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Probable consequences of high female mortality for speckled warblers living in habitat remnants

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ABSTRACT

The effects of habitat fragmentation on the Australian avifauna have been widespread with species richness and abundance declining with reduced remnant size and habitat quality and increased habitat isolation. The speckled warbler, *Chthonicola sagittata* is one species from the highly fragmented temperate woodlands of eastern Australia that has declined across its range and populations that remain appear to be patchily distributed in habitat remnants. Specific causes of decline are unknown but several aspects of its biology make the species particularly vulnerable to decline in fragmented landscapes. Here, we analyse survey data (presence/absence) of speckled warblers in a large sample of habitat remnants from three regions to identify patterns of occupancy. We explore the effects of patch size on extinction risk using population viability analyses (PVA) and detailed demographic data from a behavioural study of individuals in the Australian Capital Territory, south-eastern Australia. Patch size was a strong predictor of the persistence of speckled warblers in habitat remnants. High density populations had higher probabilities of persisting, and inclusion of an Allee effect during drought decreased the probability of persistence. In the absence of an Allee effect, only high density populations in patches greater than 300 ha and low density populations in patches greater than 700 ha had more than an 80% probability of persisting over 100 years. The accelerating decrease in population persistence below approximately 200–400 ha suggests that small populations were particularly vulnerable to stochastic demographic and environmental events. Adult female mortality was the single most important factor in driving population extinction. Our PVA model predictions matched the survey data for the Australian Capital Territory region remarkably well, but failed to predict occupancy rates in remnants in other regions. Differences in occupancy patterns between regions may, however, have resulted from inbreeding depression. This study demonstrates both the strengths and limitations of PVA analysis. PVA can predict occupancy patterns with reasonable accuracy, given good demographic data, but data for one region cannot be used universally for all regions. We highlight the need for studies of demography in different regions to interpret regional patterns of occupancy and to identify mechanisms of decline in remnant habitat.

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1. Introduction

Habitat fragmentation involves complex ecological processes that can have profound effects on the dynamics of natural populations (Fahrig, 1997; Sih et al., 2000). In particular, it can subject populations to a loss of critical resources for breeding and survival (e.g. food and shelter), change the intensity of ecological processes such as predation and competition and reduce gene flow (Andr en, 1994; Fahrig and Merriam, 1994). The impact of fragmentation on the Australian avifauna has been ubiquitous with local extinctions occurring across most guilds of birds and in most habitat types (Recher and Lim, 1990; Garnett, 1992; Lunney et al., 1997; Recher, 1999). Considerable research has focused on identifying patterns of declines, and it is clear that species richness and abundance decline with reduced remnant size and habitat quality and increased habitat isolation (Ford and Howe, 1980; Loyn, 1987; Saunders, 1989; Barrett et al., 1994; Mac Nally et al., 2000; Major et al., 2001; Lindenmayer et al., 2002; Reid, 1999).

The speckled warbler, *Chthonicola sagittata* is one of a number of species declining from the highly fragmented temperate woodlands of eastern Australia (Garnett and Crowley, 2000). Since European settlement up to 80% of the natural habitat has been cleared to make way for agriculture and grazing and this has had considerable impact on the status of species within the region (Ford et al., 2001). Specific causes of decline are unknown but thought to be linked with processes associated with fragmentation and degradation of their habitat, rather than a direct result of habitat loss, because populations continue to decline where land clearing has stopped (Reid, 1999). Speckled warblers appear to be patchily distributed in habitat remnants. The minimum patch size for viable populations is suggested to be about 100 ha, because in districts where no habitat fragments larger than 100 ha remain the species appears to be locally extinct (Barrett et al., 1994; Robinson and Traill, 1996; Traill and Duncan, 2000). However, more recent analyses of occupancy rates in patches indicate that larger remnants may be required for viable populations. In 267 remnants ranging in size from 1 ha to 2669 ha, Gardner (2002b) showed that minimum size for viable populations appeared to be about 300 ha, because the species was consistently recorded only in remnants of this size or larger. Similarly, Watson et al. (2005) showed a 50% probability of occurrence was reached only in remnants at least 180–390 ha in size, depending on the nature of the matrix surrounding the remnant.

Several aspects of their biology make speckled warblers vulnerable to population decline in fragmented landscapes. First, the species occurs at low population density and is a specialist in terms of nesting and foraging behaviour (Ford et al., 1986; Tzaros, 1996; Gardner, 2002a; Gardner et al., 2003). Second, despite being multi-brooded with the potential to fledge up to three broods each season, females have low reproductive success (Gardner, 2002a). Low success results mainly from nest predation, a phenomenon that may be elevated in habitat remnants, particularly those that are small and/or characterised by a large proportion of edge habitat where generalist predators may invade from the sur-

rounding habitat matrix (Wilcove, 1985; Paton, 1994; Gardner, 1998). Last, speckled warblers form intraspecific flocks in winter, behaviour that is likely to increase survival in harsh years (Gardner, 2004). Disruption of the structure and composition of flocks may have potential to trigger the Allee effect which is a slowing in population growth at low density or small population size (Allee, 1931; S aether et al., 1996; Courchamp et al., 1999; Stephens and Sutherland, 1999).

Here, we analyse occupancy rates of speckled warblers in a large sample of habitat remnants to identify the critical patch sizes for their persistence in different regions. We then explore the effects of patch size on extinction risk for populations using data from the individual-based behavioural study of Gardner (2002a,b) and Gardner et al. (2003). We combine the demographic parameters estimated in those studies with population viability analyses (PVA) to gain an unusually comprehensive picture of their patch size requirements. In particular, we identify the demographic attributes that make speckled warblers especially prone to extinction, but note that the demographic attributes of one population cannot necessarily be extended to predict persistence across all populations of the same species.

2. Methods

2.1. Life history of the speckled warbler

The speckled warbler is a small insectivorous passerine that breeds in the austral spring and summer. The life-history parameters used in our PVA models are largely based on a study of the breeding biology and demography of an apparently stable population occupying a large (>1000 ha) habitat remnant in the Australian Capital Territory (Gardner, 2002a). The study involved intensive monitoring of the fates of all 20–35 breeding groups living in the 250–300 ha study site and all offspring over a three-year period. All residents as well as dispersing immigrants were colour-banded to allow individual recognition.

Speckled warblers live in pairs or in trios consisting of a female with two males (Tzaros, 1996; Gardner, 2002a). The Australian Capital Territory population was male-biased in each year (mean of 59% males, range 56–62%) (Gardner et al., 2003). The species is primarily ground-dwelling, both nesting and foraging directly on the ground (Tzaros, 1996; Gardner, 2002a). All nests are built in shallow depressions that the birds appear to excavate so that the base of the entrance is almost flush with the surface of the ground (Tzaros, 1996; Gardner, 2002a). Females are multi-brooded laying clutches in up to seven months of each year, but only produce about 1.0 fledgling per season (Gardner, 2002a). All juveniles disperse from the natal territory about seven weeks after fledging, soon after reaching foraging independence (Gardner et al., 2003). Females disperse directly into breeding positions while males join an established pair as a subordinate and disperse to a breeding vacancy, usually in their second year of life. During breeding, pairs and trios defend large territories ranging in size from 6 ha to 12 ha (mean = 9 ha) (Gardner et al., 2003). Dur-

ing winter larger groups defend territories of up to 30 ha (Gardner, 2004).

2.2. Analysis of remnant size and occupancy

We compiled presence/absence data for speckled warblers from surveys of 561 habitat remnants ranging in size from 1 ha to 2669 ha from the data of Major et al. (2001), Watson et al. (2001, 2005), and Barrett et al. (1994). We divided remnants into 10 size classes and calculated occupancy rates for each. We tested whether occurrence (presence/absence) in remnants was affected by remnant area using binomial logistic regression. Because survey data were compiled from three studies, each from a different region (Northern Australian Capital Territory and surrounds, Watson et al., 2001, 2005; South Western Slopes of New South Wales, Major et al., 2001; New England Tableland, New South Wales, Barrett et al., 1994), we included region as a factor in the model as well as the area.region interaction term.

2.3. Population viability analyses

The computer program VORTEX version 9.50 (Miller and Lacy, 2005) is an individual-based simulation of the stochastic and deterministic forces affecting populations. It is primarily used to model the probability of extinction of small populations and the effects of different treatments and perturbations on population persistence. Simulations were run 1000 times (Harris et al., 1987), the time-frame for simulations was set at 100 years to ensure all long term effects were identified for this slowly breeding and potentially long-lived species (Miller and Lacy, 2005), and extinction was defined as only one sex remaining in a population.

We did not incorporate density dependence explicitly in our models, as there is no evidence that density affects survival or reproduction in “good” years. However we did include an Allee effect in drought years (see below). Our major models did not include any effects of inbreeding depression as none have been documented in this species, and anecdotal evidence suggests speckled warblers can disperse considerable distances between populations. However, in recognition of a recent analysis that showed potentially dire effects from inbreeding on small populations, we ran a sub-set of the models using 12 diploid lethal equivalents with 50% due to recessive lethals (O’Grady et al., 2006). We did not include any environmental concordance of reproduction and survival as field evidence suggests that speckled warblers may persist in the habitat even if they are unable to breed. By not including all effects of density dependence and inbreeding, we have potentially biased the model predictions towards higher rates of population persistence. Similarly, in the absence of appropriate data, our models do not consider patch connectivity or meta-population dynamics (see Section 5).

2.4. Model parameters

Table 1 shows the life-history parameters we used in our simulations of population persistence. We calculated population size for habitat remnants ranging in size from 10 to 1000 ha using two levels of population density that span the range

Table 1 – Values used for life-history parameters

Parameter	Values used
Age at first reproduction for males	1
Age at first reproduction for females	1
Maximum age of reproduction	15
Max progeny per year (independent young)	3
Sex ratio at birth (% males prior to dispersal)	47
Percentage adult females breeding	100%
Environmental variation	10%
Percentage of males in breeding population	74%
N of offspring per female per year (independent young)	0.884 ± 0.16
Mating system	Long-term monogamy
Annual mortality females (age 0–1) (independence to start of next breeding season)	22.9 ± 7.2%
Annual mortality males (age 0–1) (independence to start of next breeding season)	20 ± 7.2%
Annual mortality females (age 1–2) (from start to finish of 1st breeding season)	34.9 ± 7.6%
Annual mortality males (age 1–2) (from start to finish of 1st breeding season)	14 ± 6.3%
Annual mortality females (age 2 and above)	30 ± 7.6%
Annual mortality males (age 2 and above)	14 ± 6. %

of published data. The lower value (0.18 birds/ha) was reported by Gardner et al. (2003) from known individuals while the higher value (0.54) was based on survey data (Higgins and Peter, 2002). Putative population sizes in remnants are shown in Table 2. Carrying capacity K was allowed to be approximately 50% higher than the initial population sizes because in each year of the Australian Capital Territory study there were empty territories (those that were known to support breeding pairs or groups in previous years) or territorial males without breeding partners (Gardner et al., 2003).

Parameters for productivity were based on Gardner (2002a). We used the number of independent young (five weeks post-fledging) as our measure of reproductive success because it reflects all mortality of offspring incurred under parental care. We increased mean annual productivity from 0.65 to 0.88 independent young per female to account for differences in predation rates between territory types. Gardner (in press) showed that breeding groups suffered higher rates

Table 2 – Estimates of population sizes (N) at high and low densities used in PVA models

Remnant size (ha)	Population density	
	Low	High
10	2 (4)	5 (10)
20	4 (6)	11 (16)
50	9 (15)	27 (40)
100	18 (27)	56 (80)
200	36 (55)	108 (150)
300	56 (75)	162 (240)
400	72 (110)	216 (300)
500	90 (135)	270 (400)
1000	180 (270)	540 (720)

Carrying capacity (K) given in brackets.

of nest predation in more open habitats, resulting in lower productivity on those territories. About half of all territories were adjacent to or within 100 m of a habitat edge and therefore likely to be subject to higher predation rates, thereby leading to an underestimate of productivity for a patch this size. To be conservative in our model, we therefore calculated the difference in predation rates of eggs between territory types ($0.18/0.5 = 0.36$) and increased productivity by this proportion ($0.65 + (0.36 \times 0.65)$). The figure of 0.88 independent offspring is at the low end of the range reported for other members of the Australian Acanthizidae (1.1–3.6; Green and Cockburn, 1999) and for other Australian passerines (1.0–3.1; Rowley and Russell, 1991).

Juvenile mortality was calculated for the period from natal dispersal to the start of the following breeding season, nominally August 1. Only juveniles banded as nestlings that dispersed to vacancies within the study site ($n = 22$) were included in calculations because these individuals were regularly located throughout winter (Gardner et al., 2003). Our measure of juvenile mortality may be conservative if juveniles that disperse further incur higher mortality. Annual mortality was also calculated separately for yearling birds (1–2 years), from the start of their first breeding season to the start of their second season, and as a pooled figure for birds two years and older.

The maximum breeding age of females was estimated at 15 years and is based on records of closely related Acanthizidae species living up to 17 years in the wild (white-browed scrubwrens, *Sericornis frontalis* Magrath et al., 2000; brown thornbills *Acanthiza pusilla* Baker et al., 1999). Fifteen-year old scrubwrens are known to breed successfully (Magrath pers comm.). The oldest record of a free-living speckled warbler is at least 10 years but relatively few individuals have been banded compared with the more common and widespread scrubwrens and thornbills (Higgins and Peter, 2002).

The mating system was defined as long-term monogamy for the purpose of the model, even though speckled warblers

breed in trios comprising a female with two males, as well as in pairs. Although subordinate males are members of breeding groups they do not help to feed the offspring produced on the territory and therefore the mating system is better classified as monogamous (Gardner et al., 2004).

We modelled two types of broad scale catastrophe that are known to affect speckled warblers. The first was a disease epidemic programmed to occur at a frequency of 5% (ie one event every 20 years), decreasing annual survival of the population by 10% with no effect on reproduction. This was based on a presumed disease outbreak that was observed to have increased mortality in several species (speckled warblers, brown thornbills, white-browed scrubwrens, superb fairywrens *Malurus cyaneus*) at two sites in the Australian Capital Territory over a three-month period in 1998 (Green and Cockburn, 1999; Gardner, 2002a). Although a disease outbreak was suspected, no cause was identified. Nevertheless, all species were the subject of long-term monitoring programmes of colour-banded individuals and unusually high levels of mortality (10–40%) were recorded over the period. The assumed 10% annual mortality in our model was a conservative measure of the consequence of disease.

The second type of catastrophe modelled was a drought event with 15% frequency. This approximately 1 in 7 year interval was based on long-term (60 years) rainfall data showing years with annual rainfall below 400 mm occur with this frequency (Australian Bureau of Meteorology). Breeding in drought years was reduced to 54% of normal level with no effect on mortality. The figure is that recorded for speckled warblers in the 1997 breeding season when rainfall was just 60% (400 mm) of the average annual total recorded over the previous 10 years; the breeding season was significantly shorter with fewer nesting attempts recorded but annual adult mortality was not elevated (Gardner, 2002a).

We also examined an Allee effect that reduced survival only in drought years. The effect was modelled as a density dependent function with increasingly elevated effects on

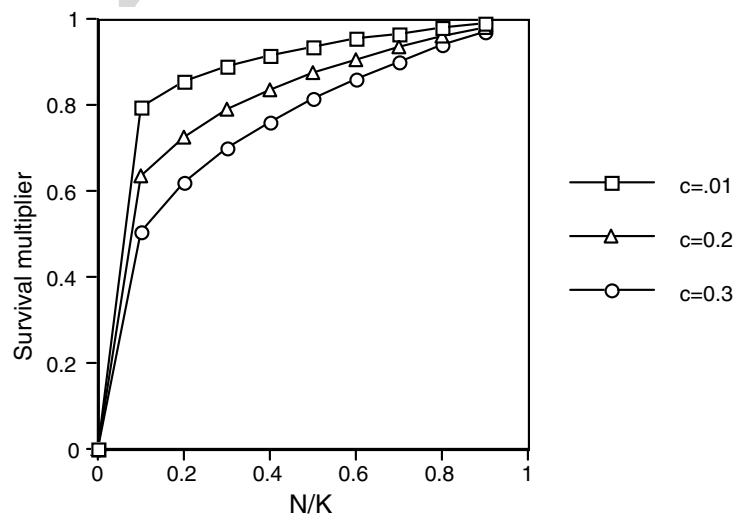


Fig. 1 – Three representative curves showing the additional effect on background survival of a drought-induced Allee effect in the PVA models. N = population size, K = carrying capacity, c establishes the severity of the multiplier for different values of N/K .

sparsely distributed populations, because such individuals would have increasing difficulty in forming flocks of an appropriate size to facilitate foraging and anti-predator strategies, given the social and spatial structure of flocks. Speckled warblers were observed to form larger flocks in drought conditions, via amalgamation of residents from several adjacent breeding territories as well as dispersing immigrants (Gardner, 2004). In the absence of precise knowledge we used a simple function $(N/K)^c$ to modify background survival rates, where N is population size at the time of the drought, K the carrying capacity of the patch, and c a constant that determines the severity of the Allee effect. Lower values of c in this function lead to larger proportional impacts on small populations. This qualitative property is important because it ensures that drought only effects a fluctuating population when its size is low by chance. We used $c=0.2$ as this achieved the desired effect of a minimal effect at high density and a severe effect at low density, but also examined the sensitivity of this parameter (below). The shape of the function is shown in Fig. 1.

We examined the sensitivity of the PVA models to juvenile and adult male and female mortality and the severity of the drought-induced Allee effect. Adult and juvenile male and female mortality were each reduced by 25% and 50%. We examined the impact of the Allee effect by varying c between 0.1 and 0.3.

3. Results

3.1. Remnant size and the presence of speckled warblers

The percentage and size of 561 habitat remnants in which speckled warblers were recorded during surveys is compiled in Table 3. Speckled warblers were more likely to be recorded in larger remnants (Logistic regression: $\chi^2_1 = 7.37$, $P = 0.007$, Fig. 2, Table 3). However, the effect of patch size on occupancy rate differed among regions (region.area interaction term $\chi^2_2 = 5.82$, $P = 0.05$). There was a strong effect of patch size on occupancy rate in the Australian Capital Territory region

($\chi^2_1 = 8.49$, $P = 0.004$), a non-significant trend for remnant size to affect rate in the South Western Slopes ($\chi^2_1 = 3.52$, $P = 0.06$), and no effect of remnant size in the New England Tablelands ($\chi^2_1 = 0.0002$, $P = 0.99$). Thus, minimum remnant sizes for viable populations will differ among regions.

4. Population viability analyses

4.1. Persistence in small habitat remnants

The probability of a population persisting in remnant habitat was correlated with patch size in all models (Fig. 3). High density populations had higher probabilities of persisting, and inclusion of an Allee effect during droughts decreased the probability of persistence (see below). In the absence of an Allee effect, only high density populations in patches greater than 300 ha and low density populations in patches greater than 700 ha had more than an 80% probability of persisting over 100 years. However, even populations in the largest

Table 3 – Proportion and size of habitat remnants in which speckled warblers were recorded during surveys (N = 561 remnants), compiled from the raw data of Major et al. (2001), Watson et al. (2001, 2005) and Barrett et al. (1994)

Remnant size class (ha)	Number remnants occupied (N surveyed)	Proportion of remnants occupied
<10	2 (60)	0.03
10–<20	2 (32)	0.06
20–<50	4 (86)	0.05
50–<100	3 (99)	0.03
100–<200	3 (87)	0.03
200–<300	3 (34)	0.09
300–<400	4 (38)	0.11
400–<500	1 (18)	0.06
500–<1000	7 (93)	0.08
>1000	3 (14)	0.21

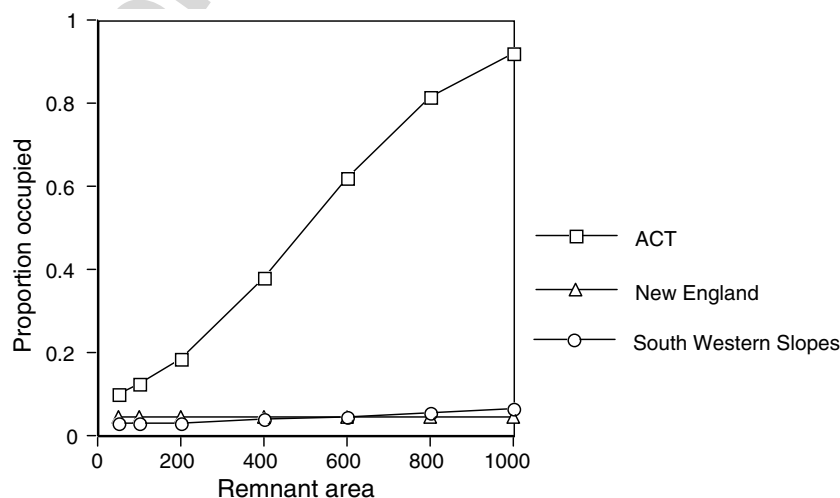


Fig. 2 – Predictions for occupancy rates of speckled warblers in habitat remnants from survey data from three regions, based on the data of Watson et al. (2001, 2005), Major et al. (2001), and Barrett et al. (1994).

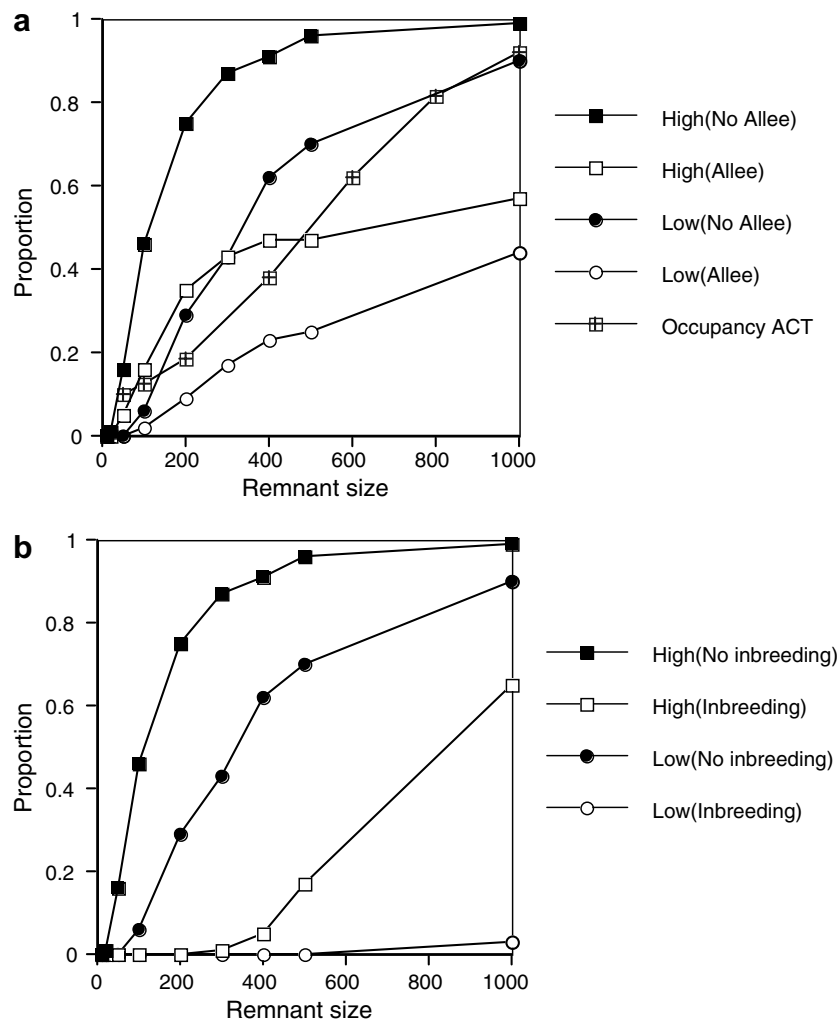


Fig. 3 – Representative curves from PVA models showing: (a) predicted persistence of populations in remnants of different sizes for high and low density populations with and without an Allee effect, together with predictions for probability of occupancy based on survey data from the Australian Capital Territory region and (b) the impact on high and low density populations if inbreeding is incorporated.

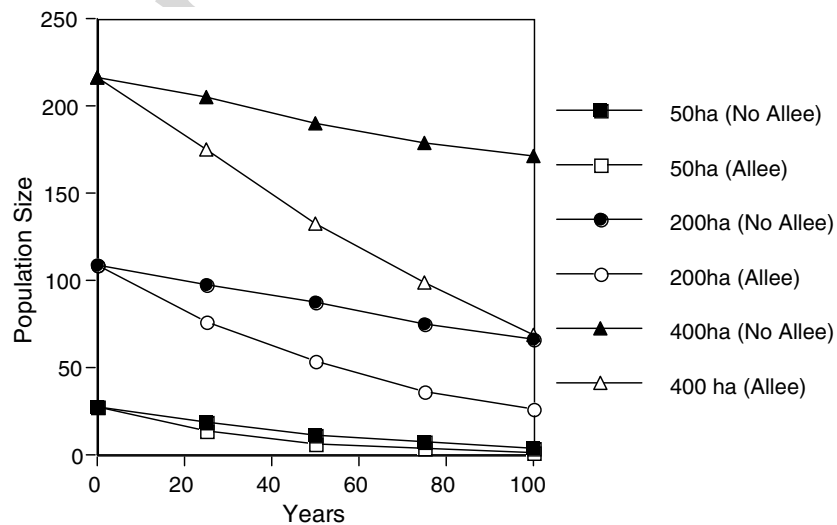


Fig. 4 – Representative curves showing the predicted population sizes for six PVA models for high density populations with and without an Allee effect.

Table 4 – Predictions of PVA models including mean annual rate of population change across simulations (r), probability of population persistence over 100 years P (persist), the mean final extant population size extant P (\pm SD), and the median time (years) to extinction, T (extinct)

Area (ha)	Density	Allee effect	r	P (persist)	Extant P	SD	T (extinct)
10	High	No	-0.015	0	0	0	8
20	High	No	-0.013	0.01	9.7	4.8	18
50	High	No	-0.011	0.16	23	11.6	45
100	High	No	-0.006	0.46	46.7	25.1	90
200	High	No	0	0.75	87.3	46.7	0
300	High	No	0.003	0.87	144.6	74	0
400	High	No	0.005	0.91	186.9	91.6	0
500	High	No	0.006	0.94	245.7	118.7	0
1000	High	No	0.008	0.99	469	208.9	0
10	High	Yes	-0.026	0	0	0	8
20	High	Yes	-0.024	0.01	9.5	5.3	15
50	High	Yes	-0.029	0.05	20.7	10.5	30
100	High	Yes	-0.026	0.17	39.2	23.7	47
200	High	Yes	-0.023	0.30	82.9	50.2	70
300	High	Yes	-0.023	0.37	112.1	71.9	82
400	High	Yes	-0.020	0.47	144.4	104	96
500	High	Yes	-0.023	0.47	195.2	138.2	96
1000	High	Yes	-0.021	0.57	354.8	262.7	0
10	Low	No	-0.016	0.01	20.8	12.1	4
20	Low	No	-0.015	0	0	0	4
50	Low	No	-0.014	0.01	10.3	5	13
100	Low	No	-0.0013	0.06	16	7.3	28
200	Low	No	-0.008	0.28	30.9	16.7	63
300	Low	No	-0.008	0.43	42.9	23.2	88
400	Low	No	-0.003	0.62	63	33.7	0
500	Low	No	-0.001	0.70	78.7	41.8	0
1000	Low	No	-0.003	0.90	159.3	81.9	0
10	Low	Yes	-0.028	0	0	0	3
20	Low	Yes	-0.026	0	0	0	5
50	Low	Yes	-0.024	0	8	0	12
100	Low	Yes	-0.028	0.02	14.8	8.2	23
200	Low	Yes	-0.027	0.09	29.6	14.7	38
300	Low	Yes	-0.024	0.17	37.7	24.5	52
400	Low	Yes	-0.025	0.23	62	36.9	55
500	Low	Yes	-0.026	0.25	73.4	48.4	61
1000	Low	Yes	-0.020	0.44	129	85.4	89

modelled patches of 1000 ha showed mean decreases over 100 years (Fig. 4).

Small populations appear particularly vulnerable to stochastic demographic and environmental events. There was an accelerating decrease in population persistence below approximately 200–400 ha in all models, regardless of density and the inclusion of an Allee effect (Fig. 3). The model simulations predicted similar persistence to the occupancy rates revealed by the Australian Capital Territory region survey data, but not those from New England or the South Western Slopes (Figs. 2 and 3a).

4.2. Effect of inbreeding

The effect of including inbreeding in the models was dramatic. Fig. 3b shows that even in the best case scenario (high density, 1000 ha) speckled warblers subject to the severity of inbreeding outlined by O'Grady et al. (2006) had only a 65% chance of persistence. This fell to 17% (versus 96% with no inbreeding) in 500 ha patches. In low density patches, speckled warblers subject to inbreeding depression had only a 3% chance of persistence.

4.3. Allee effect

Our models show that an Allee effect that only occurs in drought years markedly decreases the probability of persistence (Table 4, Fig. 3). The probability of persistence was dramatically worse in small patches, and it was approximately halved even in the largest patches (1000 ha, Fig. 3). The median extant population sizes (i.e. those that did not go extinct) were also more than halved when the Allee effect prevailed (Fig. 4). Population size for all other groups was reduced by about a half in 100 years and all were driven to extinction with the median time to extinction estimated at 3–89 years (Table 4).

4.4. Sensitivity analyses

Female mortality was the single most important factor in driving population extinction, with the greatest effect seen in adults. In a 100 ha patch at high density, adult female mortality needs only to be cut by 25% to increase the probability of persistence from 0.46 to 1.0 (Table 5). There was a similar but less dramatic effect for juveniles, with a 25% cut in mortality roughly increasing P (persist) from 0.46 to 0.76.

Table 5 – Sensitivity analyses of three major PVA parameters

Model	<i>r</i>	P (persist)	Extant P	SD	T (extinct)
1. 100 hectare, High density, no Allee	–0.014	0.46	46.7	25.1	90
2a. 75% Juvenile female mortality	0.010	0.76	58.4	22.7	0
2b. 50% Juvenile female mortality	0.033	0.93	67.0	17.6	0
3a. 75% Adult (1, 2 year-old) female mortality	0.065	1.0	75.9	9.6	0
3b. 50% Adult (1, 2 year-old) female mortality	0.100	1.0	79.4	5.1	0
4a. 75% Juvenile male mortality	–0.007	0.43	47.6	24.5	88
4b. 50% Juvenile male mortality	–0.003	0.46	48.1	23.7	93
5a. 75% Adult male mortality	–0.003	0.46	51.4	24.1	91
5b. 50% Adult male mortality	0	0.48	51.7	23.6	98
6a. 100 ha, High density, Allee (<i>c</i> = 0.3)	–0.033	0.11	41.6	26.3	42
6b. 100 ha, High density, Allee (<i>c</i> = 0.2)	–0.026	0.17	39.2	23.7	47
6c. 100 ha, High density, Allee (<i>c</i> = 0.1)	–0.016	0.29	36.0	23.5	65

Model 1 shows the output for a 100 hectare patch with high density and no Allee effect during drought. Models 2a and 2b show the effect of reducing juvenile female mortality to 75% and 50% of normal. Models 3a and 3b show the effect of reducing adult female mortality to 75% and 50% of normal. Models 4a and 4b show the effect of reducing juvenile male mortality to 75% and 50% of normal. Models 5a and 5b show the effect of reducing adult male mortality to 75% and 50% of normal. Models 6a, 6b, and 6c show the effect of varying the Allee parameter *c* during drought from 0.1 to 0.3.

The sensitivity of the models to the severity of the Allee effect during drought was also high. In a 100 ha patch at high density, a reduction of *c* from 0.2 to 0.1 (i.e. decreasing impact on mortality for larger populations, Fig. 1) changed P(persist) from 0.17 to 0.29, whereas an increase to 0.3 changed it from 0.17 to 0.11 (Table 5).

5. Discussion

Patch size is a strong predictor of the persistence of speckled warbler populations in habitat remnants. Our PVA model predictions (without inbreeding depression, see below) match the qualitative trends of survey results for the Australian Capital Territory region remarkably well, but fail to predict occupancy rates in remnants in other regions. Both Australian Capital Territory survey data and model predictions show that the persistence of populations in patches less than roughly 200–400 ha falls disproportionately. At small population sizes the unusual demography of the species appears to leave speckled warblers particularly vulnerable to stochastic events. The life history parameters used in our model are based on robust field data from known individuals, spanning years of high and low productivity, and are conservative in their estimates. This is important because parameter estimation has a strong influence on predictions of extinction risk (Sæther et al., 2005).

5.1. Female mortality

Birds show species-specific risks of extinction due to differences in life history parameters (Sæther et al., 2005). In speckled warblers, high female mortality, particularly of adults, appears to be the single most important factor in driving population decline in small remnants in the Australian Capital Territory region. Sensitivity analyses showed that a 25% decrease in adult female mortality markedly changed the probability of persistence, whereas similar changes in male mortality had negligible effects (Table 5). Only females incubate the clutch and brood the nestlings and they appear to

be vulnerable to predation at this time (Gardner, 2002a). Predators can probably approach the nest without being observed because the dome structure and location of the nest obscures the view of the sitting female. Males neither incubate nor brood the offspring and accordingly suffer lower mortality during breeding; in the non-breeding season mortality rates of males and females are similar (Gardner et al., 2003). Juvenile females (from dispersal to acquiring a breeding vacancy) have slightly higher mortality than do juvenile males, and this is probably the result of differences in dispersal patterns. Female birds generally disperse further and probably suffer higher mortality as a result (Greenwood, 1980). Our sensitivity analysis of juvenile female mortality also strongly affected the probability of persistence but not as much as did adult female mortality.

Habitat quality, in particular the structure and complexity of ground and understorey vegetation, is likely to be an important factor in the persistence of speckled warbler populations. Where understorey habitat is sparse, nests and attendant females may be more exposed to predation, especially by visually hunting predators that use parental activity as clues to locate nests (Martin et al., 2000). Most nest failure in the Australian Capital Territory population studied over three seasons was due to avian predators that probably cue on parental activity and differences in hatching success of nests are correlated with differences in habitat structure (Gardner, in press). Increasing the structural diversity and density of understorey vegetation such that female and nestling survival is increased will reduce the potential for local extinction by increasing population size in small habitat remnants, and thus is an important strategy for wildlife managers.

5.2. The allee effect

In species that show a high degree of sociality, the Allee effect may be an important mechanism in population regulation (Sæther et al., 1996; Courchamp et al., 1999; Reed, 1999; Stephens and Sutherland, 1999). Speckled warblers are highly social in winter with adjacent breeding groups amalgamating to

form flocks. Flocking probably increases survival in harsh conditions and appears to be particularly important to speckled warblers in drought conditions (Gardner, 2004). Our models may over-estimate population persistence because they only incorporate increased mortality from this source in drought years, even though such an effect may occur at some level in all years. In the absence of data that quantify the likely Allee effect we have used a simple function that leaves mortality unaffected if the population is large (e.g. near carrying capacity) but increases mortality progressively more severely in smaller populations. Thus the impact of a drought event on a population's persistence may range from negligible to drastic depending on the populations' size when the drought occurs.

Our models suggest that an Allee effect triggered by drought every seven years on average will reduce the probability of persistence for populations of all sizes (Fig. 3). It also dramatically reduces the time to extinction and the size of remaining extant populations (Fig. 4). The Allee effect with similar severity on single populations has been modelled elsewhere (Brassil, 2001). However, the severity of such effects can be drastically reduced with moderate levels of immigration. Thus, the Allee effect needs to be examined in the context of metapopulation dynamics (Brassil, 2001).

Our major models did not include metapopulation dynamics or the potential effects of inbreeding because we have no data on exchange rates among remnants. Nevertheless, there is evidence that speckled warblers can move between habitat remnants. For example, movements of 30 km have been recorded for banded individuals (Baker et al., 1999) and use of revegetated sites up to 3.5 km from source populations, measured as remnants greater than 5 ha in size, have also been documented (Bond, 2004). Whether individuals breed successfully at such sites is, however, unknown. Modelling the dynamics of metapopulations together with inbreeding in relation to patch isolation in different landscapes to assess factors driving regional extinctions would be a valuable exercise once reliable data on exchange rates and associated mortality are available. Our exploratory models based on the high number of diploid lethal equivalents recently identified for birds and mammals (O'Grady et al., 2006, Fig. 3b) showed that the effects of inbreeding are potentially profound.

5.3. Model assumptions and potential sources of error

Survey data from all three regions indicate that small remnants can support speckled warblers although it seems likely that such populations are unviable as suggested by our models. Several studies provide direct evidence that small remnants are suboptimal habitat for insectivorous birds, with associated fitness costs. First, food shortage is associated with declining remnant size (Burke and Nol, 1998), and can reduce the survival and fecundity of residents (Doherty and Grubb, 2002; Zannette et al., 2000). Zannette et al. (2003) showed experimentally that predation pressure and food shortage interacted to reduce the reproductive success of insectivorous eastern yellow robins, *Eopsaltria australis* in small habitat remnants. Furthermore, nestlings from the smaller remnants fledged at lower weights (Zannette et al., 2000; Suorsa et al., 2004), which often results in reduced survival to nutritional

independence and lower recruitment rates (Magrath, 1991; Naef-Daenzer et al., 2001).

Second, predation pressure is higher in fragmented landscapes than in continuous habitat (Ambuel and Temple, 1983; Wilcove, 1985; Andrén, 1994; Paton, 1994; Robinson et al., 1995; Gardner, 1998). Evidence for increased predation pressure comes largely from artificial nest experiments (Paton, 1994; Major and Kendall, 1996), although studies of natural populations also show increased predation of fledglings and adults in smaller remnants (Currie and Matthysen, 1998). We did not model increased fitness costs for speckled warblers living in small remnants, despite the fact that they are likely to be susceptible to both food shortage and increased predation because of their specialist nesting and foraging behaviour (Gardner, 2004). Thus, our model predictions are conservative, and suggest that the few cases of occupancy of small remnants represent nonviable populations in which individuals probably immigrated from larger remnants. The increasing and disproportionate fitness costs to living in smaller patches are likely to affect population persistence in a similar manner to an Allee effect, and may provide an alternative explanation for the observed rates of patch occupancy.

Despite the uncertainties of the status of speckled warblers in small habitat remnants, our model predictions fit those from the Australian Capital Territory survey data of Watson et al. (2005) well. For a patch of a given size the probability of occurrence of speckled warblers is influenced by both the quality of the habitat patch and the nature of the matrix surrounding the patch (Watson et al., 2005; Seddon et al., 2001), variables we did not include in our models. Nevertheless, threshold areas reported by Watson et al. (2005) of 180–390 ha for a 50% probability of occupancy match probabilities of persistence predicted by our PVA model for patches of that size.

In New England and the South Western Slopes the demography of speckled warbler populations appears to be different. This might be explained, in part, by the matrix effect described by Watson et al. (2005), whereby the properties of the matrix surrounding remnants affects occupancy rates within; occupancy rates in smaller remnants were lower in agricultural, compared with urban and peri-urban, landscapes, despite the degree of isolation and habitat quality being similar in all landscape types. A hostile matrix with reduced connectivity of patches may reduce the ability of birds to disperse between populations and have a direct bearing on the extent of inbreeding, with potentially dire effects for population persistence, as suggested by our models. New England and the South Western Slopes are agricultural regions, rather than a mixture of landscape types in the Australian Capital Territory and inbreeding may explain underlying differences in demography between regions.

This study demonstrates both the strengths and limitations of PVA analysis. PVA can predict occupancy patterns with reasonable accuracy, given good demographic data. However, such models cannot be considered universal. Clearly, there are limitations to extrapolating to regions other than those in which the demographic data were collected. Studies of the demography of individual populations in different regions are required to understand regional patterns of

occupancy and identify mechanisms of decline in remnant habitat.

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