase with

group size, up to a point, and group size is varied in response to the severity of conditions (Elgar, 1989). A reduction in population size that depletes the number of individuals available for grouping may therefore lead to a reduction in survival if groups become so small that foraging and anti-predator strategies become inefficient. Thus, the Allee effect may be an important mechanism for population regulation, especially in species that show a high degree of sociality (Sæther et al., 1996; Courchamp et al., 1999; Reed, 1999; Stephens and Sutherland, 1999).

There is evidence that the Allee effect can occur in a wide range of taxa and can greatly increase the likelihood of local and global extinction, but despite this, its importance in population ecology has traditionally been underestimated (Creel, 1998; Courchamp et al., 1999; Reed, 1999; Stephens and Sutherland, 1999). This may be due to the inherent difficulty of demonstrating an

*E-mail address:* [janet.gardner@anu.edu.au](mailto:janet.gardner@anu.edu.au) (J.L. Gardner).

imbalance between births and deaths in small populations (Courchamp et al., 1999; Stephens et al., 1999). In addition, the consequences of such an imbalance for population viability may be difficult to predict because outcomes will depend on the prevailing environmental conditions. Nevertheless, recent advances in statistical modelling have led to a better understanding of such interactions and have highlighted the importance of the Allee effect in the dynamics of small populations (e.g., McCarthy, 1997; Amarasekare, 1998).

Habitat fragmentation is one form of anthropogenic disturbance that has driven many populations to small sizes or low densities, potentially placing them at risk from the Allee effect (Courchamp et al., 1999; Reed, 1999). Habitat fragmentation alters the amount, configuration in the landscape and quality of suitable habitat available for species, thereby having potential to affect the distribution and abundance of species (Saunders et al., 1991; Fahrig, 1997). Studies of habitat fragmentation have tended to focus on description of the loss of biodiversity and changes to species composition in remnants. Much less is known about mechanisms of decline and this makes it difficult to predict the consequences of environmental change (Sutherland, 1998; Courchamp et al., 1999; Reed, 1999; Anthony and Blumstein, 2000). This limitation has led to a call for behavioural studies, including those that elucidate the causal mechanisms of the Allee effect (Courchamp et al., 1999; Stephens and Sutherland, 1999).

The speckled warbler *Chthonicola sagittata* is one of a number of declining species from the highly fragmented temperate woodlands of Australia (Garnett, 1992; Robinson and Traill, 1996; Recher, 1999; Reid, 1999). Since European settlement, up to 80% of this habitat type has been cleared to make way for grazing of livestock and agriculture, and this has had considerable impact on the status of species within the region (Ford et al., 2001). Speckled warblers have declined across a large part of their range, and in districts where no habitat fragments larger than 100 ha remain, they appear to be locally extinct (Barrett et al., 1994; Robinson and Traill, 1996; Traill and Duncan, 2000). In addition to area, habitat quality is likely to affect distribution in remnants, since presence of the species appears to be associated with a high degree of habitat complexity (Watson et al., 2001).

Specific causes of the decline of speckled warblers are unknown but thought to be linked with processes associated with the fragmentation of their habitat, rather than a direct result of habitat loss, since populations have continued to decline in areas where land clearing has stopped (Reid, 1999). The species occurs at low population density and is a specialist in terms of foraging and nesting behaviour (Ford et al., 1986; Tzaros, 1996; Gardner, 2002; Gardner et al., 2003), characteristics that are likely to result in small popu-

lation size in fragmented landscapes and thus make it prone to extinction (May, 1973; Soulé, 1987; Caughley, 1994; Mac Nally and Bennett, 1997; Reed, 1999). One aspect of behaviour that may have consequences for survival as a result of the potential for the Allee effect is the inclination to form intraspecific flocks as well as join mixed species flocks in winter. Habitat fragmentation can influence the dynamics of winter flocks because it can affect the numbers of individuals available for flocking, as well as predator abundance and the availability of food and suitable habitat (Tellerià et al., 2001).

Here, I describe the formation, structure and composition of intraspecific flocks of speckled warblers living in a large (>1000 ha) habitat remnant, based on observations of a colour-banded population over two winters. I conclude that flocking is likely to increase individual fitness and thus, under specific conditions, trigger the Allee effect. I make predictions about the context in which the Allee effect might be expressed and discuss probable consequences for populations living in small remnants of habitat.

## 2. Methods

### 2.1. Study species and site

The speckled warbler is a small (11–15 g) insectivorous passerine which is a sedentary resident of the temperate woodlands of eastern Australia (Blakers et al., 1984). It is a member of the Acanthizinae within the Pardalotidae (Christidis and Boles, 1994) or Acanthizidae, in which case the species name has reverted to *Pyrholaemus sagittatus* (Schodde and Mason, 1999). I use Acanthizinae hereafter. Males are slightly larger than females and can be distinguished on the basis of a black rather than rufous crown stripe (Blakers et al., 1984). In the population studied, speckled warblers bred in the austral spring and summer (Gardner, 2002). Most birds bred as a simple pair but up to 30% of breeding units were trios, consisting of a female with two males, in which case the second or beta male was subordinate to the alpha (Gardner et al., in press; Gardner et al., 2003). Females laid clutches in up to 7 months of each year, were multi-brooded and fledged up to three broods per season, but despite this, reproductive success was low with each female producing about 1.0 fledgling per season (Gardner, 2002). All juveniles dispersed from the natal territory about 7 weeks after fledging, soon after reaching foraging independence (Gardner et al., 2003). The population studied occurred in open eucalypt woodland, dominated by *Eucalyptus rossii*, *Eucalyptus mannifera* and *Eucalyptus macrorhyncha*, on the lower slopes of Mt. Anslie in the Canberra Nature Park, Australian Capital Territory (149°9'E, 35°16'S). The

study area was about 300 ha in size, within the larger 1500 ha reserve.

## 2.2. Field techniques

Once breeding had finished, birds were monitored weekly to record changes in social organisation and to document the arrival of immigrants. In 1998, I monitored pairs and groups from 14 breeding territories. In 1999, the same territories were monitored, although three were empty, so an additional four territories were included. Most resident birds (>90%) were already colour-banded as part of an ongoing study of breeding and demography. Unbanded immigrants were usually captured and banded as soon as they had been sighted with the same breeding group two or more times.

## 2.3. Behavioural watches

Speckled warblers foraged in stable, discrete flocks of 2–7 individuals throughout winter (see results). Flocking was achieved in two ways: first via amalgamation of the residents from several adjacent breeding territories; and second, via immigrants joining breeding pairs or groups. By mid-May changes to social organisation had stabilised and birds were observed foraging in flocks (see results). I use the term flock to refer to any non-breeding social unit of two or more individuals, consistent with studies of a variety of tit species from the genus *Parus* (Matthysen, 1990).

Behavioural watches were carried out on foraging flocks in each year (1998: 19 May–19 June; 1999: 9 June–21 July) to document flock size and composition, the range used by flocks, and the dominance behaviour of individuals. Flocks were located systematically at least once each week by walking in a clockwise direction around the flock territory, starting from one of the four pre-determined points, selected at random that day. This ensured that there was no observer bias in locating flocks. The starting points were located in roughly the north, south, east and west sections of each flock territory. I walked at a steady pace and stopped each 50 m to scan and listen for the calls of speckled warblers. Once a flock was located its position was plotted on a topographic sheet and the identity of all members recorded. Focal watches were then carried out on each member of the flock. The order of watches was random with respect to the identity of individuals and started with the first bird seen, followed by the next seen at the completion of the previous watch and so on. Watches were 15 min long, during which time I recorded on tape and map: (1) the outcome of all agonistic interactions, the identities of individuals involved and the locations at which interactions took place and (2) changes in flock composition. The location of the flock was plotted at the start and

finish of each watch, and these, along with the initial location of the flock, were used to plot the flock range. Agonistic interactions that indicated dominance status were chases and displacements. Displacements were defined as one individual approaching another and displacing it from its perch.

In 1998, I spent 37 h observing 33 individuals; each individual was observed for at least 1 h (i.e., four watches), except in the case of four birds that were observed for 1–2 focal watches only. In 1999, I spent 28 h observing 33 individuals; an additional three birds were present but were not watched.

## 3. Results

### 3.1. Flock formation and social organisation

Speckled warblers lived in flocks of 2–7 individuals throughout the winter (excluding the single case of a lone male on a territory). The nucleus of each flock was one or more breeding pairs or groups, some of which were joined by immigrants that had dispersed onto the study area (Table 1). Immigrants included juveniles that were banded as nestlings and had dispersed from their natal territories, as well as unbanded birds that had dispersed onto the study site after the previous breeding season. These unbanded birds were also likely to be juveniles since adults rarely changed territories, and if they did so moved a maximum of three territories (Gardner et al., 2003). In the five cases where there was more than one immigrant per flock, the immigrants were not siblings; this was known to be the case as all were colour-banded as nestlings.

Immigrants joined resident members of some breeding territories to form flocks in both winters, although there were fewer immigrants in 1998 (6/33: 18%) compared with 1999 (14/36: 39%; Table 1). In the two years, immigrants arrived on the study site between early January and mid-May, although one male arrived in late November of the previous breeding season; no new birds were seen on the study site after mid-May. This is consistent with the timing of natal dispersal for 55 juveniles hatched and banded on the study site over three breeding seasons; the earliest and latest dispersal dates were 14 October and 10 May, respectively, for juveniles whose dispersal dates were accurately known. In the two winters, the timing of arrival did not differ for birds hatched on the study site versus those that had dispersed from elsewhere (ANOVA:  $F_{1,13} = 0.17$ ,  $P = 0.69$ ).

Flocks also formed via amalgamation of residents and immigrants from several adjacent breeding territories, but the formation of flocks in this way was largely restricted to one of the two winters (Table 1). In 1998, residents from two or three adjacent breeding territories

Table 1  
Flock characteristics and social organisation of birds living on the study site during the two winters

Flock identity	Size of flock territory (ha)	Number of breeding territories involved	Number of individuals of different status within each flock		
			Resident adult	Immigrants	Total
<i>1998</i>					
1	30	3	7	0	7
2	22	2	4	3	7
3	19	2	3	2	5
4	28	2	3	1	4
5	15	2	4	0	4
6	20	2	4	0	4
7	9	1	2	0	2
Sub total		14	27	6	33
Means			3.9	0.9	4.7
<i>1999</i>					
1	19	2	3	3	6
2	22	2	3	1	4
3	10	1	1	4	5
4	10	1	1	2	3
5	9	1	2	1	3
6	8	1	2	0	2
7	7	1	2	0	2
8	8	1	1	1	2
9	12	1	1	1	2
10	9	1	2	0	2
11	9	1	1	1	2
12	11	1	2	0	2
13	11	1	1	0	1
Sub total		15	22	14	36
Means			1.7	1.1	2.8

amalgamated to form six flocks; only one pair remained on its breeding territory throughout winter. In contrast, in 1999 most residents remained on their breeding territories throughout winter; only residents from 4 of the 15 breeding territories amalgamated to form two flocks. The difference between the two years was significant; Fisher's Exact two-tailed test:  $P = 0.0005$ . Flock size was larger in 1998 than in 1999 (Wilcoxon's:  $Z = 2.26$   $N = 20$ ,  $P = 0.02$ ; Table 1).

Flocking of adjacent residents occurred much earlier in 1998 than in 1999. From early January in 1998 residents from several adjacent breeding territories were observed foraging together and by late April the majority (86%, 12/14) of breeding groups were observed foraging with neighbours (Fig. 1). By June, all six flocks that contained adjacent residents had formed. In contrast, of the four breeding groups that amalgamated to form two flocks in 1999, flocking was not observed until 1 June.

Membership of a flock was stable for residents but not for all immigrants. No resident ( $n = 49$ ) was observed to forage in more than one flock, while (4/17) immigrants were each seen foraging in two or three adjacent flocks (Fisher's Exact two-tailed test:  $P = 0.003$ ).

### 3.2. Flock boundaries, territoriality and range

Flock boundaries encompassed the breeding territory boundaries of residents, so flocks were largely non-overlapping (Fig. 2). Two flocks overlapped by about 10%, with one flock using the shared area when the other was foraging elsewhere. On no occasion were flocks seen to meet in these shared areas. In contrast, two adjacent flocks shared one breeding territory following the disappearance of the resident individual, and the two flocks met once in this shared area. The flocks remained as discrete groups, did not intermingle and no aggression was observed.

Seventeen cases of aggression were recorded between members of two flocks when they met at the boundaries of the flock territories. In all cases the victim of the aggression or another member of its flock retaliated and other birds often joined in until the two flocks were chasing each other high in the canopy. The flocks eventually separated and returned to forage on their own flock territories.

Because flock boundaries encompassed the breeding territory boundaries of resident flock members, the size of the flock territory was 1–3 times that of breeding territories and ranged from 7 to 30 ha (Table 1).

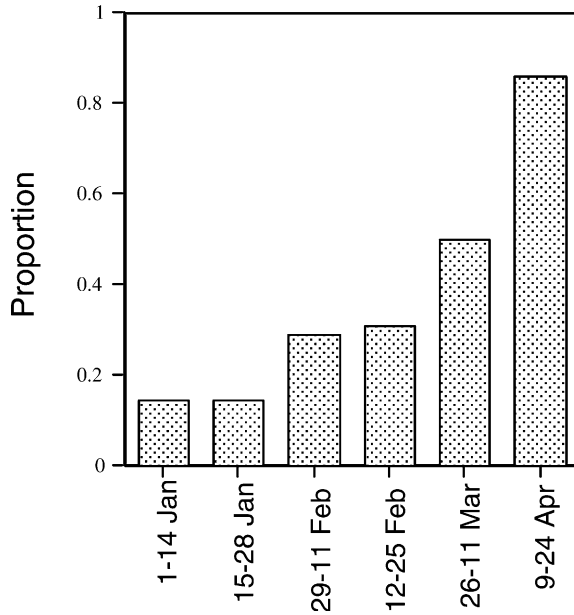


Fig. 1. Proportion of 14 breeding groups found to be foraging with neighbouring residents in flocks during weekly monitoring visits in 1998. In 1999, only 4/15 breeding territories amalgamated to form two flocks, and flocking of adjacent residents was not observed until June 1.

However, since breeding territories were up to 12 ha each (Gardner et al., 2003), the maximum area used by a single flock consisting of three breeding territories would be 36 ha.

### 3.3. Flock cohesion, dominance and aggression

Most flocks that comprised residents from two or more breeding territories were cohesive units. For six of these eight flocks, the proportion of focal watches in which members from each of the component breeding groups were found foraging together at the start of the watch ranged from 75% to 97%. The two remaining flocks were less cohesive with just 33% of watches containing representatives from each of the breeding groups belonging to the flock.

Males were dominant to females, based on all 125 aggressive interactions recorded in the two years (Table 2). Males initiated aggression toward other males and toward females but females never initiated aggression toward males, although they did so toward other females.

In flocks that comprised residents from several breeding groups, there was no consistent dominance hierarchy within the sexes; dominance was site-specific and related to breeding territories. Breeding territory residents dominated other flock members when foraging on areas of their own breeding territories and were submissive when on another's breeding territory; no resident initiated aggression unless on its own breeding



Fig. 2. Structure and layout of intraspecific winter flocks of speckled warblers in 1998. Symbols represent locations at which resident flock members were recorded during behavioural watches; each symbol type represents all members of a single flock. Solid lines represent flock boundaries and dashed lines delineate breeding territories of residents.

territory (all 78 cases of aggression in flocks comprising  $\geq 2$  breeding units). All five cases of dominance reversals between two specific individuals were the result of site-specific dominance, where dominance changed with breeding territory ownership. Subordinate males from one territory were aggressive toward alpha males from another, so age did not affect the pattern of site-related dominance, given that beta males are typically younger than alpha males (Gardner et al., 2003). However, aggression by beta male to alpha male from the same breeding group was never observed, consistent with dominance during the breeding season.

Only some immigrants appeared to have residency status. Usually, immigrants did not initiate aggression toward residents but were aggressive toward other

Table 2

Number of aggressive interactions observed and which sex initiated the aggression (28 males and 16 females)

Year	Aggression				Total
	Male to male	Male to female	Female to female	Female to male	
1998	40	36	23	0	99
1999	25	1	0	0	26
Total	65	37	23	0	125

Includes only those aggressive interactions in which all individuals involved were identified.

immigrants (five cases involving two females in 1998 and one male in 1999). Two immigrant males that initiated aggression toward breeding residents (five occasions) from adjacent territories did so on the breeding territories to which they became betas in trios, but not on other territories, suggesting that both had residency status.

In all 83 (82 in 1998, 1 in 1999) aggressive encounters observed within flocks the victim never retaliated, nor did any member of the flock regardless of how close they were to the encounter, or their relationship with the victim. For example, the breeding partner of a female victim did not retaliate when another male was aggressive toward her.

### 3.4. Fate of non-residents

There was a trend for immigrants that arrived on the study site early (before March 14) to be more successful at gaining breeding vacancies (7/7) than those that arrived late (6/11; Fisher's Exact two-tailed test:  $P = 0.10$ ). Eleven (of 13) birds that gained a vacancy (eight females as breeders and five males as betas in trios) did so in the flock in which they spent the winter. The remaining two males gained vacancies in one of the several adjacent flocks that they visited during the winter. Birds hatched on the study site were no more successful at gaining vacancies (6/7) than were those that dispersed into the study area from elsewhere (7/13; Fisher's Exact two-tailed test:  $P = 0.33$ ). All seven birds that failed to gain vacancies on the study site disappeared by August. Two were known to have dispersed at the end of winter, in August, since both were subsequently re-sighted outside the study site.

### 3.5. Rainfall

Rainfall for the 12-month period to June 1998 was 428 mm, which was substantially lower than the average rainfall calculated for the previous 10 years (mean  $\pm$  SD:  $668 \pm 165$  mm) and lower than the minimum recorded over that period (range: 441–1023 mm). In contrast, rainfall for the 12-month period to June 1999 was 690 mm, slightly higher than the long-term average.

## 4. Discussion

### 4.1. Function of flocking

Speckled warblers lived in discrete, stable flocks throughout winter, the nucleus of which was the residents from one or more adjacent breeding territories. Residents were joined by immigrants that had dispersed after the previous breeding season. Boundaries of the flock territory encompassed the breeding territory boundaries of residents so flocks were largely non-overlapping. Exclusive ranges were maintained through avoidance, although when flocks occasionally met at boundaries all members of the flock contributed to defense by chasing the intruders.

The structure of speckled warbler flocks is similar to that reported for other acanthid species, but flocks differ in the relatedness of flock members, suggesting that the primary function of flocking may be different for speckled warblers. Buff-rumped thornbills *Acanthiza reguloides* also form stable, exclusive flocks with the residents from several adjacent breeding territories forming the nucleus of the flock (Bell and Ford, 1986). Striated *Acanthiza lineata* and yellow-rumped thornbills *Acanthiza chrysorrhoa* also appear to conform to this pattern but their social organisation is less well known (Bell, 1985; Bell and Ford, 1986; D. Ebert, pers. comm.). Although similar in structure, speckled warbler flocks were comprised largely of non-relatives since all young dispersed from the natal territory soon after reaching foraging independence, before the start of winter (Gardner et al., 2003). In contrast, buff-rumped and yellow-rumped thornbill offspring delay dispersal and remain on the natal territory throughout winter so flocks are comprised of kin (Bell, 1985; Bell and Ford, 1986; D. Ebert, pers. comm.). One hypothesis proposed to explain intraspecific flocking and exclusive flock membership in kin groups is that it allows control of access to breeding vacancies arising within the flock (Ekman, 1979; Smith, 1984). Flock members gain indirect genetic benefits via relatedness to subsequent young produced. Although shorter dispersal distances by speckled warbler males, compared with females (Gardner et al., 2003), would result in greater relatedness among males within flocks, flocks do

not typically comprise clans of first and second order male relatives, so genetic benefits would be relatively small compared with those for buff-rumped and yellow-rumped thornbills. Consequently, this is an unlikely explanation for flocking in speckled warblers.

Flocking in speckled warblers is likely to relate to individual fitness, rather than that of kin groups, potentially through improved predator detection and increased foraging efficiency (see Section 1). Compared with foraging alone, individuals in groups can spend less time looking out for predators without increasing personal risk of predation, and therefore more time foraging which increases survival when food is least abundant or when predator numbers are elevated (Elgar, 1989). In species where intraspecific flocking relates to survival, flock size increases in more severe conditions when birds have difficulties in meeting their energy requirements (Saitou, 1978; Hogstad, 1988; Matthysen, 1990; Lens and Dhondt, 1992; Brotons et al., 2000). This is consistent with behaviour observed in speckled warblers; flock size was significantly larger in 1998 when rainfall was the lowest recorded in 12 years and substantially lower than that for 1999. Reduced rainfall is likely to reduce the abundance of invertebrates available to speckled warblers, which are primarily insectivorous (Ford et al., 1986), thereby making meeting their energy requirements more difficult.

Although flocking in speckled warblers might relate primarily to foraging efficiency, there are likely to be secondary benefits relating to the formation and maintenance of social bonds for breeding. The correspondence of winter and breeding territories observed in speckled warblers is predicted in species where there are benefits of mate retention and site fidelity for all members of a breeding group (Matthysen, 1990). In a relatively long-lived species like the speckled warbler (Gardner et al., 2003) whose breeding territories and groups are stable from year to year (Gardner et al., 2003), such benefits are likely to apply. Flocks also appear to facilitate access to breeding vacancies since most juveniles that gained vacancies did so in the flock in which they lived, and those that joined flocks early tended to gain vacancies compared with those that joined late. Early arrival may be correlated with dominance, which has been shown to increase success in gaining breeding vacancies (Drent, 1987).

## 4.2. The Allee effect and implications for population viability

### 4.2.1. Increased mortality

If flocking acts to increase survival in harsh winters, then speckled warblers living in remnants smaller than the area required by a flock are predicted to suffer the Allee effect via increased levels of winter mortality, and this may be a contributing factor in population decline.

In this study, flock area ranged from 6 to 30 ha with potential for single flocks to use areas as large as 36 ha, suggesting that remnants less than about 40 ha may be unsuitable habitat. Because flock size appeared to increase in response to the severity of conditions, areas required for the largest flocks must be used to estimate minimum remnant sizes suitable for flocks. In this case, the largest flocks resulted from amalgamation of two or three breeding territories. In remnants smaller than 40 ha there may be too few birds available to form flocks of an appropriate size to facilitate increased foraging efficiency or predator detection when conditions are most extreme, leading to increased mortality. Although I did not distinguish between the predation and foraging hypotheses in this study, the effect is the same: survival is reduced. Social disruption to either foraging or anti-predator behaviour can trigger an Allee effect in flocking birds and has been documented for a variety of species (reviewed in Sæther et al., 1996; Reed, 1999; Stephens and Sutherland, 1999).

In practice, remnants suitable for speckled warblers may need to be larger than the minimum 40 ha required for a flock if habitat quality affects food availability and results in a need for larger flock size or larger flock territories. Even in remnants as large as 55 ha, Zanette et al. (2000) found that the invertebrate biomass of surface-dwelling invertebrates was about half that recorded in remnants of 400 ha, accounting for reduced foraging success of Eastern Yellow Robins *Eopsaltria australis* in the smaller remnants. Larger remnants may also be required if only a proportion of available habitat is of suitable quality. For example, remnant edges may make poor foraging sites due to weed invasion, increased numbers of predators or structural changes due to grazing (Saunders et al., 1991; Major et al., 2001). Grazing may also reduce food availability for insectivores, since the diversity of invertebrates is reduced in grazed, compared with ungrazed remnants (Abensperg-Traun et al., 1996; Bromham et al., 1999).

Speckled warblers are likely to be vulnerable to differences in habitat quality and food availability because they forage almost exclusively on the ground year-round (Ford et al., 1986; Tzaros, 1996; unpublished data). They do not use multiple substrates or change their foraging niche seasonally, as do other acanthizid species with which they share habitat (Ford et al., 1986; Bell and Ford, 1990). In addition, they do not dig for prey or sift leaf litter like white-browed scrubwrens *Sericornis frontalis* (Higgins and Peter, 2002) but move across the ground gleaning prey off the surface (Tzaros, 1996; pers. obs.). Such limited foraging behaviour suggests that they are unlikely to compensate for poorer quality habitat by exploiting other substrates, as at least some thornbill species appear to do (Bell and Ford, 1990) and may therefore need larger territories, or larger flocks in winter when food is least abundant.

Regardless of habitat quality, speckled warbler populations may only be viable in remnants that are large enough to support multiple flocks, to enable rapid recruitment to breeding vacancies and thus provide adequate numbers of birds for flocking.

#### 4.2.2. Reduced reproductive success

In remnants where survival is reduced as a result of disruption to flocking behaviour, the consequences of several other behaviours may compound the Allee effect. Increased mortality is likely to affect females disproportionately because of dominance behaviour and therefore result in excessively skewed sex ratios, leading to a reduction in effective population size. Speckled warbler males dominated females, so females are likely to have reduced access to resources (food or protection from predators) and may suffer higher mortality when conditions are harsh, consistent with patterns of dominance behaviour and survival recorded for other winter flocking avian species (e.g., Ekman and Askenmo, 1984; Desrochers et al., 1988; Desrochers, 1989; Ekman, 1990; Koivula et al., 1996; Lahti, 1998). Skewed sex ratios will result in a lack of mates for breeding and reduce reproductive success of the population.

As a consequence of a skewed sex ratio and therefore increased numbers of unpaired males in the population, harassment of females could occur thereby disrupting breeding attempts, leading to a further reduction in breeding success. Competition among males for fertile females is a component of the mating system, and most unpaired males in this study undertook extra-territorial forays to visit fertile females (Gardner et al., in press). This normal aspect of male behaviour may become maladaptive when males greatly outnumber females. Similar behaviour has been recorded in the endangered Seychelles magpie robin, *Copsychus sechellarum* (Komdeur, 1994). In that case, an increase in the number of offspring produced resulted from providing supplemental food to breeders. Because of a lack of suitable territories many of those 'excess' offspring became floaters (individuals that do not belong to any particular territory but move between territories in search of vacancies) and disrupted the breeding attempts of residents.

#### 4.3. Interactions with mixed species flocks

The disappearance of speckled warblers from remnants could affect the survival of other species with which they forage in mixed species flocks in winter. As well as foraging in intraspecific flocks, speckled warblers forage in mixed species flocks in winter that include a range of insectivorous species (Bell, 1980; unpublished data). Given that speckled warblers are foraging specialists it is likely that they would be among the first to disappear from such flocks. In mixed flocks of tit species, those species that were foraging specialists disappeared first in

remnants, thereby changing the structure and composition of flocks (Tellerià and Santos, 1995; Tellerià et al., 2001). Changes in the structure and composition of winter flocks in fragments affected the anti-predator behaviour and energy management strategies of the commonly occurring blue tit *Parus caeruleus* (Tellerià et al., 2001). Social disruption of this sort has been proposed to reduce the survival of mixed species flocks of birds (Reed, 1999), and there is some experimental evidence to support this idea. Reducing the size of mixed species flocks by removal of two nuclear Parid species resulted in a reduction in body condition and a tendency to increased winter mortality in white-breasted nuthatches *Sitta carolinensis* (Dolby and Grubb, 1998). Since such changes to flock dynamics are predicted to occur in other fragmented habitat types (Tellerià et al., 2001) this could be a contributing factor in the disappearance of a variety of insectivores in remnants less than 20 ha in the temperate woodlands of Australia (Mac Nally et al., 2000; Major et al., 2001). Although these declines have been attributed to the aggressive noisy miner *Manorina melanoccephala* (Mac Nally et al., 2000; Major et al., 2001), and the re-establishment of such species following the removal or reduction of miners provides convincing support for the hypothesis (Grey et al., 1997, 1998), it may not be the only factor involved. Given that speckled warblers are a foraging and nesting specialist, conserving habitat suitable to their requirements could ultimately result in protection of a range of insectivorous species with similar life histories.

#### Acknowledgements

I thank Rob Magrath, Penny Olsen, Todd Soderquist, Richard Major, Denis Saunders and two anonymous referees for comments on the draft manuscript, and Peter Marsack for assistance in the field. Rainfall data were provided by the Bureau of Meteorology. The study was supported by an ANU Graduate Scholarship, a Stuart Leslie Bird Research Award (Birds Australia) and a Cayley Memorial Scholarship (Gould League of New South Wales). Bird trapping and banding were carried out under license from the Australian Bird and Bat Banding Scheme, the ACT Parks and Conservation Service and the ANU Animal Experimentation and Ethics Committee; all work complied with current Australian laws.

#### References

- Abensperg-Traun, M., Smith, G.T., Arnold, G.W., Steven, D.E., 1996. The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the Western Australian wheatbelt. 1. Arthropods. *Journal of Applied Ecology* 33, 1281–1301.



- Allee, W.C., 1931. *Animal Aggregations. A Study in General Sociobiology*. University of Chicago Press, Chicago.
- Amarasekare, P., 1998. Allee effects in metapopulation dynamics. *American Naturalist* 152, 298–302.
- Anthony, L.L., Blumstein, D.T., 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce  $N_e$ . *Biological Conservation* 95, 303–315.
- Barrett, G.W., Ford, H.A., Recher, H.F., 1994. Conservation of woodland birds in a fragmented rural landscape. *Pacific Conservation Biology* 1, 245–256.
- Bednekoff, P.A., Lima, S.L., 1998. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. *Proceedings of the Royal Society of London* 265, 2021–2026.
- Bell, H.L., 1980. Composition and seasonality of mixed-species feeding flocks of insectivorous birds in the Australian Capital Territory. *Emu* 80, 227–232.
- Bell, H.L., 1985. The social organization and foraging behaviour of three syntopic thornbills *Acanthiza* spp. In: Keast, A., Recher, H.F., Ford, H., Saunders, D. (Eds.), *Birds of Eucalypt Woodlands: Ecology, Conservation, Management*. RAOU and Surrey Beatty and Sons, Chipping Norton.
- Bell, H.L., Ford, H.A., 1986. A comparison of the social organization of three syntopic species of Australian thornbill, *Acanthiza*. *Behavioral Ecology and Sociobiology* 19, 381–392.
- Bell, H.L., Ford, H.A., 1990. The influence of food shortage on interspecific niche overlap and foraging behavior of three species of Australian warbler. *Studies in Avian Biology* 13, 381–388.
- Blakers, M., Davies, S.J.J.F., Reilly, P.N., 1984. *The Atlas of Australian Birds*. Melbourne University Press, Melbourne.
- Bromham, L., Cardillo, M., Bennett, A.F., Elgar, M.A., 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. *Australian Journal of Ecology* 24, 199–207.
- Brotons, L., Orell, M., Lahti, K., Koivula, K., 2000. Age-related microhabitat segregation in willow tit *Parus montanus* winter flocks. *Ethology* 106, 993–1005.
- Caughley, G., 1994. Directions in conservation biology. *Journal of Animal Ecology* 63, 215–244.
- Christidis, L., Boles, W., 1994. *The Taxonomy and Species of Birds of Australia and its Territories*. Royal Australasian Ornithologists Union, Melbourne.
- Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* 14, 405–410.
- Creel, S., 1998. Social organisation and effective population size in carnivores. In: Caro, T. (Ed.), *Behavioural Ecology and Conservation Biology*. Oxford University Press, New York, pp. 246–265.
- Desrochers, A., 1989. Sex, dominance and microhabitat use in wintering black-capped chickadees: a field experiment. *Ecology* 70, 636–645.
- Desrochers, A., Hannon, S.J., Nordin, K.E., 1988. Winter survival and territory acquisition in a northern population of black-capped chickadees. *Auk* 105, 727–736.
- Dolby, A.S., Grubb, T.C., 1998. Benefits to satellite members in mixed-species foraging groups – an experimental analysis. *Animal Behaviour* 56, 501–509.
- Drent, P.J., 1987. The importance of nest boxes for territory settlement, survival and density in the great tit. *Ardea* 75, 59–71.
- Ekman, J., 1987. Exposure and time use in willow tit flocks: the cost of subordination. *Animal Behaviour* 35, 445–452.
- Ekman, J., 1990. Alliances in winter flocks of willow tits – effects of rank on survival and reproductive success in male-female associations. *Behavioral Ecology and Sociobiology* 26, 239–245.
- Ekman, J.B., 1979. Coherence, composition and territories of winter social groups of the willow tit *Parus montanus* and the crested tit *Parus cristatus*. *Ornis Scandinavica* 10, 56–68.
- Ekman, J., Askenmo, C., 1984. Social rank and habitat use in willow tit groups. *Animal Behavior* 32, 508–514.
- Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* 64, 13–33.
- Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61, 603–610.
- Ford, H.A., Barrett, G.W., Saunders, D.A., Recher, H.F., 2001. Why have birds in the woodlands of Southern Australia declined? *Biological Conservation* 97, 71–88.
- Ford, H.A., Noske, S., Bridges, L., 1986. Foraging of birds in eucalypt woodland in north-eastern New South Wales. *Emu* 86, 168–179.
- Gardner, J.L., 2002. Breeding biology of the speckled warbler, *Chthonicola sagittata*. *Australian Journal of Zoology* 50, 169–181.
- Gardner, J.L., Magrath, R.D., Kokko, H., 2003. Stepping stones of life: natal dispersal in the group-living but non-cooperative speckled warbler. *Animal Behaviour* 66, 521–530.
- Gardner, J.L., Magrath, R.D., Olsen, P.D., in press. Speckled warblers break cooperative rules: absence of helping in a group-living member of the Pardalotidae. *Animal Behaviour*.
- Garnett, S., 1992. Threatened and extinct birds of Australia. RAOU Report No. 82.
- Grey, M.J., Clarke, M.F., Loyn, R.H., 1997. Initial changes in the avian communities of remnant eucalypt woodlands following a reduction in the abundance of noisy miners, *Manorina melanocephala*. *Wildlife Research* 24, 631–648.
- Grey, M.J., Clarke, M.F., Loyn, R.H., 1998. Influence of the noisy miner *Manorina melanocephala* on avian diversity and abundance in remnant grey box woodland. *Pacific Conservation Biology* 4, 55–69.
- Higgins, P.J., Peter, J.M., 2002. *Handbook of Australian, New Zealand and Antarctic Birds. Pardalotes to Shrike-thrushes*, vol. 6. Oxford University Press, Melbourne.
- Hogstad, O., 1988. Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. *Ibis* 130, 45–56.
- Koivula, K., Orell, M., Rytönen, S., 1996. Winter survival and breeding success of dominant and subordinate willow tits *Parus montanus*. *Ibis* 138, 624–629.
- Komdeur, J., 1994. Conserving the Seychelles warbler *Acrocephalus sechellensis* by translocation from Cousin Island to the Islands of Aride and Cousine. *Biological Conservation* 67, 143–152.
- Lahti, K., 1998. Social dominance and survival in flocking passerine birds: a review with an emphasis on the willow tit *Parus montanus*. *Ornis Fennica* 75, 1–17.
- Lens, L., Dhondt, A.A., 1992. The effect of a severe storm on a population of crested tits *Parus cristatus* in Belgium. *Bird Study* 39, 31–33.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation – a review and prospectus. *Canadian Journal of Zoology* 68, 619–640.
- Mac Nally, R., Bennett, A.F., 1997. Species-specific predictions of the impact of habitat fragmentation: local extinction of birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation* 82, 147–155.
- Mac Nally, R., Bennett, A.F., Horrocks, G., 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation* 95, 7–29.
- Major, R.E., Christie, F.J., Gowing, G., 2001. Influence of remnant and landscape attributes on Australian woodland bird communities. *Biological Conservation* 102, 47–66.

- Matthysen, E., 1990. Non-breeding social organisation in *Parus*. *Current Ornithology* 7, 109–249.
- May, R.M., 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- McCarthy, M.A., 1997. The Allee effect: finding mates and theoretical models. *Ecological Modelling* 103, 99–102.
- Pulliam, H.R., 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38, 419–422.
- Recher, H.F., 1999. The state of Australia's avifauna: a personal opinion and prediction for the new millennium. *Australian Zoologist* 31, 11–27.
- Reed, J.M., 1999. The role of behavior in recent avian extinctions and endangerments. *Conservation Biology* 13, 232–241.
- Reid, J., 1999. Threatened and declining birds in the New South Wales Sheep-wheat belt: diagnosis, characteristics and management. Final Report to NSW National Parks and Wildlife Service, Canberra.
- Robinson, D., Traill, B.J., 1996. Conserving woodland birds in the wheat and sheep belts of southern Australia. RAOU Conservation Statement No. 10, Melbourne.
- Sæther, B.E., Ringsby, T.H., Røskoft, E., 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* 77, 217–226.
- Saitou, T., 1978. Ecological study of social organisation in the great tit *Parus major* L.I. Basic structure of the winter flock. *Japanese Journal of Ecology* 28, 199–214.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation – a review. *Conservation Biology* 5, 18–32.
- Schodde, R., Mason, I., 1999. *The Directory of Australian Birds*. CSIRO, Victoria.
- Smith, S.M., 1984. Flock switching in chickadees: why be a winter floater? *American Naturalist* 123, 81–98.
- Soulé, M.E., 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Stephens, P.A., Sutherland, W.J., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* 14, 401–405.
- Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect? *Oikos* 87, 185–190.
- Sutherland, W., 1998. The importance of behavioural studies in conservation biology. *Animal Behaviour* 56, 801–809.
- Tellerià, J.L., Santos, T., 1995. Effects of forest fragmentation on a guild of wintering passerines – the role of habitat selection. *Biological Conservation* 71, 61–67.
- Tellerià, J.L., Virgos, E., Carbonell, R., Perez-Tris, J., Santos, T., 2001. Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. *Oikos* 95, 253–264.
- Traill, B., Duncan, S., 2000. Status of Birds in the New South Wales Temperate Woodlands Region. Australian Woodlands Conservancy, Chiltern, Vic.
- Tzaros, C., 1996. Nesting and ecology of the speckled warbler. *Australian Birdwatcher* 16, 221–225.
- Watson, J., Freudenberger, D., Paull, D., 2001. An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. *Conservation Biology* 15, 1364–1373.
- Zanette, L., Doyle, P., Tremont, S.M., 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81, 1654–1666.