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Gap-crossing decisions of forest birds in a fragmented landscape

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Abstract Habitat loss and fragmentation are recognized as primary drivers of biodiversity loss worldwide. To understand the functional effects of habitat fragmentation on bird populations, data on movement across gaps in habitat cover are necessary, although rarely available. In this study, we used call playback to simulate a conspecific territorial intruder to entice birds to move through the landscape in a predictable and directional manner. We then quantified the probability of movement in continuous forest and across cleared gaps for two forest-dependent species, the grey shrike-thrush (*Colluricincla harmonica*) and the white-throated treecreeper (*Cormobates leucophaeus*). Fifty-four playback trials were conducted for each species across distances ranging from 25 to 480 m in continuous forest and 15–260 m across gaps in a forest-agricultural landscape in southern Victoria, Australia. The probability of movement was significantly reduced by gaps in forest cover for both species. Shrike-thrushes were six times more likely to move 170 m in continuous forest than to cross 170-m gaps. The mean probability that treecreepers would cross any gap at all was less than 0.5, and they were three times less likely to move 50 m across a gap than through continuous forest. Both species displayed non-linear responses to increasing gap distance: we identified a gap-tolerance threshold of 85 m for the shrike-thrush and 65 m for the treecreeper beyond which individuals were most unlikely to cross. The presence of scattered paddock trees increased functional connectivity for the shrike-thrush, with individuals crossing up to 260 m when scattered trees were present. We conclude that gaps in habitat cover are barriers to movement, and that characteristics of the intervening matrix influence landscape permeability.

Key words: call playback, *Colluricincla harmonica*, *Cormobates leucophaeus*, functional connectivity, gap-tolerance, habitat fragmentation.

INTRODUCTION

Habitat loss and fragmentation has been demonstrated to have profound implications for the distribution and occurrence of woodland and forest birds worldwide (Donald *et al.* 2001; Ford *et al.* 2001; Fahrig 2003; Hannah *et al.* 2007). Population declines associated with habitat fragmentation are often attributed to reduced functional connectivity: that is, the degree to which a landscape facilitates or impedes the movement of organisms (Taylor *et al.* 1993; Tischendorf & Fahrig 2000). Functional connectivity is determined by the physical arrangement of the species' habitat (structural connectivity), the resistance of areas of non-habitat to movement and behavioural attributes of the species in question (Merriam 1991; Uezu *et al.* 2005). However, the mechanisms by which habitat fragmentation impinges on functional connectivity remain unclear. Of particular interest in this regard is the impact of landscape structure on gap-crossing behaviour because ultimately, functional connectivity is the outcome of successive gap-crossing decisions made by individuals at patch boundaries.

Habitat fragmentation reduces structural connectivity by creating areas of cleared land (gaps) between habitat patches. For forest-dependent species, this might reduce functional connectivity because the behaviour and morphology of forest specialists are seldom adapted to movement in open areas (Gobeil & Villard 2002). Functional connectivity can be maintained for some species by the retention or restoration of movement corridors (Saunders & de Rebeira 1991; Bennett 1999; Haddad & Tewksbury 2006). Other species are able to use small remnants (Date *et al.* 1991; Haas 1995) or scattered paddock trees (Law *et al.* 2000; Fischer & Lindenmayer 2002) as 'stepping stones' to move through fragmented landscapes. A species' ability to cross gaps, therefore, is a crucial component of functional connectivity, and hence response to habitat fragmentation, and will be a

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function of a species behaviour, mobility and motivation to cross a gap (Bélisle *et al.* 2001). This ability can be quantified by 'gap-tolerance': the maximum distance of cleared land between two habitat patches that an individual will cross (Desrochers & Hannon 1997; Brooker *et al.* 1999).

The most direct means for estimating functional connectivity is derived from data on individual movements (Fagan & Calabrese 2006). However, relatively few studies have empirically examined how individual movement pathways are influenced by landscape structure (Desrochers & Hannon 1997; Robichaud *et al.* 2002; Shirley 2006). Mark-recapture, radio-telemetry and translocation studies provide critical information on long-distance movements and have established that movement might be disrupted by habitat fragmentation (e.g. Brooker *et al.* 1999; Cooper & Walters 2002; Gobeil & Villard 2002). Genetic approaches are able to show the demographic consequences of constrained movement in fragmented landscapes (Stow *et al.* 2001; Banks *et al.* 2005; Walker *et al.* 2007). However, these approaches do not explicitly examine movement pathways. This requires organism-based studies examining responses to variation in landscape structure to identify barriers to, or conduits for, movement across fragmented landscapes.

Individual-based modelling approaches (Tracey 2006), such as least-cost pathway analysis (Adriaensen *et al.* 2003) or cellular automation (Aurambout *et al.* 2005), indirectly examine movement pathways by integrating spatial information with population modelling. These approaches allocate movement costs to each 'cell' in a digital map of the landscape. Simulations are then run to find the path with the lowest movement costs (least resistance), or ascertain the probability of movement from source to destination, and thus identify likely movement pathways through fragmented landscapes. However, the attributes of the model species, the motivation for movement, and movement costs for different land-uses are rarely based on empirical data. Thus, the true costs of alternative pathways remain undefined (Epps *et al.* 2007). There is a demonstrative need for empirical data on movement behaviour to inform these potentially powerful management tools.

Call playback experiments, during which recorded bird calls are used to stimulate movement across gaps, are an organism-based approach used to derive empirical data pertaining to gap-crossing decisions. They are useful for examining movement behaviour because they are repeatable, standardize the destination and motivation for movement and provide a quantitative measure of inter-patch movement. Most call playback studies have been conducted in the closed forests of Europe and the Americas and have showed that relatively small gaps in forest cover (often <100 m) severely restrict avian movement (e.g. Desrochers & Hannon 1997; Rail *et al.* 1997; Bélisle & Desrochers 2002; Creegan & Osborne 2005). However, many Australian forests and woodlands have a more open canopy than the forests referred to above. Furthermore, many rural landscapes in Australia are characterized by fuzzy patch boundaries rather than distinct edges (McIntyre & Barrett 1992). Thus, Australian birds might be more inclined to cross patch boundaries and traverse larger gaps. The regular occurrence of a range of species (including our study species) in scattered trees and small remnants in agricultural landscapes (Fischer *et al.* 2005) supports this contention.

In this study, we used call playback experiments to investigate the gap-crossing decisions of two species, the grey shrike-thrush (*Colluricincla harmonica* Latham, 1802) and the white-throated treecreeper (*Cormobates leucophaeus* Latham, 1802), at relatively small spatial scales in different contexts in a fragmented landscape. Although this study was conducted in a forest setting, both species are widespread in woodlands and forests throughout south-eastern Australia. Our objective was to examine the behavioural processes underlying the choice of movement pathways, and thus, provide a process-oriented understanding of the impact of habitat fragmentation on functional connectivity and ultimately, the persistence of forest bird populations. Specifically, we asked:

1. Are cleared gaps a barrier to movement?
2. Are there characteristics of gaps that facilitate or militate against movement?
3. Is there a threshold distance beyond which gaps are impassable?
4. What is the gap-tolerance of the target species?

METHODS

Study region

This study was conducted on the inland slopes of the Otway Ranges in southern Victoria, approximately 150 km south-west of Melbourne. The inland slopes experience a mild (mean daily max. temp: January 24.5°C; July 11.7°C) and mesic (mean annual rainfall: 1040 mm) climate; coastal regions are slightly drier with less seasonal variation in temperature (Bureau of Meteorology 2006). A rain shadow affects the northern foothills of the region (mean annual rainfall: 740 mm). At higher altitudes, vegetation consists of wet sclerophyll forest dominated by mountain ash (*Eucalyptus regnans*), mountain grey gum (*E. cypellocarpa*), Tasmanian blue gum (*E. globulus*), narrow-leaved peppermint (*E. radiata*) and manna gum (*E. viminalis*). Lower on the slopes, this is replaced by riparian forests of manna gum and messmate (*E.

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obliqua), and dry forests and heathy woodlands consisting of messmate, brown stringybark (*E. baxteri*) and red stringybark (*E. marcrorhyncha*) (Department of Sustainability and Environment 2006).

Most of the contiguous forest of the Otway Ranges is contained within the Great Otway National Park (103 000 ha) and the Otways Forest Park (40 000 ha). These parks extend to the coast to the south but the northern edge is bordered by agricultural land (dairy, beef, agro-forestry, horse studs, vegetable crops), resulting in an artificial and abrupt forest edge. The fertile valleys have been preferentially and extensively cleared but some native vegetation remains along the creeks and drier ridges. The extent of habitat loss increases with distance from the contiguous forest, such that three distinct landscape patterns are apparent: contiguous forest, a band of highly fragmented forest patches within agricultural land, and extensively cleared agricultural land. Most forest remnants within the agricultural landscape are small (<20 ha) and many have been modified by grazing.

Study species

The grey shrike-thrush is a common, widely distributed, medium-sized passerine (65 g) that occupies a range of habitats, including wet and dry sclerophyll forests and woodlands (Higgins & Peter 2002). It is primarily insectivorous, foraging by gleaning, probing and sallying in foliage, branches and tree trunks and on the ground, but will also prey on small frogs and lizards, eggs and young birds (Higgins & Peter 2002). In Victoria, breeding occurs between August and January, although pairs defend permanent territories using songs and displays (Higgins & Peter 2002). Territory size is variable, ranging from 5 to 18 ha, depending on region and habitat (Higgins & Peter 2002). The shrike-thrush is sedentary (Griffioen & Clarke 2002) but little is known about local movement patterns.

The white-throated treecreeper is a small (22 g) sedentary bird that occurs across eastern Australia in rainforest, wet and dry sclerophyll forests, woodland and riparian habitat (Doerr & Doerr 2001; Griffioen & Clarke 2002). It is almost entirely arboreal, gleaning invertebrates (mostly ants) from the surface and under the bark of trunks and branches. Breeding occurs between August and January when pairs occupy and defend the territory together. However, outside the breeding season, males and females avoid each other and might divide the territory, sometimes engaging in agonistic behaviour. Territories range from 2 to 12 ha during the breeding season (slightly smaller during the non-breeding season) and are vigorously defended with calls and displays (Noske 1991; Doerr & Doerr 2001). Dispersal has been studied in continuous habitat (Doerr & Doerr 2004) and young birds might move up to 2 km from their natal territory during exploratory forays (Doerr & Doerr 2001) but little is known about movement pathways in fragmented habitat.

Call playback experiments

Call playback experiments involved the broadcast of conspecific calls simulating a territorial intruder to stimulate target birds to move towards the call. For each species, a series of 'control' and 'gap' playback trials were conducted over a range of distances, where 'distance' refers to the linear distance between the target bird and the broadcast speaker when playback commences. Control trials were conducted in continuous forest within the Great Otways National Park. Birds were located by walking along walking trails, 4WD tracks and management roads. Once a target bird was identified, its location was marked with flagging tape and the distance from bird to speaker was recorded later. By communicating via two-way radios, an observer monitored the target bird while an assistant operated the call broadcast from a prescribed distance. Gap trials were conducted across clearings between forest patches. After locating the target bird in a forest patch (source patch), calls were broadcast from a second forest patch (speaker patch) across the gap. Gap distance – the shortest distance between forest canopy edges – was measured using a rangefinder.

For all trials, conspecific calls were broadcast intermittently for 1 min followed by 1 min silence, for a total of 10 min. The pause in playback was intended to imitate natural patterns of calling and allow target birds to reply. A trial ended when either (i) the target bird moved to within 10 horizontal metres of the speaker (success); or (ii) the target bird failed to arrive at the speaker after 10 min (failure). Observers minimized interference by concealing themselves, keeping a reasonable distance from the target bird, and taking care not to 'chase' the target bird towards the speaker. A maximum of one trial for each species was conducted at each site. Trials for the shrike-thrush and treecreeper at the same site were conducted at different times.

A 15-W megaphone hardwired to a portable CD player (Faunatech) was used to broadcast recorded calls. The broadcast operator crouched low to the ground, holding the speaker at knee-height, facing the direction of the target bird. For all trials, calls were broadcast at a constant volume, considerably louder than the normal calls of both species. Sound attenuation is greater through forest than cleared land: thus, true differences in movement propensity between continuous forest and gaps might be underestimated because of a slightly weaker stimulus through continu-

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ous forest. Nonetheless, playback was clearly audible to 500 m through continuous forest. For the shrike-thrush, we used a 5-min recording of calls and song, long sequence phrases and a duet of the nominate race *C. harmonica* (Plowright 2003a). For the treecreeper, we used a 5-min recording of the nominate race *C. leucophaeus* that included prolonged trills, song, notes, rolling trills and adults with fledglings (Plowright 2003b). All trials were conducted between 07.30 and 12.00 hours or 16.00 and 17.30 hours from 1 May to 5 August 2006. Trials were not conducted during rain or high wind because of sound degradation.

Study sites

Gap sites were initially identified from a digital map of forest cover in a geographical information system. However, gaps less than 50 m were difficult to identify from the geographical information system, so additional gap sites were selected once in the field. Most source patches were extensive forests within the park system but some remnants (minimum 20 ha) within agricultural land were also used. Source patches were checked just before playback to ensure the target species was present. The location of control sites was determined by access along tracks and walking paths but all sites were at least 500 m apart.

Land-use in the gap between the source and speaker patches was always grazed pasture, although bracken fern (*Pteridium esculentum*) was present at some sites. Scattered paddock trees were sometimes also present in the gap. No minimum size was set for speaker patches; they were usually small remnants but also included linear vegetation along roads and creeks. Patches with non-native vegetation and gaps with sealed roads or buildings were excluded. At each site, the gap distance, patch size and presence of paddock trees, bracken and conspecifics was recorded (Table 1).

Table 1. Variables recorded for each gap trial

Variable	Description
Response	Success: target bird moves within 10 m of speaker Failure: target bird not within 10 m of speaker after 10 min
Distance	Distance (m) across gap between canopy edges
Paddock trees	Present: paddock trees (living or dead) in gap Absent: no paddock trees in gap
Bracken	Present: bracken covers a majority of the gap Absent: pasture grasses cover majority of the gap
Speaker patch size	Small: <20 ha including riparian or roadside vegetation Large: >20 ha
Conspecifics	Present: conspecifics (excluding the target bird) observed in the speaker patch during the trial Absent: conspecifics not observed in speaker patch

Data analysis

1. Are cleared gaps a barrier to movement? We examined the effects of landscape structure (continuous forest *vs*. gap) and distance on the probability of movement (success *vs*. fail) using logistic regression (McCullagh & Nelder 1989). We constructed models with distance entered initially as a simple linear term and then as a polynomial with up to three degrees of freedom. We compared these models using Akaike's information criterion (AIC) and two estimates of model performance: (i) the area under the receiver operating characteristic (ROC) curve; and (ii) Miller's calibration slope (Wintle *et al.* 2005). The ROC area measures the ability of a model to correctly predict positive and negative responses, and ranges from 1 (perfect discrimination) to 0.5 (no better than random discrimination) (Fielding & Bell 1997). Miller's calibration slope measures the ability of a model to accurately predict the proportion of cases that are expected to be positive for a given predicted probability (Wintle *et al.* 2005). Bootstrapped estimates of ROC area and Miller's calibration slope were obtained using functions in Wintle *et al.* (2005) implemented in the R statistical platform (R Development Core Team 2005).
2. What are the characteristics of gaps that influence movement? We examined the influence of gap characteristics (Table 2) on the probability of movement using data from the gap trials only. We used logistic regression with all possible subsets selection (Genstat 8.1, Lawes Agricultural Trust 2005) to identify the most parsimonious model (based on AIC) of gap-crossing for each species.
3. Does gap-crossing exhibit a threshold response? We adapted the approach of Rail *et al.* (1997) to assess non-monotonic responses in gap-crossing in relation to gap distance. Using the model identified in (2) for each species, we compared model fit (AIC and percent deviance explained) across a series of models in which distance was treated first as a continuous variable and then as a dichotomous factor greater or smaller than a threshold distance. Twenty threshold distances in 10-m increments (5, 15 . . . 195) were examined. Support for a threshold response would be provided if model fit was highest when distance was entered as a dichotomous factor.

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Table 2. Land-use and mean (±SD) gap distance of the grey shrike-thrush ($n = 32$) and white-throated treecreeper ($n = 25$) gap trial sites

	Paddock trees		Bracken		Patch size		Conspecifics	
Variable	Present	Absent	Present	Absent	Small	Large	Present	Absent
Grey shrike-thrush								
Number of sites	6	26	15	17	18	14	13	19
Mean distance	191 ± 49	95 ± 56	110 ± 49	115 ± 80	93 ± 60	138 ± 67	111 ± 66	114 ± 68
White-throated treecreeper								
Number of sites	2	23	8	17	16	9	7	18
Mean distance	217 ± 60	101 ± 61	93 ± 46	119 ± 76	106 ± 67	118 ± 73	126 ± 90	104 ± 59

Table 3. Comparison of model performance and bootstrapped estimates of model discrimination (ROC) and calibration (MCS)

Species	Model	% dev exp	AIC	ROC	MCS
Grey shrike-thrush	Gap + Distance	29.5	58.7	0.837	0.988
Grey shrike-thrush	Gap + poly(Distance, 3)	44.8	51.3	0.812	0.596
White-throated treecreeper	Gap + Distance	25.2	55.1	0.767	0.864
White-throated treecreeper	Gap + poly(Distance, 2)	28.4	55.0	0.732	0.660

The expression 'poly(Distance, *x*)' refers to a polynomial term with *x* degrees of freedom; '% dev exp' is the percent deviance explained (i.e. 100 * (null dev – residual dev)/null dev). AIC, Akaike's information criterion; ROC area, the area under the receiver operating characteristic curve; MCS, Miller's calibration slope.

RESULTS

Twenty-two control trials with distances ranging from 35 to 480 m and 32 gap trials ranging from 15 to 260 m were conducted for the shrike-thrush. Positive responses were observed for distances up to 315 m in control trials, and up to 260 m in the gap trials. However, in the absence of paddock trees, positive responses in the gap trials were limited to 80 m. For the treecreeper, we conducted 29 control trials over 25 to 200 m and 25 gap trials from 25 to 260 m. Positive responses were consistently recorded up to 120 m in the control trials, whereas only three positive responses were obtained in the gap trials, ranging from 35 to 65 m.

Gaps as a barrier to movement

For both the shrike-thrush and the treecreeper, explained deviance was higher and AIC lower when distance was entered as a polynomial term (Table 3), indicating a better fit to the observed data. However, the area under the ROC curve and the calibration statistics were much higher when distance was entered as a linear term (Table 3), suggesting these models have greater discriminatory and predictive value and are less sensitive to atypical responses in the observed data. Thus, we present the linear models here because they have better predictive discrimination.

There was a significant effect of landscape structure on the probability of success for both species; individuals were much less likely to cross gaps in response to the call playback (Table 4). The largest discrepancy in the probability of success between the control and gap trials was over distances of 50–200 m for the shrike-thrush, and 0–100 m for the treecreeper (Fig. 1). For example, shrike-thrushes were 2.5 times less likely to cross 100-m gaps and nearly six times less likely cross 170-m gaps compared with similar distances in continuous forest (Fig. 1a *cf.* 1b). The mean probability that treecreepers would cross any gap at all was less than 0.5, and they were two times less likely to cross 20-m gaps and three times less likely to cross 50-m gaps than for equivalent distances in continuous forest (Fig. 1c *cf.* 1d).

The probability of success for either species also decreases with increasing distance in both continuous habitat and across gaps (Table 4). However, the rate of decline with distance did not differ significantly between control and gap trials: that is, the interaction between landscape structure and distance was not significant for either species (grey shrike-thrush: change in deviance = 0.072, $P = 0.788$; white-throated treecreeper: change in deviance = 1.05, $P = 0.384$).

What are the characteristics of gaps that influence movement?

The single best model of shrike-thrush gap-crossing included distance and paddock trees (Table 5). In fact,

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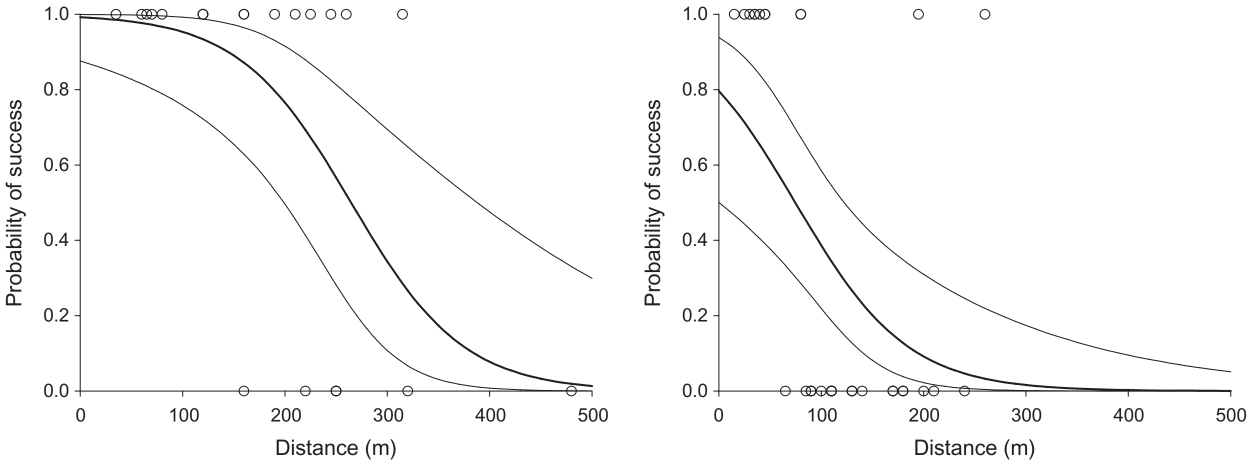
Table 4. Influence of landscape structure and distance on the probability of a positive response to call playback for the grey shrike-thrush and white-throated treecreeper

Variable	Estimate	SE	*t*-value	*P*
Grey shrike-thrush				
Intercept	4.84	1.46	3.30	<0.001
Gap	−3.47	1.06	−3.27	0.001
Distance	−0.018	0.006	−3.06	0.002
White-throated treecreeper				
Intercept	1.94	0.92	2.10	0.035
Gap	−1.99	0.80	−2.48	0.013
Distance	−0.024	0.01	−2.48	0.013

The parameter estimate for 'Gap' is relative to continuous forest.

(a) Grey shrike-thrush – control trials

(b) Grey shrike-thrush – gap trials



(c) White-throated treecreeper – control trials

(d) White-throated treecreeper – gap trials

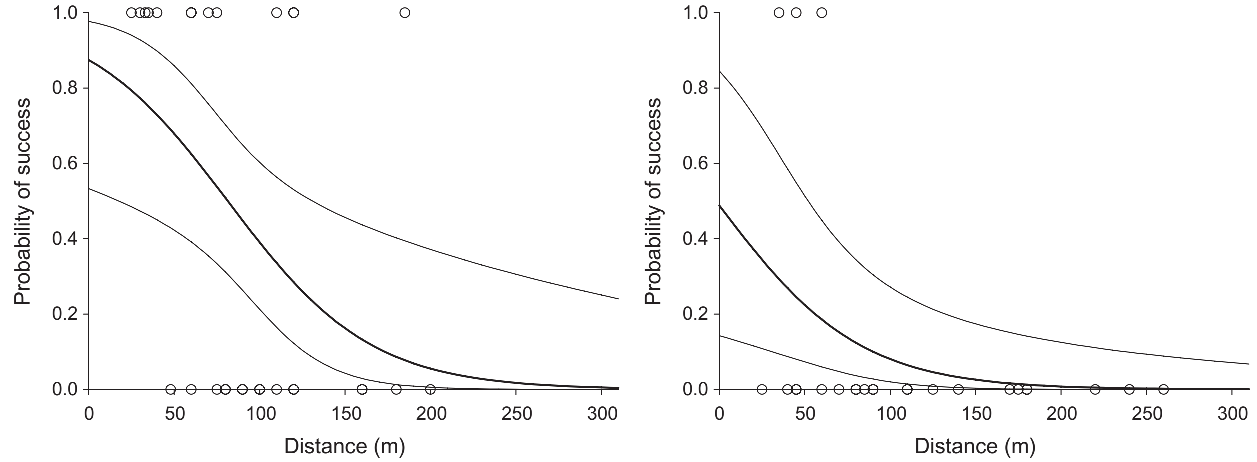


Fig. 1. Probability of success as a function of distance for the Grey Shrike-thrush in (a) control trials and (b) gap trials and the White-throated Treecreeper in (c) control trials and (d) gap trials. Light solid lines indicate 95% confidence intervals. Observed responses (○) are also indicated.

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Table 5. Influence of gap characteristics on the probability of a positive response to call playback for the grey shrike-thrush and white-throated treecreeper

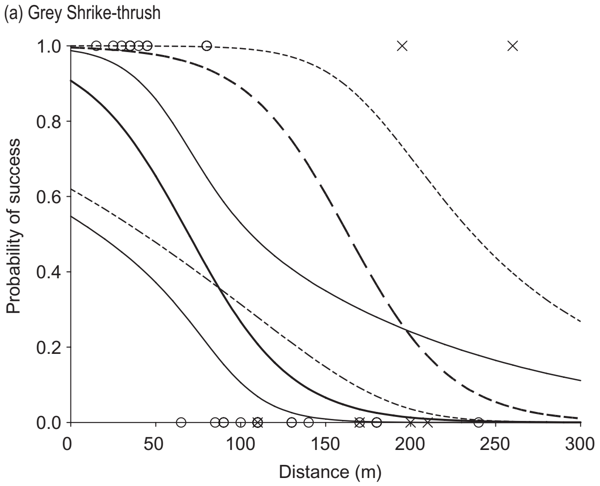
Variable	Estimate	SE	*t*-value	*P*
Grey shrike-thrush				
Intercept	2.28	1.06	2.15	0.032
Distance	–0.033	0.012	–2.68	0.007
Paddock trees (present)	3.08	1.74	1.77	0.076
White-throated treecreeper				
Intercept	2.20	2.14	1.03	0.304
Distance	–0.042	0.035	–1.20	0.230
Bracken (present)	–11.0	97.0	–0.11	0.910
Patch size (large)	–10.7	84.4	–0.13	0.899

Parameter estimates for Paddock trees (present) are relative to Paddock trees (absent), Bracken (present) relative to Bracken (absent) and Patch size (large) relative to Patch size (small).

the 10 best models all included distance, and four of the five best models also included paddock trees. The probability of shrike-thrush movement decreased rapidly with gap distance but increased when paddock trees were present, such that at a distance of 150 m the mean probability of gap-crossing was less than 0.1 in the absence of scattered paddock trees but 0.6 with scattered trees (Fig. 2a). The most parsimonious model based on AIC for treecreeper gap-crossing included distance, bracken and patch size. However, this model was a poor fit that overestimated at low probabilities and underestimated at high probabilities, with very high standard error to estimate ratios for bracken and patch size (Table 5). This raised concerns about including these terms in the model: the change in deviance associated with removing either bracken (change in deviance = 2.54, d.f. = 1, P = 0.111) or patch size (change in deviance = 2.38, d.f. = 1, P = 0.123) was marginal. Thus, for simplicity, we preferred a model that included only distance (estimate = –0.05 ± 0.03, change in deviance = 5.49, d.f. = 1, P = 0.019) (Fig. 2b). However, as indicated by the very wide confidence intervals (Fig. 2b), the precision of this model remains very low because of the small number of positive responses recorded.

Does gap-crossing exhibit a threshold response?

The fit of the shrike-thrush gap-crossing model was better when distance was considered as a dichotomous factor with a threshold distance of 85 m (Adj. R^2 = 63.8%, AIC = 20.3) than when distance was entered as a continuous variable (Adj. R^2 = 22.9%, AIC = 36.5) (Fig. 3). Indeed, threshold distances of 55 m (Adj. R^2 = 49.0%, AIC = 26.2), 95 m (Adj. R^2 = 38.4%, AIC = 30.4), 75 m (Adj. R^2 = 33.8%, AIC = 32.2), 105 m (Adj. R^2 = 32.5%, AIC = 32.7) and 45 m (Adj. R^2 = 30.2%, AIC = 33.7) were all better fits than the continuous model (Fig. 3). The pattern for the



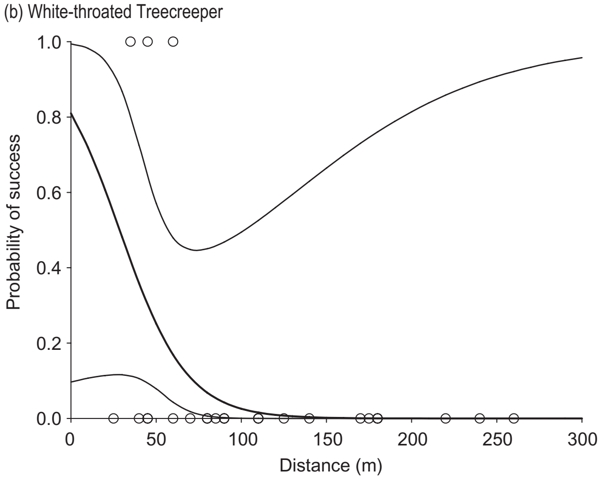


Fig. 2. Probability of gap-crossing as a function of distance for the (a) grey shrike-thrush when paddock trees are absent (heavy solid line) and present (heavy dashed line) and (b) white-throated treecreeper. Light solid lines indicate 95% confidence intervals when paddock trees are absent; light dashed lines indicate 95% confidence intervals when paddock trees are present. Observed responses without (○) and with (×) paddock trees indicated for the shrike-thrush.

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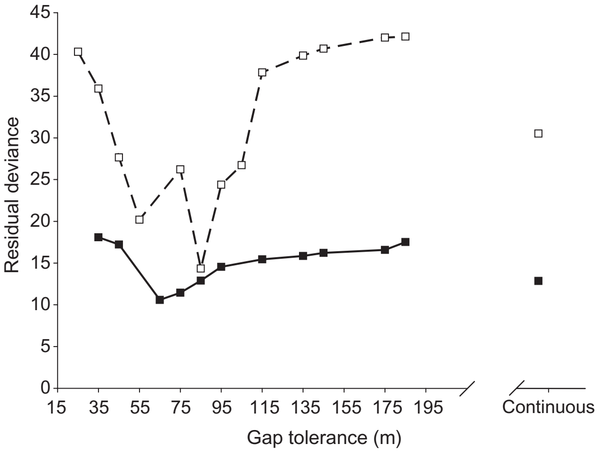

Fig. 3. Residual deviance from logistic regression models of gap-crossing for the grey shrike-thrush (□) and white-throated treecreeper (■) when distance is treated as a dichotomous factor split at different gap-tolerance thresholds, and as a continuous variable. Note that 'Paddock trees' was also included in the shrike-thrush models.

treecreeper was similar although less striking: the best fits were achieved when distance was treated as a dichotomous factor with threshold distances of 65 m (Adj. R^2 = 39.8%, AIC = 14.6) or 75 m (Adj. R^2 = 34.8%, AIC = 15.5), compared with the fit when considered as a continuous variable (Adj. R^2 = 26.9%, AIC = 16.8) (Fig. 3).

DISCUSSION

Cleared land as a barrier to movement

This study provided empirical, individual-based evidence that gaps in forest cover constrain the movement of the grey shrike-thrush and the white-throated treecreeper. Individuals were less likely to move through the landscape in response to the stimulus of a simulated territorial intruder as distance between the target bird and the stimulus increased. Pertinently, individuals were more likely to move through continuous habitat than discontinuous habitat (i.e. gap trials). Our results clearly showed that cleared land is a barrier to the movement of individuals, and that gaps greater than 100 m might significantly reduce functional connectivity for the study species.

Contrary to expectations, our results were remarkably consistent with gap-crossing studies from forested ecosystems in other parts of the world that show that gaps of less than 100 m might severely impede the movement of forest birds. For example, understory passerines were reluctant to enter open pasture in Chile (Seiving *et al.* 1996), Amazonian rainforest birds failed to recolonise patches isolated by as little as 80 m (Laurance *et al.* 2002), and 100-m gaps inhibit the movement of many forest songbirds in North American boreal forests (Desrochers & Hannon 1997; Rail *et al.* 1997). What are the behavioural mechanisms behind this reluctance to cross gaps?

Forest specialists are often hesitant to cross boundaries marked by extreme structural contrast, such as the interface between forest and cleared land (Wiens *et al.* 1985; Norris & Stutchbury 2001; Shirley 2006). A contributing factor might be that forest species have had little reason to traverse clearings in their evolutionary history; therefore the avoidance of such areas might be an innate response (Greenberg 1989). The current study was conducted in a region that was heavily forested until European settlement less than 200 years ago. Thus, there might be a 'hard-wired' aversion to gaps in forest cover in populations endemic to this region. It would be intriguing to ascertain whether conspecific populations in more open woodland habitat are similarly constrained by gaps in habitat cover. There are also likely to be contemporary fitness benefits from avoiding gaps. Forest birds are more vulnerable to raptors in open areas, so there is greater perceived and actual predation risk in gaps (Lima & Dill 1990; Desrochers & Hannon 1997; Yoder *et al.* 2004). The energetic cost of movement might also be higher in open areas (Grubb & Doherty 1999; Graham 2001) particularly for the smaller treecreeper, which is a relatively weak flier and normally advances by a series of short tree-to-tree flights.

Gaps in forest cover were not totally impermeable for the study species: there was a better than 50% chance that the shrike-thrush would cross gaps up to 70 m, and the treecreeper was observed crossing gaps up to 60 m. However, the probability of gap-crossing decreased precipitously with increasing distance. This suggests movement reflects a trade-off between the energetic costs and exposure to predators which increase with gap distance and the benefit of gap-crossing, which in this study, was to defend their territory from a potential intruder. Thus, the permeability of the landscape not only depends on land-use (forest or pasture) but also on the configuration of forest patches in the landscape that determines gap distance (Gobeil & Villard 2002). The motivation for movement might also influence landscape permeability. It might be that individuals are willing to accept greater risk and cross larger gaps during dispersal or when searching for a mate than when defending a territory. There might also be seasonal influences: during the breeding season, costs associated with territory intrusion might rise (e.g. extra-pair fertilizations, divorce, challenge for territory) precipitating movement across larger gaps. Thus, given particular constraints or inducements to move, the ability of individuals to disperse through fragmented landscapes might be better than the results of this study suggest. However, landscape configura-

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tion is likely to influence the ease with which individuals are able to move with smaller gaps and multiple pathways offering less resistance to movement and facilitating functional connectivity (McRae & Beier 2007).

Response to call playback might have been curtailed by territory boundaries (Betts *et al.* 2005). Although the trials in continuous forest were designed to control for this effect, territory boundaries might often be located along the forest edge, reducing the impetus for an individual to respond to an intruder in an adjacent patch. Furthermore, it is likely that some of the distance travelled by individuals through continuous forest in response to call playback were within part of its territory, whereas this was unlikely to be the case for cleared land. This raises the possibility that we underestimated the gap-crossing ability of our study species. For example, some Neotropical forest birds are able to cross treeless gaps of several hundred metres (Norris & Stutchbury 2001; Fraser & Stutchbury 2004). Perhaps the relevant indicator is the distance birds will move beyond their territory boundary in response to an intruder. However, this is difficult to measure and the fact that shrike-thrushes crossed gaps of 200–260 m when scattered trees were present indicated that the motivation for crossing remained strong.

Influence of paddock trees on gap-crossing

For some forest-dependent species, the presence of scattered trees can 'soften' the barrier to movement imposed by the matrix (Fischer *et al.* 2005). Individuals might rest and forage in paddock trees, seek refuge from predators, or use them to survey the landscape for predators. The presence of scattered paddock trees improved functional connectivity for the grey shrike-thrush. Paddock trees were present in the only cases in which shrike-thrushes crossed gaps greater than 80 m. Birds were observed perching momentarily in dead or living trees before crossing to the speaker patch. However, paddock trees did not ensure movement with birds failing to cross several gaps between 110–210 m even though paddock trees were present. Fischer and Lindenmayer (2002) found that paddock trees were used as stepping stones by a range of bird species and inferred that paddock trees increased landscape connectivity. Our results corroborate these findings. Paddock trees are likely to be critical elements for inter-patch movements in fragmented or variegated landscapes (McIntyre & Barrett 1992; Manning *et al.* 2006).

Thresholds in gap-crossing and gap-tolerance

The probability of gap-crossing in relation to gap distance was non-monotonic for both the shrike-thrush and the treecreeper. The dichotomous (threshold) models were better approximations of movement behaviour than models in which distance was considered as a continuous gradient. Based on the fit of the dichotomous models, gap tolerance was estimated to be 85 m for the shrike-thrush and 65 m for the treecreeper. The low incidence with which treecreepers crossed gaps of any size suggests 65 m might be an overestimate. However, at this distance, the predicted mean probability of gap-crossing was 0.15, indicating that although gaps of this distance might not preclude movement, the likelihood of crossing is very low.

These results have direct management implications because they indicate the grey shrike-thrush and white-throated treecreeper might be sensitive to fragmentation that isolates patches by more than 85 and 65 m, respectively. Managers seeking to improve functional connectivity therefore need to implement strategies to minimize the occurrence of gaps greater than the identified gap-tolerance limits. The preference that both species displayed for moving through continuous habitat in this study suggests habitat corridors might be effective for increasing movement. However, this study was not designed to test movement through corridors and there are fundamental differences between corridors and continuous forest. For example, width might influence the distance an individual moves along a corridor (Bennett 1999) but such constraints do not apply to individuals moving through continuous habitat. Moreover, corridors might not be the most cost-effective way to increase connectivity if individuals are able to use small patches or scattered trees as stepping stones to move through the landscape.

Few studies have quantified the gap-tolerance of Australian birds. Brooker and Brooker (1997) used mark-recapture to quantify dispersal distances of blue-breasted fairy-wrens (*Malurus pulcherrimus*), and then applied an individual-based simulation model on this and other data to identify likely gap-tolerance distances of 60 m for the fairy-wrens and 270 m for the white-browed babbler (*Pomatostomus superciliosus*) (Brooker *et al.* 1999). Radford and Bennett (2006) inferred a gap-tolerance of 450 m for the white-browed treecreeper (*Climacteris affinis*) from patterns of patch occupancy. Gap-tolerance for less mobile taxa (e.g. arboreal mammals, reptiles, amphibians, terrestrial invertebrates) is likely to differ considerably from those identified for birds, although the gap-tolerance of 75 m identified for the squirrel glider (*Petaurus norfolcensis*) in agricultural landscapes (van der Ree *et al.* 2003) was coincidentally similar to the results obtained here.

The treecreeper appeared less inclined to leave forest cover and had a lower gap-tolerance than the shrike-thrush. This disparity might be due to differences in foraging mode, mobility and morphology.

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Certainly, the shrike-thrush has faster and stronger flight than the treecreeper, and gap-tolerance might be positively related to body mass (Creegan & Osborne 2005) although this relationship requires further testing. Interestingly, both species studied here are commonly observed in relatively small and isolated patches and are generally considered 'tolerant' to fragmentation. Neither species breeds cooperatively, and thus young are expelled from their natal territories which might increase their ability and motivation to disperse across gaps. More fragmentation-sensitive species, many of which are cooperatively breeding species (e.g. brown treecreeper, Cooper & Walters 2002) or ground-dwelling and cover-dependent species (e.g. speckled warbler, Gardner 2002), are likely to have shorter gap-tolerances and be less inclined to cross gaps. Species-specific differences in movement capacity are well documented (Rail *et al.* 1997; Bélisle & Desrochers 2002; Creegan & Osborne 2005), and reinforce the perils of ascribing community-wide functional connectivity on the basis of one or two species. However, empirical data should be considered when available, and gap-crossing studies can make a valuable contribution towards improving our knowledge of gap-tolerance and functional connectivity for a guild of species. This will provide more robust data on which to base representations of landscape connectivity and to inform spatially dynamic models.

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