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Abstract

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Keywords

southeastern, natural, across, australia, communities, edge, bird, species, ecotonal, effect

Disciplines

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THE EDGE EFFECT AND ECOTONAL SPECIES: BIRD COMMUNITIES ACROSS A NATURAL EDGE IN SOUTHEASTERN AUSTRALIA

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Abstract. Ecotones have been considered as unique environments, and the concepts of edge effect and ecotonal species have been widely used, especially in avian community ecology. We studied the patterns of bird densities across heath–wood edges at replicated sites in three locations in southeastern Australia. Multivariate analysis showed that the bird community in the ecotone was intermediate between the heath and wood communities, indicating that the ecotone contained a mixing of species rather than a unique bird community. ANOVA showed a modest increase in bird density at the wood side of the ecotone, which may be partly due to sampling biases rather than to some inherent habitat value in the ecotone. The outstanding pattern was that bird density and species richness in the wood habitat were twice as high as in the heath habitat. Of a total of 86 species, 31 occurred in sufficient numbers to categorize according to their habitat association (generalist, or heath or wood specialist) and their density at the ecotone (ecotone neutral, ecotone shy, or ecotone conspicuous). Three of these were habitat-generalist–ecotone-neutral. Fourteen species were ecotone neutral but were habitat specialists on either the wood (13 spp.) or the heath (1 sp.). Three species were ecotone shy. Although 11 species were ecotone conspicuous, they also occurred in either heath or wood or both. Thus, no species could be categorized as entirely ecotonal. We conclude that there is little evidence from this or other studies of avian communities to support an edge effect of increased density and species richness, and no evidence of entirely ecotonal species.

Key words: Australia; Australian bird community; bird densities; *Dasyornis brachypterus*; *Eastern Bristlebird*; ecotonal species; ecotone; generalist vs. specialist; heathland; species richness; woodland.

INTRODUCTION

The term ecotone has a long history and is widely used in ecology (e.g., Holland et al. 1991, Schilthuizen 2000), yet its use and definition are imprecise. Clements (1907, cited in Harris 1988) first described the junction between two adjacent communities as a stress line or ecotone. More recently, the concept has been broadened to include biotic and abiotic factors at various scales (Holland and Risser 1991, Risser 1995) and a considerably refined definition has now become accepted. An ecotone is the zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between the systems (Holland 1988, Risser 1993).

To avoid the ambiguities caused when the terms edge and ecotone are used interchangeably (e.g., Clements 1907, Odum 1958, Yahner 1988), we define *edge* as the line used to demarcate two adjacent ecosystems and *ecotone* as the two- or three-dimensional zone of tran-

sition between the ecosystems. This transition may be abrupt or gradual (Ratti and Reese 1988, Lennon et al. 1997), extending varying distances on either side of the edge. In practice, both the location of the edge and the extent of the ecotone will need to be defined in each case.

One consequence of ecotones for fauna has been described as the *edge effect*, first defined by Odum (1958) as the tendency for increased population density and species richness at the junction zone between two communities. This formalized Leopold's writings, in which ecotones were presented as beneficial to wildlife (Leopold 1933, cited in Harris 1988). The edge effect described by Odum may occur simply because the ecotone contains representatives of species characteristic of both of the adjacent communities. This view of ecotones is pervasive in the literature, despite the paucity of empirical support for the existence of these sorts of edge effects (Guthery and Bingham 1992). A meta-study by Murcia (1995) concluded that there was no general pattern in the direction or intensity of edge effects in the 24 studies that she reviewed. Odum (1958) suggested that edge effects were especially applicable to bird communities, yet there have been few studies in which bird population density and species richness have been measured across natural habitat edges (Sisk and Margules 1993).

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FIG. 1. Location of study sites (Budderoo National Park, Booderee National Park, and Nadgee Nature Reserve) in southeastern Australia.

Explicit in Odum's view of the edge effect was the existence of a set of species characteristic of the ecotone. These he defined as primarily or entirely *ecotonal species*, based on studies (Beecher 1942, Johnston 1947, Johnston and Odum 1956) about heterogeneity of bird habitat. Once again, many texts and papers use the concept of ecotonal bird species (e.g., Gates and Gysel 1978, Frith 1979, Brewer 1988, Chan 1995, Griggs 1997), despite the few studies specifically designed to test for ecotonal species. Two studies came to opposite conclusions. In Arizona, Laudenslayer and Balda (1976) concluded that none of the 11 bird species breeding in an ecotone between pinyon pine/juniper woodland and ponderosa pine forest was ecotonal. In southeastern Australia, Bramwell et al. (1992) concluded that the Eastern Bristlebird (*Dasyornis brachypterus*) was ecotonal because they detected significantly more birds in the ecotone than in either of the adjacent communities of heathland and woodland. However, this study was confounded by the heterogeneity of the heath-wood mosaic and was limited to a single 66-ha site studied during just one spring.

Given the widespread references in the literature to the concepts of ecotone, edge effects, and ecotonal species, and the scarcity of supporting empirical studies, we considered that a replicated and more detailed study was needed. We therefore investigated the patterns in the bird communities (composition and species richness) and in densities of individual species across naturally occurring heath-wood edges, using replicated sites in three locations in southeastern Australia. Specifically, we asked the following questions. (1) Is the bird community in the ecotone intermediate between those in the heath and the wood? (2) Are bird density and species richness greater in the ecotone than in either the heath or the wood? (3) How do densities of individual bird species respond to the ecotone? (4) Can any species, particularly the Eastern Bristlebird, be

considered as primarily or entirely ecotonal (sensu Odum 1958)?

METHODS

Site selection

In coastal regions of southeastern Australia, there are large *Eucalyptus*-dominated wooded areas interspersed in a few places with narrow (usually <1 km) patches of treeless heathland/sedgeland (Costermans 1981). There are typically sharp boundaries between the wood and heath plant communities, providing an opportunity to examine the ecotone in detail. The one bird species described as ecotonal, the Eastern Bristlebird (*Dasyornis brachypterus*; Bramwell et al. 1992), is a small, cryptic, semi-flightless, rare passerine endemic to southeastern Australia, with substantial populations at only three locations (Baker 1997): Budderoo National Park/Barren Grounds Nature Reserve (Budderoo), the Jervis Bay area centered on Booderee National Park (Booderee), and Nadgee Nature Reserve (Nadgee), all of which have heath-wood edges.

The study was conducted at four sites at Budderoo (150°40' E, 34°40' S), four at Booderee (150°40' E, 35°10' S), and three at Nadgee (150°00' E, 37°30' S; Fig. 1). Across the sites, the heath was closed heathland/sedgeland with variable heights of 0.4–0.8 m and emerging shrub clumps at 0.6–1.4 m; the wood was forest, open forest, woodland, and open woodland with a variable (10–35 m) canopy, shrubby understory (average height 2.1 m), and herbaceous ground cover (average height 0.4 m; Fig. 2). The floristics at each location are described in Baker (2000). The sites were chosen because they had distinct, relatively straight heath-wood edges at least 600 m long dividing relatively large, homogenous areas of vegetation extending for at least 200 m each side of the edge. The sites were separated by 0.25–2.2 km at Budderoo, 1.3–3.1 km at Booderee, and 1.5–2.7 km at Nadgee.

FIG. 2. Example of a heath-wood edge at Budderoo.

Surveys

At each site, pairs of plots 25×400 m were marked on either side of three parallel transects: along the heath-wood edge and 100 m on either side of the edge, in the heath, and in the wood areas (Fig. 3). The width and separation of our survey plots were similar to those of other edge studies of birds (e.g., Bramwell et al. 1992, Sisk and Margules 1993, Kruger and Lawes 1997, Luck et al. 1999). A bird survey was conducted at every site during eight periods between September 1995 and July 1997 at ~ 3 -mo intervals. Each survey was completed within 4 h after sunrise in suitable weather conditions. The order in which the transects were walked was varied systematically to avoid bias related to time of day. Each pair of plots was surveyed for 1 h and all birds seen or heard were counted in the first plot where they were detected, taking care not to double count individuals.

Data analysis: whole communities

The total data set was used in two ways. First, for each survey period, the data for each pair of plots were combined to allow consideration of the ecotone as one zone, separate from the heath and the wood (called pairs of plots). Second, all six plots at each site were considered in order to separate the edge effect on the opposite sides of the heath-wood edge (called plots). The bird communities across the heath-wood edge were described using multivariate techniques, and then species density and richness were examined in detail using ANOVA.

The multivariate analysis was undertaken using PRIMER (Carr 1996). The attributes of the bird communities were the cumulative number of detections over the eight visits for each species. Differences in the composition of the communities were tested using a two-way analysis of similarity (ANOSIM) with location and distance (either plots or pairs of plots) as factors. Similarity among the plots (or pairs of plots) was determined by ordination using nonmetric multidimensional scaling (MDS; Kruskal and Wish 1978) and was displayed in two dimensions.

Bird density was derived from the mean density of individuals per plot (or pair of plots) over the eight surveys. Species richness was assessed by the mean number of species per plot (or pair of plots) over the eight surveys. A second measure of species richness was obtained by calculating the cumulative number of species across all sites for the total period of the study. Nested, three-factor ANOVAs ($\alpha = 0.05$) were conducted on density and species richness with location, site within location, and distance (plot or pair of plots) as the factors (Table 1). The number of sites within locations was unequal; therefore successive sites from each of Budderoo and Booderee were paired at random and excluded from the data set (as recommended by Underwood 1997). Four iterations of balanced ANOVAs with three sites within locations were performed. Tukey's HSD was used ($\alpha = 0.05$) where the ANOVAs found significant differences among means, although this procedure is less powerful than ANOVA and may fail to detect differences between any pair of means (Zar 1984). The data were not transformed because each of the data sets met the ANOVA assumptions of normality, homoscedasticity, and additivity (Zar 1984).

Data analysis: individual species

For each site, the density per hectare of each bird species at each of the six plots was expressed as the

FIG. 3. Survey layout at each site showing six plots (making three pairs of plots).

TABLE 1. ANOVA summary table for bird density and species richness across a natural edge in southeastern Australia.

Source of variation	F
Distance (fixed)	Distance MS/Location $\times$ Distance MS
Location (random)	Location MS/Site within Location MS
Site within Location (random)	
Location $\times$ Distance	Location $\times$ Distance MS/Site within Location $\times$ Distance MS
Site within Location $\times$ Distance	

average over the eight surveys. Then, for each species, the bird density per plot was calculated as the mean (and standard error) for the sites (usually 11 sites) and was displayed as a histogram. When a species was detected at fewer than the three locations, the density was calculated for the number of sites at the locations where the species occurred.

Based on the intuitive categorization proposed by Sisk and Margules (1993), we distinguished that bird species at ecotones can be (1) ecotone neutral, (2) ecotone conspicuous, or (3) ecotone shy, and can be divided further into habitat generalists or habitat specialists of one or other side of the edge. This gives nine hypothetical responses for species density across the edge between two habitats (see *Results*). Ecotone-conspicuous birds have apparently increased density at the ecotone, whereas ecotone-shy birds have apparently decreased density at the ecotone. The density of ecotone-neutral birds is apparently unchanged across the ecotone, except for species that are habitat specialists. Habitat-specialist-ecotone-neutral birds have reduced density across the ecotone, as the amount of suitable habitat decreases. A tenth hypothetical response is that of an entirely ecotonal species, which would be expected to have high density at the ecotone and be absent from the habitats on either side (see *Results*).

Species that were rarely detected (less than an average of one detection per two site visits; i.e., cumulative total <44 detections) were not considered further. For the remaining species, the histogram pattern of variation in bird density across the six plots from heath to ecotone to wood was used to categorize them into one of the models of ecotone response according to the following decision rules. Species with >75% of detections at the three plots on the heath side of the edge were called heath specialists; those with >75% of detections at the three plots on the wood side of the edge were called wood specialists; the remainder were considered to be habitat generalists. Species with >50% of detections at the two ecotone plots were called ecotone conspicuous; those with <25% of detections at the two ecotone plots were called ecotone shy; and the remainder were considered to be ecotone neutral.

The density data for each species were analyzed using the same ANOVA design as for the whole-communities analysis previously described. If there were

no records for a species at a location, that location was excluded from the analysis. The White-cheeked Honeyeater (*Phylidonyris nigra*) did not occur at Nadgee, so the ANOVA was balanced and there was no need for the iteration procedure. The White-eared Honeyeater (*Lichenostomus leucotis*) occurred at only one location; hence, a single-factor ANOVA ($\alpha = 0.05$) was used to compare bird density to distance. All data were transformed using the square root of $(x + 0.375)$ because the variances were proportional to the means and because some data were small or zero (Zar 1984). Tukey's HSD was used ($\alpha = 0.05$) where ANOVAs found significant differences among means.

RESULTS

Multivariate overview of the bird communities

Overall, 86 bird species were recorded in the study, and the number of detections by location and distance are given in the Appendix. Nomenclature follows Christidis and Boles (1994). The composition of the bird communities differed significantly among locations (for plots, Global $R = 0.582$, $P < 0.001$; for pairs of plots, Global $R = 0.468$, $P < 0.001$) and with distance (for plots, Global $R = 0.717$, $P < 0.001$; for pairs of plots, Global $R = 0.570$, $P < 0.001$; Clarke and Warwick 1994). For pairs of plots, ANOSIM at each location determined that the wood and ecotone were not significantly different, but were different from the heath (Budderoo, $P = 0.029$; Booderee, $P = 0.029$; Nadgee, insufficient data for analysis). In pairwise tests of plots for Budderoo and Booderee, there was no difference between the two wood plots or the two heath plots. Moreover, the significance of the difference between each of the two wood plots and the plot at the wood side of the ecotone was variable, as was the difference between each of the heath plots and the heath side of the ecotone. For pairs of plots at Nadgee, there were insufficient data for the analysis, but trends in the data were similar to those of the other locations.

The two-dimensional ordination for pairs of plots confirms that the composition of the community at the ecotone was intermediate between the wood and the heath communities (Fig. 4). The ordination for plots shows that the composition of the community at the heath side of the ecotone was intermediate between the heath community and the community of the wood com-

FIG. 4. Two-dimensional ordination of the bird community across the heath-wood edge (pairs of plots) showing Budderoo (squares), Booderee (diamonds), and Nadgee (circles) at the wood (black symbols), ecotone (hatched symbols), and heath (open symbols) plots.

FIG. 5. Two-dimensional ordination of the bird community across the heath-wood edge (plots) showing Budderoo (squares), Booderee (diamonds), and Nadgee (circles) at both wood plots (black symbols), the wood side of the ecotone (bold symbols), the heath side of the ecotone (hatched symbols), and both heath plots (open symbols).

bined with the wood side of the ecotone (Fig. 5). Both ordinations had low stress values (0.12 and 0.14, respectively) which give good two-dimensional representation of the spread of objects (Clarke and Warwick 1994). The ordinations also demonstrate that these patterns were consistent among locations. The similarity indices for pairs of plots at each location were high (47–65%) within the wood, ecotone, and heath and between the wood and the ecotone intermediate (18–34%) between the ecotone and heath; and low (10–22%) between heath and wood (Table 2).

Bird density

Using the three pairs of plots at each site, the ANOVAs of bird density showed a significant effect of distance (four iterations gave a range of $F_{2,4} = 25.1$ – 45.1 , $P < 0.02$), no effect of location (four iterations, range of $F_{2,6} = 1.18$ – 3.60 , $P > 0.1$) and no interaction (four iterations, range of $F_{4,12} = 0.424$ – 0.783 , $P > 0.5$). Tukey's HSD revealed that the density (mean $\pm$ 1 SE) at the ecotone (34.4 ± 4.04 birds/2 ha) and the wood (28.2 ± 2.59 birds/2 ha) were similar and both significantly greater than at the heath (14.7 ± 2.73 birds/2 ha; Fig. 6a). This pattern of the ecotone and the wood being similar and approximately double the density at the heath was consistent across all sites.

Using the six plots, four iterations of the ANOVAs of bird density showed a significant effect of distance (range of $F_{5,10} = 20.2$ – 29.8 , $P < 0.001$), no effect of location (range of $F_{2,6} = 0.834$ – 4.05 , $P > 0.2$), and no interaction (range of $F_{10,30} = 0.112$ – 1.47 , $P > 0.5$). Tukey's HSD showed that the density (mean $\pm$ 1 SE) at the wood side of the ecotone (23.5 ± 2.53 birds/ha) was significantly greater than at all other distances and

~67% greater than at the wood plots. The remaining paired comparisons gave ambiguous results, with the abundances for two wood plots (15.4 ± 1.64 and 12.8 ± 1.12 birds/ha), the heath side of the ecotone (10.8 ± 1.93 birds/ha) and the two heath plots (8.17 ± 1.43 and 6.55 ± 1.35 birds/ha) not clearly separable (Fig. 6b). The wood side of the ecotone had greater density than both of the wood plots across all of the sites. Density at the heath side of the ecotone was ~47% greater than at the heath plots, but this difference was not significant. Although the pattern held across the three locations, it did not hold across all sites.

Species richness

Using the three pairs of plots at each site, four iterations of the ANOVAs of the average species rich-

TABLE 2. Average Bray-Curtis similarities between sites within a distance (pairs of plots).

Study area and site	Wood	Ecotone	Heath
Budderoo			
Wood	57	52	10
Ecotone		53	18
Heath			53
Booderee			
Wood	55	47	22
Ecotone		50	34
Heath			51
Nadgee			
Wood	65	48	14
Ecotone		62	28
Heath			58

FIG. 6. Edge effect: bird density (a, b) and species richness (c, d), and cumulative species richness (e, f) showing bird density or species richness (mean $\pm$ 1 SE) at each distance (three pairs of plots or six plots). ANOVA results (summarized) are shown for differences among the means: * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. From Tukey's HSD, unambiguously different means at plots (or pairs of plots) are shown by separate levels of underlining.

ness showed a significant effect of distance (range of $F_{2,4} = 56.7-203$, $P < 0.01$), no effect of location (range of $F_{2,6} = 0.961-4.75$, $P > 0.2$), and no interaction (range of $F_{4,12} = 0.345-1.30$, $P > 0.5$). Tukey's HSD revealed that the average richness (mean $\pm$ 1 SE) at the wood (10.7 ± 0.699 spp./2 ha) and the ecotone (10.6 ± 0.724 spp./2 ha) were similar and both significantly greater than at the heath (4.19 ± 0.647 spp./2 ha; Fig. 6c). This pattern of the ecotone and the wood being similar and approximately double the average species richness at the heath was consistent across all sites.

Using the six plots, four iterations of the ANOVAs of the average species richness showed a significant effect of distance (range of $F_{5,10} = 25.8-62.0$, $P < 0.001$), no effect of location (range of $F_{2,6} = 1.05-5.81$, $P > 0.08$), and no interaction (range of $F_{10,30} = 0.873-3.25$, $P = 0.02$, $P > 0.15$, $P > 0.5$, $P > 0.5$). Tukey's HSD revealed that the average species richness (mean $\pm$ 1 SE) at the two wood plots (7.36 ± 0.548 and 6.41 ± 0.374 spp./ha) and the wood side of the ecotone (8.86 ± 0.586 spp./ha) were significantly greater than at the heath side of the ecotone (4.11 ± 0.537 spp./ha) and

the two heath plots (2.75 ± 0.472 and 3.15 ± 0.481 spp./ha; Fig. 6d). The three wood plots had a greater average species richness than the three heath plots across all sites.

The cumulative species richness for the pairs of plots clearly grouped the wood (69 species) with the ecotone (68 species), being nearly double the 40 species at the heath. Using six plots, the two wood plots with 61 and 58 species grouped with the wood side of the ecotone (65 species), and these were approximately double the number of species at the heath side of the ecotone (37) and the two heath plots (36 and 33). Total species richness was similar among locations: Budderoo, 56 species; Booderee, 62 species; and Nadgee, 58 species.

Response of species across heath-wood edges

Of the 86 bird species recorded, 31 were present in sufficient numbers to be categorized into one of the models of ecotone response (Fig. 7; see Appendix). Three species, the Little Wattlebird (*Anthochaera chrysoptera*), White-cheeked Honeyeater (*Phylidonyris nigra*), and Beautiful Firetail (*Stagonopleura bella*) were habitat generalist-ecotone neutral. Fourteen of the 31

FIG. 7. Models of response for birds across the edge between two habitats (adapted from Sisk and Margules [1993]) and examples applying the models to species, showing the density (no. birds/ha, mean ± 1 SE) at each distance (plot).

FIG. 8. Model of the density response of an entirely ecotonal species compared to the density (no. birds/ha, mean $\pm$ 1 SE) of the Eastern Bristlebird at each distance (plot).

species were categorized as ecotone neutral, but showed a marked change in density across the edge. Thirteen species were wood specialist–ecotone neutral and one was heath specialist–ecotone neutral. Eleven species were ecotone conspicuous and three were ecotone shy. No species was categorized as habitat generalist–ecotone shy (which may be considered an oxymoron anyway), heath specialist–ecotone conspicuous, or entirely ecotonal.

The ANOVAs showed significantly different mean densities among the distances for 14 species. For 10 of these species, $P < 0.05$ for all four iterations of the ANOVA; for the remaining four species, $P < 0.1$ for one iteration and < 0.05 for the other three (see Appendix). Tukey's HSD made unambiguous distinctions among the means for only the White-throated Tree-creeper (*Cormobates leucophaeus*), which was clearly a wood-specialist–ecotone-neutral species, and the Southern Emu-wren (*Stipiturus malachurus*), which was a heath-specialist–ecotone-neutral species overall. The Emu-wren was the only species that showed a significant effect of distance and distance $\times$ location interaction. This was due to the high density of the species on the heath side of the ecotone at Nadgee relative to the other two locations. Applying the decision rules to the densities at each location, the Emu-wren was an ecotone-shy species at Budderoo and Booderee and an ecotone-neutral species at Nadgee only.

Ecotonal species

Eleven species, including the Eastern Bristlebird (*Dasyornis brachypterus*), were categorized as ecotone conspicuous and were therefore potentially ecotonal species. However, all of these species were also found in the wood and/or the heath; hence, none was entirely ecotonal.

The Eastern Bristlebird was detected at all sites. Overall, 65% of the records were at the ecotone, 24% were at the heath, and 11% were at the wood (Fig. 8). This density pattern is not consistent with an entirely ecotonal species. Although the decision rules categorized the species as an ecotone-conspicuous species, the ANOVAs did not show a significant effect of distance (four iterations gave a range of $F_{5,10} = 1.90$ – 2.95 , $0.15 < P < 0.3$). At each location, Eastern Bristlebirds

were detected at the heath or the wood or both, although, among locations, there was variation in density on either side of the edge and the ANOVAs showed a significant effect of the distance $\times$ location interaction ($F_{10,30} = 5.45$ – 6.39 , $P < 0.001$).

Two species, the White-eared and White-naped Honeyeaters (*Lichenostomus leucotis* and *Melithreptus lunatus*), had histograms most like the ecotonal species model, although neither showed a significant effect of distance in the ANOVAs ($P > 0.1$) and the results were highly variable among sites. There were 67 records for the White-eared Honeyeater and it occurred only at Budderoo. Most of the records (61%) were at the ecotones of two sites. The White-naped Honeyeater occurred at seven sites; the ecotones at four sites accounted for most (83%) of the 125 records.

DISCUSSION

Bird communities across edges

Odum (1958) suggested that, in terrestrial communities, the concept of the edge effect was especially applicable to bird communities. However, in the present study, there was only limited evidence for the traditionally held concept of an edge effect of increased density and species richness. The multivariate overview of the bird communities across the heath–wood edge indicated that the bird community composition at the ecotone was intermediate between the communities at the heath and the wood, not unique from them.

When the ecotone was taken as a 50 m wide zone spanning both sides of the heath–wood edge, there was no evidence for greater bird density or species richness at the ecotone. Rather, the ecotone and the wood were similar and they had twice the bird density and richness of the heath. This result highlights the importance of comparing the community at the ecotone with the communities in both of the adjacent ecosystems. Had we compared only the bird community at the heath to that at the heath–wood ecotone, we may have falsely concluded that there was a strong edge effect.

When the ecotone was divided into two 25 m wide zones, one on either side of the edge, there was some evidence for an edge effect. Taking the six plots spanning the edge, there was an underlying pattern that the density and species richness for the wood side of the

edge were greatest at the ecotone plot and, similarly, the density and richness for the heath side of the edge were greatest at the ecotone. This pattern was statistically significant in only one case; bird density at the wood side of the ecotone was greater than at the wood plots, and the trend was consistent across all sites. This was the strongest evidence for the traditional view of an edge effect. However, we will show that this pattern is largely explained by the density patterns of only eight species.

The ecological significance of this evidence of an edge effect may be that the wood side of the ecotone is particularly important habitat because it accommodates an increased density of birds of some species. However, two insights counter this explanation. (1) At the edge, there is greater visibility than in the adjacent wood and the birds may be both easier to detect and more readily attracted to an observer. Hence, some of the apparent higher density may be an artifact of sampling. (2) The wood side of the ecotone may provide only a brief resting place for birds that are moving between habitats or within the wood habitat. For example, the New Holland Honeyeater (*Phylidonyris novaehollandiae*) was frequently recorded in feeding sallies and aggressive displays over the heath that began and ended in trees at the wood side of the ecotone. The mostly migratory Yellow-faced Honeyeater (*Lichenostomus chrysops*) was recorded flocking along heath-wood edges and perching briefly in the trees at the wood side of the ecotone. Also, a feeding pattern noted for some species (e.g., White-throated Treecreeper *Cormobates leucophaeus*) was to move from the wood to the wood side of the ecotone, then along the ecotone and back into the wood again. These are examples of what Soulé and Gilpin (1991) described as the sticky nature of edges, which suggests that the ecotone does not provide more important habitat than the wood.

In three studies of natural edges, each from a different continent, there was no support for increased diversity at the ecotone. Laudenslayer and Balda (1976) concluded that the bird diversity in the ecotone between pinyon pine/juniper woodland and ponderosa pine forest in Arizona was no greater than that in either of the adjacent habitats. Terborgh et al. (1990) found no evidence for increased species richness at ecotones in forests in Peru. Luck et al. (1999) concluded that the bird diversity at the ecotone between mallee and shrubland in south-central Australia was not generally greater than in the mallee. Comparisons with studies involving anthropogenic forest edges provide little additional support for the concept of edge effect. In a regrowth forest in Uganda, Africa, Dale et al. (2000) found no change in the abundance of understory birds moving from the edge of a 15-ha clearing to 500 m into the forest. However, they found a significant increase in species richness, with fewer, more common species near the edge and more, less common species at the forest interior. At forest-pastoral edges in

KwaZulu-Natal, South Africa, Kruger and Lawes (1997) had raw data showing a modest, nonsignificant increase (21%) in bird density near the edge and found that bird species richness was the same for the forest interior and near the forest edge. At forest-agricultural edges in Illinois, Marini et al. (1995) found a modest, nonsignificant increase (44%) in bird density and no difference in species richness near the forest edge compared to the interior. At clearings in mallee eucalypt in south-central Australia, Luck et al. (1999) found no increase in diversity near the mallee edge.

Bird species across edges

The models of avian response to ecotones were useful for describing the localized (each site spanned 10 ha) density patterns of 31 bird species in this study, although the statistical evidence for associating species with particular models was definitive only for the White-throated Treecreeper, which was wood specialist-ecotone neutral. For the dichotomy of generalist-specialist, most (68%) of the species were habitat specialists of either the heath or the wood. At the ecotone, the density of most species (65%) was either unaffected or reduced. Of the ecotone-conspicuous species, all four of the wood specialists and four of the seven habitat generalists showed relatively high density only at the wood side of the ecotone and might be better described as conspicuous at the wood side of the ecotone, as exemplified by the Grey Shrike-thrush (*Colluricincla harmonica*) and New Holland Honeyeater, respectively (Fig. 7). There were no ecotone-conspicuous birds among the three species categorized as heath specialists, and two additional heath specialists, the Ground Parrot (*Pezoporus wallicus*) and Striated Field-wren (*Calamanthus fuliginosus*), were detected in low numbers at only the heath plots (Appendix). Hence, the heath specialists contributed little to the bird species richness at the ecotone; the intermediate nature of the ecotone bird community described by the multivariate analysis was almost entirely due to the habitat-generalist and the wood-specialist species.

Results from the present study were comparable to those of Sisk and Margules (1993), who could definitively assign few species to their models on the basis of unambiguously different mean bird densities across an edge. Nevertheless, both studies identified a considerable percentage of species that were neutral or conspicuous at the ecotone, fewer species that were ecotone shy, and some species that were omitted from the categorization (Table 3). In particular, we found that 35% of species were ecotone conspicuous and Sisk and Margules (1993) categorized ~50% of species as ecotone exploiters. These results are analogous to Odum's (1958) conclusion that 40% of the regionally common birds in Georgia were ecotonal. However, all three studies measured the pattern of bird density rather than the birds' functional utilization of ecotones. Hence, all three studies have detected about the same

TABLE 3. Summary of results compared to Sisk and Margules (1993), showing the percentage of bird species in each of three categories of response to the ecotone.

Study and response	No. species studied	No. species categorized	Percentage of species
Present study	86	31	
Ecotone neutral			55
Ecotone conspicuous			35
Ecotone shy			10
Sisk and Margules (1993)			
Hard edge	38	26	
No response			35
Edge exploiter			54
Edge avoider			12
Soft edge	36	24	
No response			33
Edge exploiter			46
Edge avoider			21

percentage of ecotone-conspicuous bird species, but none has measured how these species might be ecotonal or exploiting the ecotone.

Entirely ecotonal species? None

None of the 11 ecotone-conspicuous species investigated at Budderoo, Booderee, and Nadgee showed strong evidence of being entirely ecotonal. The Eastern Bristlebird (*Dasyornis brachypterus*) was a habitat generalist, with twice as many records in the 50 m wide ecotone as in the adjacent wood plus heath. At Budderoo, Bramwell et al. (1992) made 52% of 132 detections in a 40 m wide ecotone, with the remaining 48% of detections in the adjacent woodland and heathland. The White-eared and White-naped Honeyeaters (*Lichenostomus leucotis* and *Melithreptus lunatus*), for which there were few records other than at the ecotone, were not entirely ecotonal species. Problems with under-sampling honeyeaters (Meliphagidae) have been noted in the literature (e.g., Mac Nally 1997, Taylor et al. 1997) and, in the present study, the distribution patterns of these two honeyeaters may have been artifacts of small sample sizes or skewing due to large numbers at just a few sites. Nevertheless, other studies (Chan 1995, Luck et al. 1999) support our categorization of the White-eared and White-naped Honeyeaters as ecotone conspicuous.

We found no entirely ecotonal species and there are several possible explanations. (1) Ecotonal species occurred but were not detected. We reject this explanation. Scrutiny of the 55 species recorded but not analyzed in detail in our study (see the Appendix) and scrutiny of the extensive species lists for Budderoo (Jordan and Jordan 1987), Booderee (Anonymous 1986), and Nadgee (Gosper and Baker 1997) revealed no species that we consider to occur only at heath-wood ecotones. (2) The 50 m wide ecotone was too narrow and 100 m on either side of the edge was too close to distinguish ecotonal species. This is theoret-

ically possible. Scale needs to be biologically significant (Paton 1994) and ecotones defined at a fraction of bird territory widths may be problematic (Terborgh 1985). However, to conduct the comparison at a larger scale would be difficult at Nadgee and impossible at Budderoo and Booderee, because of the natural scale of heterogeneity of the heath-wood mosaic. Besides, the scale we used did detect significant differences in densities for some species even between adjacent 25 m wide transects at the edge. (3) The 50 m wide ecotone zone was too wide. This explanation is rejected because a smaller scale is inappropriate for measuring bird density, and having a narrower ecotone zone would not promote the detection of any additional species. (4) Across heath-wood edges at Budderoo, Booderee, and Nadgee, there are no entirely ecotonal bird species. This explanation is the most likely.

Other studies have similarly failed to find entirely ecotonal species. McFarland (1988) reported no species (of 54 recorded) restricted to the ecotone between wet and dry heathland in southeastern Queensland, Australia. Luck et al. (1999) reported no species (of 53 recorded) restricted to mallee woodland ecotones in central-south Australia. Chapman and Harrington (1997) reported no species (of 16 recorded) restricted to the wet sclerophyll-rainforest ecotone in northeastern Queensland, Australia. Kruger and Lawes (1997) regarded the eight species (of 49 recorded) that they found at a forest edge in KwaZulu-Natal, South Africa, as typical of the adjacent grassland, the forest, or the woodland-savannah. For 88 bird species at montane rain forest-cloud forest ecotones in the Andes, Terborgh (1985) found that ecotones limited the distribution of some bird species, but the study gave no evidence of any ecotonal species. In the northeastern United States, Able and Noon (1976) found that of ~40 bird species, half had their altitudinal limit coinciding with three ecotones, beech/maple-birch/spruce, birch/spruce-balsam fir, and the tree line, but they noted no ecotonal species. Sisk and Margules (1993) reported no species (of ≥38 recorded) restricted to the oak woodland ecotones in central-coastal California (USA). Laudenslayer and Balda (1976), who tested specifically for ecotonal species in the southwestern United States, found none.

Conclusions

Avian communities across heath-wood edges in southeastern Australia provided little support for Odum's (1958) theories of edge effect and ecotonal species. The other bird studies that we reviewed also failed to give strong support to these theories.

The strongest pattern of the communities we studied was that bird density and species richness in the wood habitat were twice those of the heath habitat. The wood has more vegetation stories and a correspondingly more diverse bird community than the heath, which supports

the habitat complexity theory of MacArthur and MacArthur (1961).

Birdwatchers find that many species are more conspicuous at edges (Griggs 1997). However, being conspicuous at an edge does not make a species ecotonal or an ecotone exploiter. These terms imply some habitat function beyond the simple observation of a pattern of occurrence. The distinction is important for several reasons: it clarifies the difference between pattern and ecological process and it cautions against describing or managing birds as ecotonal species in landscapes that are becoming increasingly fragmented and, often, increasingly ecotonal (Laurance 2000).

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APPENDIX

A table showing bird numbers in six plots across heath–wood edges at three locations in southeastern Australia is available in ESA's Electronic Data Archive: *Ecological Archives* E083-058-A1.