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ELEVATED RATES OF PREDATION ON ARTIFICIAL NESTS IN LINEAR STRIPS OF HABITAT

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Abstract.—Artificial nests monitored with automatically triggered cameras were used to determine the intensity of nest predation and the identity of nest predators in linear remnants and large remnants of woodland in the wheatbelt of New South Wales, Australia. Nests were constructed from wire, grass, and bark to mimic those of the Red-capped Robin (*Petroica goodenovii*) and were stocked with eggs made from modelling clay. The incidence of predation was significantly higher in linear remnants (62% predation) than in large remnants (34%). Forty-seven independent photographic events were recorded, and nine species of bird accounted for all predation. Two species of predator, the Grey Shrike-thrush (*Colluricincla harmonica*) and the Grey Butcherbird (*Cracticus torquatus*), were responsible for 70% of predation and were detected at nests in both linear and large remnants. The remaining seven species of predator were detected only at nests in linear remnants. Bird surveys conducted in the same sites revealed that of the species of predator identified from photographs all, with two exceptions, were present in both linear remnants and large remnants. However, the abundance of identified predators was significantly higher in linear remnants. This study suggests that linear strips of vegetation, despite providing habitat in which birds can live, or a conduit through which they can move, may have limited value as breeding habitat. The current enthusiasm for protection and creation of corridors should not be at the expense of restoration and sympathetic management of large areas of native vegetation.

TASAS ELEVADAS DE DEPREDACIÓN EN NIDOS ARTIFICIALES EN PARCELAS LINEARES DE HABITAT

Sinopsis.—Se usaron nidos artificiales monitoreados con cámaras de control automático para determinar la intensidad de la depredación de los nidos y la identidad de los depredadores en remanentes lineares y en grandes parcelas remanentes en el "cinto de trigo" de la Nueva Gales del Sur en Australia. Los nidos se construyeron de alambres, hierbas y corteza para imitar los de Petroica goodenowii y se apertrecharon con huevos hechos de plastilina. La incidencia de depredación fué significativamente grande en remanentes lineares (62% depredados) que en las grandes parcelas remanentes (34%). Cuarentisiete eventos independientes se registraron fotográficamente y se documentó que hay nueve especies de aves depredadoras. Dos especies depredadoras, *Colluricincla harmonica* y *Cracticus torquatus*, fueron responsables del 70% de la depredación y se detectaron en tanto en nidos en remanentes lineares como en remanentes grandes. Las otras siete especies depredadoras se detectaron solamente en remanentes lineares. Muestreos de aves conducidos en los mismos lugares revelaron que las especies depredadoras identificadas por fotografías, con dos excepciones, estaban presentes tanto en remanentes lineares como en remanentes grandes. Sin embargo, la abundancia de depredadores identificados fué significativamente mayor en remanentes lineares. Este estudio sugiere que parcelas lineares de vegetación, además de proveer habitat en el cual las aves pueden vivir, o un conducto a través del cual se puede mover, pueden tener valor limitado como habitat reproductivo. El entusiasmo actual para la protección y creación de corredores no debiera ser al costo de la restauración y del manejo sensible de áreas grandes de vegetación nativa.

One of the most prominent explanations for the continued decline of songbirds following habitat fragmentation, is that elevated rates of nest predation prevent recruitment levels that maintain populations (Martin 1992, Paton 1994). Several North American and European studies have demonstrated a negative correlation between nest predation and the size of vegetation remnants (Wilcove 1985, Small and Hunter 1988, Gibbs 1991, Donovan et al. 1995). Two main hypotheses have been proposed to explain why predation is higher in fragmented habitats.

First, habitat fragmentation results in an increase in habitat edge (Sisk and Margules 1993) and nest predation is frequently higher near edges (e.g., Gates and Gysel 1978, Møller 1989, Gibbs 1991, but see Angelstam 1986, Small and Hunter 1988). This may be because edges (Soulé and Gilpin 1991), or the adjoining matrix (Andren et al. 1985), favor some major nest predators, such as corvids. Second, small habitat islands lack "interior habitat" and are unable to support large predators such as large felids, wolves, large hawks, and owls (Wilcove 1985, Soulé et al. 1988). In their absence, smaller mesopredators such as skunks, raccoons, jays, and crows become abundant as their populations are no longer limited by the large predators (mesopredator release; Soulé et al. 1988, Litvaitis and Villafuerte 1996).

Research on habitat fragmentation in Australia has also demonstrated that many bird species are adversely affected by increased habitat fragmentation (Loyn 1987, Lynch and Saunders 1991, Barrett et al. 1994), with higher predator activity along habitat edges (Gardiner 1998; Luck et al., in press). However, little is known about the relative importance of different species of nest predators in Australia (but see Laurance and Grant 1994, Major and Gowing 1994, Gardiner 1998). Such information is crucial to understanding the mechanism responsible for elevated predation in fragmented habitats.

The shape of the resulting remnants is also an important contributor to the amount of habitat edge in a landscape. In the wheatbelt of New South Wales, Australia, land tenure has strongly influenced the shape of remnants. Much of the private land, except that on rocky hill-tops and along water courses, has been cleared for crops and grazing. Public land, under the jurisdiction of the Rural Lands Protection Board, can exist as linear Travelling Stock Routes, some of which contain remnant vegetation. Other public land containing remnant vegetation is in the form of linear road reserves controlled by local councils. Both of these remnant types are narrow, linear and have a high edge to area ratio. We refer to these as *linear remnants.* If nest predation is more intense along edges, birds nesting in linear remnants will be particularly vulnerable. Other public land in the wheatbelt is managed by State Forests for selective logging. These remnants are large, non-linear, and provide relatively little edge habitat. We refer to these as *large remnants.*

There were three main aims to this study. First, we compared relative rates of nest predation between the interior of large remnants and linear remnants of woodland in the wheatbelt of New South Wales. Second, we attempted to determine the relative contribution of different species of nest predator to total nest predation pressure. Third, we measured the abundance of these nest predators in the two remnant types. In particular, we focused on one prey species, the Red-capped Robin (*Petroica goodenovii*), a species that has declined in fragmented woodlands in several parts of Australia (Hoskin et al. 1991, Robinson 1993, Saunders and Ingram 1995, Egan et al. 1997) and is typical of the ground-foraging guild of birds that is declining (Recher and Lim 1990).

Experiments using artificial nests have become popular for answering a variety of evolutionary, ecological, and land-management questions, although they are prone to a number of biases (Major and Kendal 1996). One of the chief strengths of this study is that the experimental design incorporated the photographic identification of nest predators at a large sample of nests. As well as providing information on mechanisms explaining differences in predation rates between large non-linear remnants and linear remnants, this approach provides partial validation of deploying artificial nests because anomalous predators can be detected.

STUDY AREA AND METHODS

Study area.—This study was carried out in ten woodland remnants near Forbes in the wheatbelt of New South Wales. Five linear remnants were located in Travelling Stock Routes or Roadside Reserves 50–90-m wide, 4.5–16-km long and 40–105 ha in area. The other five remnants were State Forests 640–1860 ha in area. Sites were chosen that contained Red-capped Robins and had vegetation as similar as possible to each other. Red-capped Robins nested in all our chosen remnants during the period of the study.

All selected sites have been classified by Sivertsen and Metcalfe (1995) as either Peneplain Box Woodlands or Peneplain White Cypress Pine Woodlands. All sites had *Callitris glaucophylla* (White Cypress Pine) as the dominant tree and understory species. Other common tree species included *Eucalyptus populnea* (Bimble Box), *E. microcarpa* (Grey Box), *E. intertexta* (Red Box), *Brachychiton populneus* (Kurrajong) and *Allocasuarina luehmannii* (Bull Oak). Common shrubs included *Acacia deanei* (Deane's Wattle) and *Dodonaea viscosa* (Broad-leaf Hopbush). All trees and shrubs were recorded in a 1-m wide strip along five 250-m transects in each site. Differences between linear and large remnants for four dominant vegetation attributes were determined by nested ANOVA with Remnant Type and Site (nested within Remnant Type) as factors.

Nests and eggs.—Artificial nests and eggs were used in this experiment because of the difficulty of finding and monitoring an adequate sample of natural nests in the two types of remnant. Nests were constructed from a 4-cm diameter cup of 1-cm diameter wire mesh around which fine grass and fibres of eucalypt bark were wound on the inside and outside. Small pieces of lichen were attached to the outside of the nests so that they closely resembled those of the Red-capped Robin (Beruldsen 1980). All materials were set in place with Fuller's Spray Bond Plus, pressure-pack adhesive.

Eggs were made from modelling clay and speckled with paint following

Major et al. (1996). One or two eggs, measuring approximately 19 × 16 mm, were placed in each nest and one egg was attached to a triggering system (Major and Gowing 1994). Movement of the egg activated a camera, which photographed the nest and any associated predator. Cameras were located 1–2 m from each nest which were otherwise unflagged.

Sampling design.—Five nests and cameras were set out at 100-m intervals along two transects at each site. Color-banding of male robins in the same sites indicated that robin territories were approximately 1.2 ha (unpubl. data). Thus a nest spacing of 100 m was compatible with the expected spacing of natural robin nests. Transects in the large remnants were at least 500 m from the edge of the remnant. Transects in the linear remnants were between 5 and 40 m from the edge of the remnant. Nests were generally placed in forks adjoining the trunk of *Callitris glaucophylla* trees at a height of 1.5–2 m above the ground. Occasionally nests were placed in branch forks of larger trees. Both nest placements were typical of those of Red-capped Robins in the study sites, although natural nests were usually built farther from the ground. However, it is not uncommon for Red-capped Robins to nest at this height (29% of 572 nests reported in the Birds Australia Nest Record Scheme were less than 2 m from the ground).

Only ten cameras were available for the study and, because we wished to monitor each nest photographically, only two transects could be monitored at a time. In each period of nest exposure, one transect in a large remnant and one transect in a linear remnant were monitored simultaneously. Both transects within each remnant were monitored in the same month. Thus one linear remnant and one large remnant were monitored each month from August to December 1995 spanning the breeding season of the Red-capped Robin (Beruldsen 1980).

Each nest was exposed for an average of 15 d, ranging between 9 and 19 d. Because linear remnants and large remnants were monitored simultaneously, nests in each remnant type were sampled at the same intensity over the same time period obviating any need to calculate daily survival probabilities (Mayfield 1975). Nests were considered depredated if an egg was damaged or removed. Statistical differences in the number of nests preyed upon in large versus linear remnants were assessed by Chi-square analysis.

Predator surveys.—Two bird censuses were conducted on each transect during the month in which the artificial nests were exposed. Censuses consisted of strip-transects 50-m wide, 500-m long, and lasting 50 min. All birds seen or heard within (but not flying through or over) the transect were included in subsequent analyses. A mean abundance of each species was calculated from the two surveys of each transect. The two transects in each site were used as replicates in a nested ANOVA with Remnant Type and Site (nested within Remnant Type) as factors. All species names follow Christidis and Boles (1994).

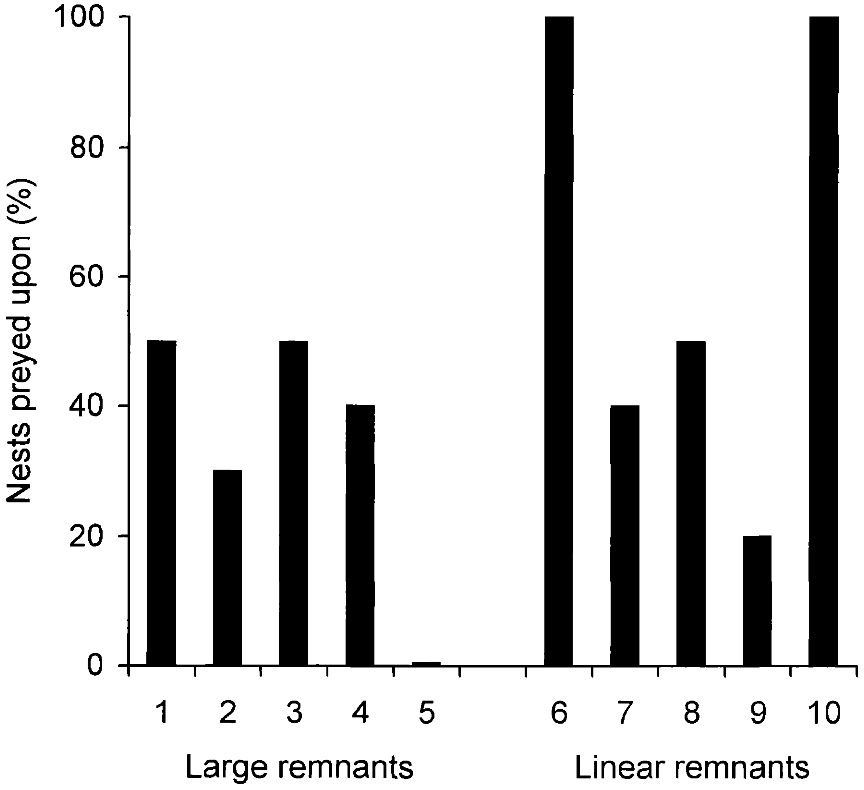

FIGURE 1. Variation in the incidence of nest predation between Linear Woodland Remnants and Large Woodland Remnants, New South Wales, Australia.

RESULTS

Effect of remnant type.—Of the 100 nests set out in this experiment, 48 showed evidence of predation. The predation rate, calculated from pooled sites within each remnant type, was significantly higher in linear remnants (62% predation) than in large remnants (34%) ($\chi^2 = 6.77$, df $= 1$, $P < 0.01$). To prevent saturation of a site with nests, and to achieve greater generality, we deliberately opted to minimize the number of nests per site and maximize the number of sites. The consequence of this was that there was insufficient power to allow meaningful comparison of each site independently. Although not tested statistically it is clear that the pattern of predation was not uniform across all sites of each remnant type (Fig. 1).

Identity of nest predators.—More than one photograph was normally taken at each nest, but only independent photographic events are analyzed below. We considered events to be independent if they occurred at dif-

TABLE 1. Observations of photographed predators of artificial eggs in Linear Woodland Remnants and Large Woodland Remnants in New South Wales Australia, 1995.

	Photographed at nests			Detected in surveys		
	Linear	Large	Total	Linear	Large	Total
Grey Shrike-thrush *Colluricincla harmonica*	15	10	25	12	7	19
Grey Butcherbird *Cracticus torquatus*	5	3	8	1	0	1
Australian Raven *Corvus coronoides*	6	0	6	3	0	3
Apostlebird *Struthidea cinerea*	1	0	1	3	0	3
Pied Butcherbird *Cracticus nigrogularis*	1	0	1	2	0	2
Australian Magpie *Gymnorhina tibicen*	1	0	1	11	6	17
Pied Currawong *Strepera graculina*	1	0	1	0	0	0
Grey-crowned Babbler *Pomatostomus temporalis*	1	0	1	15	0	15
Rufous Whistler *Pachycephala rufiventris*	1	0	1	59	37	96
Total	34	13	47	106	50	156

ferent nests or if different species of predator were recorded at the same nest.

Predators were photographically identified in 47 independent events (Table 1). Nine species of predator were identified depredating artificial nests. The Grey Shrike-thrush (*Colluricincla harmonica*) was the most frequently photographed predator in both large remnants (ten events) and linear remnants (15 events). The Grey Butcherbird (*Cracticus torquatus*) was the next most frequently photographed predator, again recorded at nests in both large remnants (three events) and linear remnants (five events).

The remaining seven predators were observed only at nests in linear remnants (Table 1). Thus nine different species of predator were identified from linear remnants but only two in large remnants.

Distribution and relative abundance of predators.—The combined abundance of all the above mentioned predators was significantly higher in linear remnants ($F_{1,8} = 9.20$, $P < 0.025$) (Fig. 2) than in large remnants. Small sample sizes prevented the statistical analysis of variation between linear remnants and large remnants in the abundance of individual species of identified nest predator. However, each identified predator, except the Pied Currawong, was more abundant in surveys of linear remnants (Table 1).

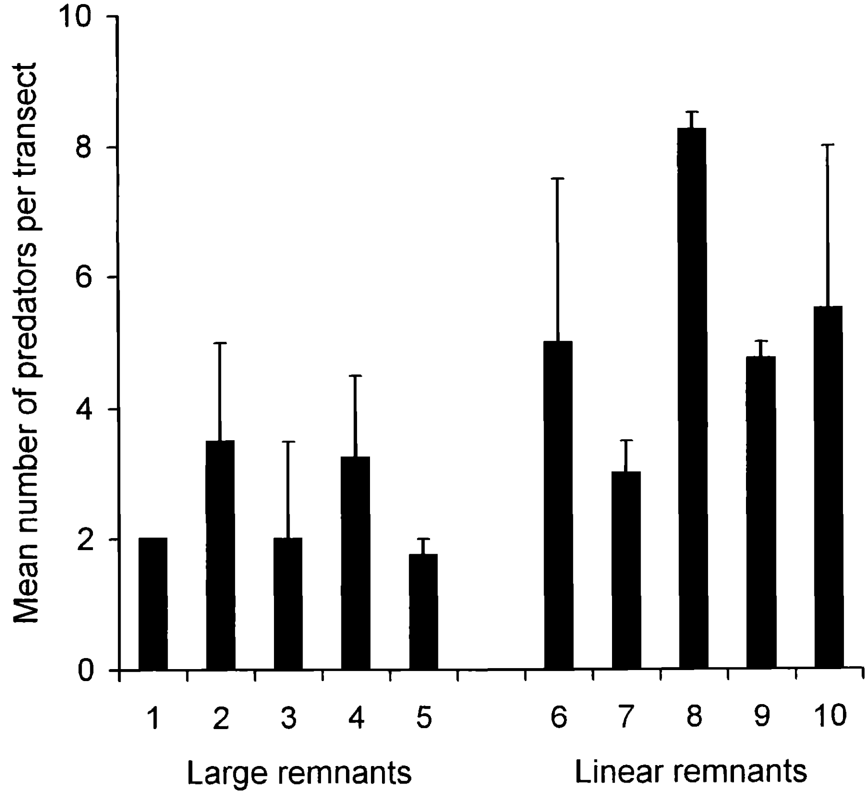

FIGURE 2. Variation in the abundance of identified predators between surveys conducted in Linear Woodland Remnants and surveys conducted in Large Woodland Remnants, New South Wales, Australia. Error bars represent standard error of the mean.

DISCUSSION

Explanations for variation in predation.—In terms of predation risk, linear remnants in our study represented poorer nesting habitat than large remnants. Part of the reason for the higher rate of predation in linear remnants was the greater activity of predators that exploit the agricultural matrix surrounding the remnant (hereafter called *matrix invaders*).

Four species of predator, together accounting for 19% of predation, probably derive extra foraging opportunities from the agricultural matrix. Australian Ravens, Australian Magpies, and Pied Butcherbirds were frequently observed in single trees and on fences in paddocks, and appear to benefit from land clearance. In the Western Australian wheatbelt, these three species use remnants of native vegetation as breeding and roosting sites, but depend upon paddocks for most of their feeding (Lynch and Saunders 1991, Saunders and Ingram 1995). The Pied Butcherbird has even extended its range into the Western Australian wheatbelt as a result of agricultural development (Saunders and de Rebeira 1991). In fragmented agricultural land in Victoria the Australian Magpie feeds mainly in paddocks (Loyn 1985), and in an urban situation Australian Magpies and Pied Butcherbirds are considered to be edge species (Catterall et al. 1991). Apostlebirds, the fourth potential matrix invader, were frequently seen foraging in paddocks adjoining roadside vegetation. We never encountered Apostlebirds in our large remnants, but they were found in four out of five of our linear remnants.

However, although 19% of predation was by potential matrix invaders, the bulk of predation was the result of forest-dependent birds. Seventy per cent of predation was due to the Grey Shrike-thrush and Grey Butcherbird, species which we observed to inhabit woodland and not adjoining paddocks. This was also the case for Rufous Whistlers and Grey-crowned Babblers. The Grey Shrike-thrush, Grey Butcherbird and Rufous Whistler are considered to be forest species (Catterall et al. 1991, Loyn 1985), dependent upon remnant vegetation in agricultural areas (Lynch and Saunders 1991, Saunders and de Rebeira 1991). Pied Currawongs, despite being voracious nest predators (Langmore and Mulder 1992), were photographed only once (in a linear remnant) and were not recorded in surveys. Although Pied Currawongs have benefited from urbanization, we are not sure whether they benefit from an agricultural matrix. They were probably a minor predator in our study area, which is on the western edge of their range (Blakers et al. 1984). Thus proximity to the matrix cannot be a unitary explanation for the increase in predation in the linear habitats.

The other prominent explanation, mesopredator release (Soulé et al. 1988, Litvaitis and Villafuerte 1996), cannot account for our results because large predators, which may potentially limit the abundance of mesopredators in this region, are no more abundant in large remnants than linear remnants. The Dingo (*Canis lupus dingo*), might conceivably have once regulated small mammal abundance, but it is now absent from large remnants as well as linear remnants (Brad Hazel, Rural Lands Protection Board, pers. comm.). The only other large mammalian predators that occur in our study area are the introduced cat (*Felis catus*) and fox (*Vulpes vulpes*). However, these species are not restricted to large remnants and therefore cannot be agents explaining mesopredator release. Furthermore, unlike many North American studies, no predation by mammals was observed in this study, and small mammals, rather than increasing, represent a group that has experienced a dramatic decline in response to land clearance in Australia (Dickman 1994).

Raptorial birds are likely to be the most significant predators of the medium-sized birds which accounted for all nest predation in this study. Raptors are therefore the most likely agent of mesopredator release in small remnants. Several species of raptor were seen in the study area: Black-shouldered Kite (*Elanus axillaris*), Black Kite (*Milvus migrans*), Spotted Harrier (*Circus assimilis*), Brown Goshawk (*Accipiter fasciatus*), Wedge-tailed Eagle (*Aquila audax*), Little Eagle (*Hieraaetus morphnoides*),

TABLE 2. Variation in density of vegetation between Linear Woodland Remnants and Large Woodland Remnants, New South Wales, Australia, 1995. Means are expressed as number of individuals per hectare.

Habitat variable	Linear mean	Large mean	*F*	df	*P*
Eucalyptus[a]	80	79	0.02	1, 8	0.89
Large *Callitris*[b]	213	217	0.01	1, 8	0.93
Small *Callitris*[c]	3389	4220	0.14	1, 8	0.72
Total Shrubs[d]	3753	4991	0.35	1, 8	0.57

[a] All Eucalyptus species combined.
[b] *Callitris glaucophylla* greater than 5-m high.
[c] *Callitris glaucophylla* less than 5-m high.
[d] All plants between 1 m and 5 m.

Brown Falcon (*Falco berigora*), Australian Hobby (*F. longipennis*), Black Falcon (*F. subniger*), and Nankeen Kestrel (*F. cenchroides*). However, none appeared to be confined to, or show a preference for, large remnants of vegetation. If anything, we would expect their impact to be higher in linear strips because fleeing birds would be more visible there than in the more extensive woodland provided by large remnants. Overall we can find no evidence that mesopredator release explains the observed differences in predation rates.

It is possible that other mechanisms related to patch size might have been responsible for differences in predation. Remnant size and type were necessarily confounded in our experiment. Linear remnants in this study were an order of magnitude smaller in area than the large remnants, thus any differences due to linearity are confounded with remnant size. For example, if the minimum area requirement for a competitor, which controls the abundance of nest predators, was not met by our linear remnants, it is possible that habitat size rather than shape was responsible for the variation in predation. We consider this unlikely because our linear strips were quite large (>40 ha in area) so that they were likely to be above the minimum area requirement of the species which might be conceived to fit into this category. However, these variables of size and shape remain confounded.

A further possible explanation is that variation in vegetation between large and linear sites might have influenced predator abundance or efficiency. Several different vegetation variables have been shown to influence rates of nest predation (Yahner and Wright 1985, Sugden and Beyersbergen 1986, Yahner and Cypher 1987). However, we attempted to minimize habitat variation when selecting sites, and none of the habitat characteristics we measured differed significantly between remnant types (Table 2).

Limitations of artificial nests.—A fundamental problem with using artificial nests is that, unlike real nests, they are not defended by a parent bird (Major and Kendal 1996). This makes them vulnerable to attack from animals which are not true nest predators. Knowing the identity of the predators provides some reassurance that this was not the case in this study. Grey Shrike-thrushes (Major 1991a), Grey Butcherbirds (Morris 1971), ravens (Major 1991b), Apostlebirds (Whitmore 1981), Pied Butcherbirds (Wyndham 1981), Pied Currawongs (Langmore and Mulder 1992), Australian Magpies (Vestjens and Carrick 1974), and Grey-crowned Babblers (Lord 1936) are all known predators of natural nests. We are unaware of any records of Rufous Whistlers as nest predators, but given that even smaller birds, such as Brown-headed Honeyeaters (*Melithreptus brevirostris*), have been recorded preying on eggs (Hobbs 1990), it is conceivable that Rufous Whistlers are occasional predators. Furthermore, Rufous Whistlers were the most common bird observed in our surveys yet they were recorded only once at nests. This suggests that they are infrequent predators.

Several studies deploying artificial nests have found that some important mammalian predators of natural nests are under-represented at artificial nests compared with avian predators (Willebrand and Marcstrom 1988, MacIvor et al. 1990). This is another potential source of bias in our experiment, particularly as no mammalian predation was observed. During previous work with a similar "artificial" methodology, but in different habitats, we observed that two species of rat and one small marsupial found artificial nests and eggs attractive (Major 1991c, Major et al. 1994). Ringtail Possum (*Trichosurus vulpecula*) predation has also been recorded at artificial nests (Matthews et al. 1999). We suspect that the reason for a lack of mammalian predation in our study was because of a genuine lack of mammalian predators in our study area. Intensive surveys in state forests in the same region produced a very low trap rate (Paul Wells, Forbes District Forester, pers. comm.). We therefore consider it unlikely that the use of artificial nests was the reason for the absence of mammalian predation. The absence of parental activity at artificial nests may also result in the under-representation of reptilian nest predators. Lace Monitors (*Varanus varius*), and Eastern Brown Snakes (*Pseudonaja textilis*) were occasionally observed in the study area, but they were never photographed at nests.

Implications for conservation.—The results of this study support the contention that increasing the amount of edge habitat in a landscape has the potential to result in a decline in reproductive success of birds. Our results are not explained by mesopredator release but are consistent with the notion that there are predators which are more abundant or forage more effectively along edges. These predators may be edge specialists or they may invade the remnants from the agricultural matrix. Furthermore, we suggest that the search pattern of predators may be simplified by what is essentially a one-dimensional habitat, resulting in higher predation efficiency. Whether an increase in nest predation in linear remnants would result in smaller populations and therefore a higher extinction probability is dependent upon two things: firstly, the degree to which available habitat is already occupied by adults and secondly, whether recruits to a remnant are produced within the remnant or whether they have emigrated from other areas.

Much of the woodland of the cereal-growing areas of Australia has been cleared, producing a consequent rise in the water table. The land is currently under threat from widespread salination. Responding to this and other environmental threats, programs of habitat reconstruction are under way and considerable resources are being directed towards tree-planting. Based on personal observation, discussion with land holders, the newsletters of government agencies, and references in recent legislation and policy, linear strips of vegetation are often the preferred habitat configuration in reconstruction programs. While providing other benefits such as windbreaks and shelter belts, the results of our study suggest that a strategy preoccupied with essentially narrow linear strips may be misguided in terms of nature conservation. Justification on the grounds that linear strips will serve as wildlife corridors is not a convincing argument while the evidence regarding the value of narrow, integrated corridors is inconclusive (Nicholls and Margules 1991) and such corridors may in fact be detrimental (Merriam 1991, Soulé and Gilpin 1991). We recognise that land managers must act now in the absence of adequate knowledge, but a mixed strategy is recommended as an appropriate course of action. Large non-linear "controls" must be reconstructed so that the value of linear strips can be evaluated. Our results from existing remnants of these configurations indicate that, at least for small birds, the value of linear strips could easily be over-estimated.

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