

RESEARCH ARTICLE

Predation risk for reptiles is highest at remnant edges in agricultural landscapes

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Abstract

1. Preventing biodiversity loss in fragmented agricultural landscapes is a global problem. The persistence of biodiversity within remnant vegetation can be influenced by an animal's ability to move through the farmland matrix between habitat patches. Yet, many of the mechanisms driving species occurrence within these landscapes are poorly understood, particularly for reptiles.
2. We used scented and unscented plasticine lizard models and wildlife cameras to (a) estimate predation risk of reptiles in four farmland types (crop field, pasture paddock, restoration tree planting and areas with applied woody mulch) relative to the patch edge and remnant vegetation, and (b) examine how predation risk was influenced by temporal change in the matrix (crop harvesting).
3. Birds (55.1%), mammals (41.1%), reptiles (3.4%), and invertebrates (0.5%) attacked models, of which 87% were native species. Mammalian predators were 60.2% more likely to attack scented models than unscented models. Bird predators were not influenced by scent.
4. We found predator attacks on models were highest at edges (49%, irrespective of adjacent farmland type, with a reduced risk within farmland (29%) and remnant patches (33%) ($p < 0.01$). Both mammal and bird predators contributed to high numbers of predation attempts at edges.
5. Removal of crops did not increase predation attempts in crop fields or other farmland types, although predation attempts were significantly lower along the crop transect after harvesting, compared to the woody debris transect. However, numbers of predation attempts were higher in edge habitats, particularly prior to harvesting.
6. *Synthesis and applications.* Reptiles are at risk of predation by birds and mammals in both remnant patches and the farmland matrix, particularly in edge habitat. Our results demonstrate that edge habitats are potentially riskier for lizards than the farmland. Vulnerability to predation may be increased by a lack of shelter within edge habitats such as by increasing visibility of reptiles to predators. Therefore, to benefit reptiles, land managers could provide shelter (rocks, logs, and grasses), particularly between remnants and linear plantings which could improve landscape connectivity.

KEYWORDS

edge effects, edge habitat, farming, landscape connectivity, matrix, mortality, predation risk, reptile

1 | INTRODUCTION

Habitat loss and fragmentation resulting from intensive agricultural production is a major threat to global biodiversity (Ellis & Ramankutty, 2008; Venter et al., 2016). Habitat patches can be surrounded by a highly modified agricultural matrix (defined as an extensive, nonnative land cover type which cannot sustain some species dependent on patches of remnant native vegetation; Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013) comprised of different farmland types. The long-term persistence of fauna populations within these landscapes can depend on the ability of animals to move between remnant patches of habitat (Kay, Driscoll, Lindenmayer, Pulsford, & Mortelliti, 2016; Pulsford, Driscoll, Barton, & Lindenmayer, 2017). However, some matrix environments could represent a barrier to movement (Prevedello & Vieira, 2010; Pulsford et al., 2017), particularly if there is high mortality risk during dispersal (Anderson & Burgin, 2008; Daly, Dickman, & Crowther, 2008). Despite increasing research on the impact of matrix heterogeneity on some fauna species (Driscoll et al., 2013; Watling, Nowakowski, Donnelly, & Orrock, 2011), empirical data on the mechanisms explaining reduced use of some matrix types is lacking in agroecosystems (Driscoll et al., 2013).

The risk of elevated mortality, such as individuals being killed by harvesting machinery (Rotem, 2012), increased risk of desiccation (Cosentino, Schooley, & Phillips, 2011), or predation (Schneider, Krauss, & Steffan-Dewenter, 2013; Shtickzelle & Baguette, 2003), at different times and within different matrix environments may be an important driver of matrix use by fauna in agricultural areas (Driscoll et al., 2013; Ewers & Didham, 2006; Pita, Beja, & Mira, 2007). Predation is one of the most important factors influencing mortality (Castilla & Labra, 1998) and population persistence (Purger, Csuka, & Kurucz, 2008; Suhonen, Norrdahl, & Korpimäki, 1994). Predation risk may reduce an individual's willingness to emigrate (Stevens, Le Boulengé, Wesselingh, & Baguette, 2006), their likelihood of reaching a new patch (Pita, Mira, Moreira, Morgado, & Beja, 2009), and their safe return from exploratory forays into the matrix (Ewers & Didham, 2006; Rotem, 2012). These factors increase the effective isolation of remnant patches (Pita et al., 2009). Yet, agricultural lands can vary markedly in spatial and temporal vegetation structure. This can affect the ability of predators to traverse and forage between several habitat types and, in turn alter the exposure of prey to predation (Cosentino et al., 2011; Storch, Woitke, & Krieger, 2005). Predator responses to habitat edges also may vary depending on the species, landscape type, and scale (Driscoll et al., 2013; Rand, Tylianakis, & Tscharntke, 2006).

The effects of habitat structure on predation risk have been reasonably well explored for birds (Purger et al., 2008; Whittingham & Evans, 2004) and mammals (Norrdahl & Korpimäki, 1998; Pita et al.,

2009). However, knowledge of the influence of predation risk on reptiles within agricultural areas is limited (Daly et al., 2008; Driscoll et al., 2013; Sato et al., 2014). Most reptile species have limited dispersal abilities when compared to birds and mammals, and depend on specific microhabitat features to avoid predation (Manning, Cunningham, & Lindenmayer, 2013; Michael et al., 2015). Reptiles also have specific thermal requirements that make them dependent on basking opportunities and, in turn, exposing them to predation risk (Anderson & Burgin, 2008; Sato et al., 2014). Therefore, predation risk may be a key ecological driver which may impact reptile movement and habitat selection in agricultural landscapes, and in turn, influence the effectiveness of management approaches aimed at improving reptile persistence (Driscoll et al., 2013; Vandermeer & Carvajal, 2001).

Since the understanding of predation risk on reptiles in agroecosystems is limited, we used scented and unscented plasticine models of a patch-dependant gecko species, *Gehyra versicolor*, to test if predation risk varied between differing types of farmland, at different distances from edges and before and after crop harvesting. *G. versicolor* is a small, nocturnal, arboreal and saxicolous species and occurs widely throughout eastern Australia (Cogger, 2014; Michael & Lindenmayer, 2010). This species can be relatively common in fragmented agricultural landscapes and is strongly associated with woodland remnants, rocky outcrops, logs, and shrubs (Cogger, 2014; Gruber & Henle, 2004). Previous studies found that *G. versicolor* (syn. *G. variegata*) disperses readily through natural habitat, but farmland may represent a barrier to movement (Sarre, Smith, & Meyers, 1995). Using a landscape-scale field experiment we addressed two specific questions:

1. Does differing farmland type (cropped paddocks, pasture paddocks, linear plantings, and applied woody mulch) influence predation risk in contrast to the adjacent edge ecotone and remnant patch? We hypothesized that predation rates would be greater in the farmland matrix and edge habitats. Many empirical studies have documented increased avian and insect predation rates near patch edges and within farmland for a suite of taxa (Driscoll et al., 2013; Ries Jr., Battin, & Sisk, 2004; Storch et al., 2005). We postulated that structurally simplified farmland types (crops and paddocks) would have higher rates of predation (Purger et al., 2008; Storch et al., 2005), compared to structurally complex linear plantings and woody debris treatments. This was because lizards in such areas would be more exposed and visible to predators (Michael et al., 2015; Wilson, Whittingham, & Bradbury, 2005). Previous studies have supported the idea that the potential food subsidies provided by crops may increase generalist predators

within paddocks, resulting in elevated predation rates and reducing prey populations within agricultural habitats (Andren, 1992; Rand et al., 2006; Rotem, 2012). Furthermore, while temporary vegetation cover (e.g., cereal crop, pasture grasses) may conceal prey from visual predators (e.g., corvids, raptors), the cover afforded may increase predation by animals which use olfactory cues such as mammals (Stoate et al., 2009; Wilson et al., 2005).

In agricultural environments, edge habitats may be inhabited by a large suite of mammalian and avian predators using edges as hunting areas, movement corridors, or transitory zones to cross-forage between patches and farmland, which in turn, increases predation risk (Anderson & Burgin, 2008; Sewell & Catterall, 1998). These mechanisms may increase hunting opportunities for these predators in edge areas compared to core remnants (Anderson & Burgin, 2008; Storch et al., 2005). While the impact of these predators on reptile prey is well known (Anderson & Burgin, 2008; Barrows & Allen, 2007), the contribution of edge habitats to predation risk for reptiles in agroecosystems is unclear.

2. Does crop harvest increase predation risk? Harvesting may influence predation rates in all farmland types as predators may move opportunistically to new foraging habitat (spillover effects) (Storch et al., 2005), or compensatory shifts due to the prey source being killed during the mechanical harvesting of crops (Rotem, Ziv, Giladi, & Bouskila, 2013; Thorbek & Bilde, 2004). For example, rodent predators increased in habitat surrounding crop fields after crop harvesting due to the decline in resource availability within cropped fields (Jacob, Ylönen, & Singleton, 2004). Therefore, we tested if attacks on reptile models would be higher in crop paddocks prior to harvesting, due to an increase in prey abundance (Rand et al., 2006), with the converse effect after harvesting due to the rapid removal of resources (Rotem et al., 2013). Consequently, we expected predators to spillover or shift to nearby habitats and farmland types in search of foraging opportunities (e.g., linear plantings and woody debris; Storch et al., 2005; Thorbek & Bilde, 2004). We also expected the addition of woody mulch to a bare crop paddock would provide additional shelter for reptiles (i.e., models) after harvesting, therefore reducing exposure of models to predators and reducing attacks on models.

2 | MATERIALS AND METHODS

2.1 | Study species

Gehyra versicolor is a medium-sized (mean SVL = 55 mm) nocturnal, arboreal, and saxicolous gecko in the family Gekkonidae (Gruber & Henle, 2004). Currently, its population status is unknown due to recent taxonomic reclassification (Duckett, Wilson, & Stow, 2013).

This species may alter its habitat use in response to availability of food and shelter resources, antagonistic behaviour, mating opportunities (Henle, Davies, Kleyer, Margules, & Settele, 2004) and uses the matrix ecotone (observed from a previous study; N.A. Hansen, unpublished data).

2.2 | Study areas

Our study area is located within western New South Wales, Australia and is bounded by the coordinates 33° 55' 58.249" S; 147° 53' 48.729" E (Grenfell) and 34° 10' 34.776" S; 146° 50' 7.522" (Ardlethan; Figure 1a,b). Mixed farming dominates the landscape, characterized by intensive cereal cropping (wheat, canola, lupins, and barley) and grazing by sheep (*Ovis aries*) and cattle (*Bos taurus*). The dominant native vegetation types within the remnant patches in the western part of our study area include mallee woodland and shrubland with some White Cypress Pine (*Callitris glaucophylla*). The eastern part of our study area is dominated by patches of Box Gum and White Cypress Pine woodland, including threatened White Box (*Eucalyptus albens*) woodland, Yellow Box (*Eucalyptus melliodora*) woodland, Blakely's Red Gum (*Eucalyptus blakelyi*) woodland, and derived grasslands.

2.3 | Gecko models

Plasticine models are useful for estimating rates of predation (Daly et al., 2008; Sato et al., 2014). We created a prototype model of *G. versicolor* using nontoxic sculpting clay (Chavant NSP Hard Clay). The models were based on mean morphological measurements taken from adult specimens previously recorded in the field (N.A. Hansen, unpublished data). We used a prototype to create silicon moulds for mass model production. We then painted the models with nontoxic paint to mimic the body colour of *G. versicolor* (see Supporting Information Figure S1a in Appendix S1). We deployed a total of 540 models.

Several studies have used plasticine models to estimate predation rates, typically targeting visual predators like diurnal birds or mammals (Bateman, Fleming, & Wolfe, 2016; Daly et al., 2008; Purger et al., 2008; Sato et al., 2014). However, *G. versicolor* is a nocturnal species (Cogger, 2014; Gruber & Henle, 2004) and predation of this species is largely by nocturnal predators (Henle, 1990). Therefore, to evaluate potential impacts of predators that use olfaction for hunting such as nocturnal mammals and reptile predators, we synthesized and applied *G. versicolor* odour to one of the two models at each plot ($n = 10$ models per transect). We synthesized odour by fermenting skin, faeces, and bedding from captive *G. versicolor* individuals in water, for at least 4 weeks. We then strained the liquid and soaked plasticine models overnight in the mixture to produce a scented model. Separate latex gloves were used for each model to ensure no human scent was transferred on to models, or cross-contamination of gecko scent between scented and unscented models.

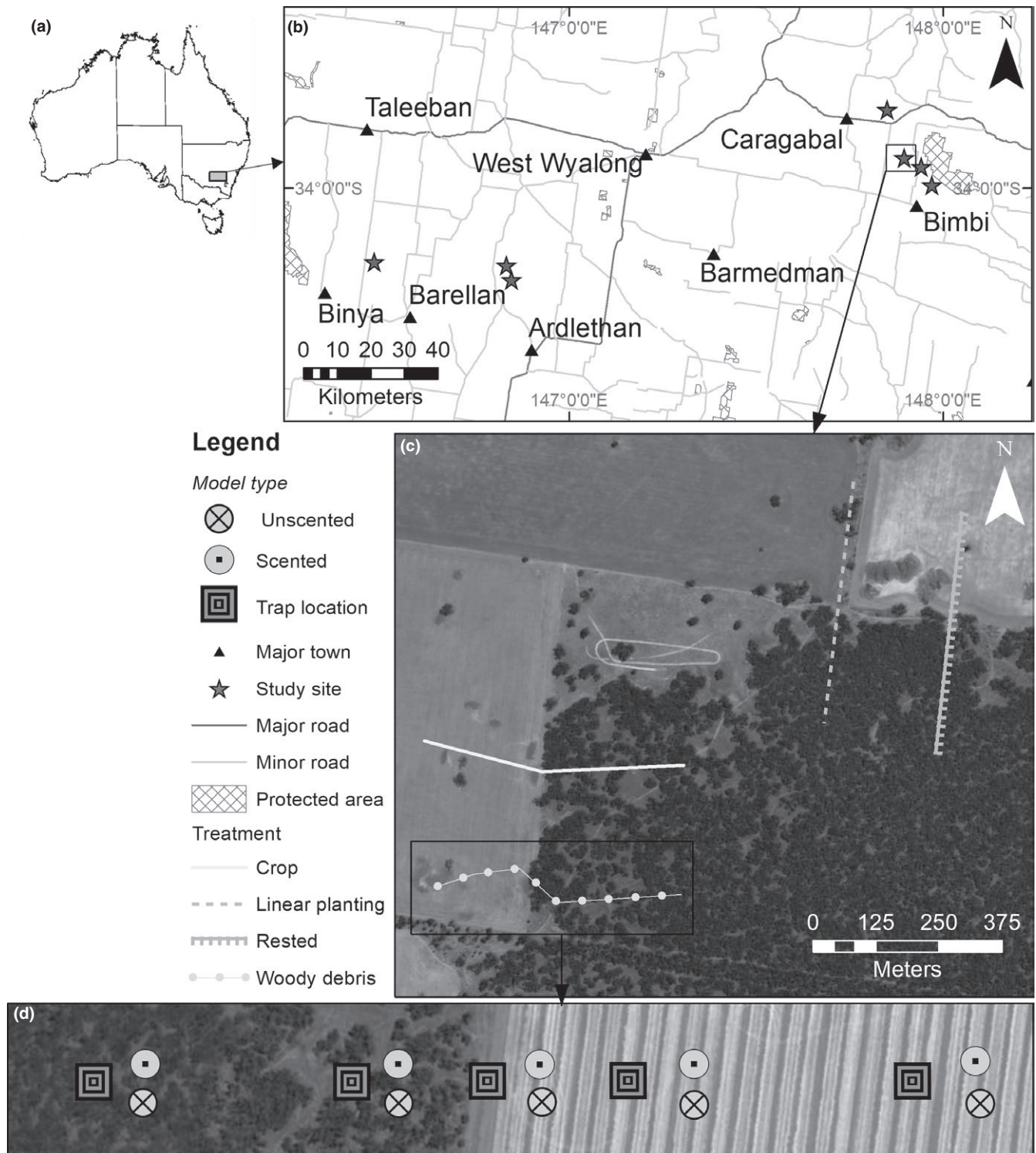


FIGURE 1 (a) The geographical location of the study area in New South Wales, Australia. (b) The approximate locations of study locations (represented by the open circles). (c) Location layout for each block design; coloured lines indicate each transect (or treatment) examined during the study. Each treatment extends from the remnant into four farmland types (planting, pasture, woody debris, and crop). (d) Configuration of models and cameras for each treatment

2.4 | Experimental design and survey protocol

We established a blocked experiment with seven replicate study locations (Figure 1b,c). Each location comprised a remnant patch of

native vegetation surrounded by a matrix of three different farmland types: (a) “cropping”: a cereal crop paddock (largely wheat and some barley), (b) “linear plantings”: a linear strip of fenced restoration vegetation, predominantly *Acacia* midstorey with occasional

TABLE 1 Summary of species captured on camera or identified by attack marks

Group	Scientific name	Common name
Invertebrate	<i>Iridomyrmex</i> sp.	Meat-eating ants ^a
Bird	<i>Aquila audax</i>	Wedge-tailed Eagle ^a (Brooker & Ridpath, 1980)
	<i>Corcorax melanorhamphos</i>	White-winged chough ^a (Anderson & Burgin, 2008)
	<i>Corvus coronoides</i>	Australian Raven ^a (Sato et al., 2014)
	<i>Cracticus tibicen</i>	Australian Magpie ^a (Anderson & Burgin, 2008)
	<i>Cracticus torquatus</i>	Grey butcherbird ^a (Anderson & Burgin, 2008)
	<i>Dacelo novaeguineae</i>	Laughing Kookaburra ^b (Anderson & Burgin, 2008)
	<i>Dromaius novaehollandiae</i>	Emu ^a
	<i>Grallina cyanoleuca</i>	Magpie-lark
	<i>Pomatostomus temporalis</i>	Grey crowned babbler
Mammal	<i>Struthidea cinerea</i>	Apostle bird ^a (Chapman, 2001)
	<i>Vulpes vulpes</i>	Red Fox ^{a,b} (Henle, 1990)
	<i>Macropus giganteus</i>	Eastern Grey Kangaroo
		Swamp/rock wallabies
	<i>Trichosurus vulpecula</i>	Brush-tail Possum (How & Hillcox, 2000)
	<i>Mus musculus</i>	House mouse ^{a,b} (Henle, 1990)
	<i>Lepus europaeus</i>	European hare
	<i>Sminthopsis murina</i>	Common Dunnart ^a
		Livestock (cow, sheep)
	<i>Capra hircus</i>	Feral goat
Reptile	<i>Antechinus flavipes</i>	Yellow-footed antechinus ^a
	<i>Varanus gouldii</i>	Sand monitor ^{a,b} (Henle, 1990)
	<i>Varanus varius</i>	Lace monitor ^{a,b} (Guarino, 2001; Henle, 1990)
	<i>Tiliqua Scincoides</i>	Eastern Blue-tongue lizard

^aKnown to include reptiles as prey.^bPotential predator of *Gehyra versicolor*.

eucalypt species, grassy ground cover, occasionally subject to disturbance by sheep grazing, (c) “grazed pasture”: a rotationally grazed paddock, cleared of midstorey and canopy cover with the occasional paddock tree (Figure 1c). We created a fourth experimental farmland type by apply a native woody mulch (hereafter “woody debris”) to a cropped paddock after crop harvest to examine if we could temporarily provide shelter and protection for reptiles in the cropping farmland type. Forest cover across the study area is <11% and remnant patch size range between 64.89 ha and 23,073 ha (mean patch size = 6759.94 ± SE 4,212.50 ha). The dominant predators recorded (Table 1) are widespread generalists found throughout farmland patches and matrix alike so, patch size is unlikely to influence the main of predators recorded (Anderson & Burgin, 2008; Arthur, Henry, & Reid, 2010; Daly et al., 2008; Storch et al., 2005).

At each location, we located five paired sets of plasticine models along 400 m transects centred on, and running perpendicularly to, the edge of a remnant patch. We placed model sets at the edge (0 m), and at 20 m and 200 m into both the remnant patch and the adjacent farmland type (Figure 1d). We positioned models near to, but not completely obscured by, ground cover (e.g., crop row, mulch, or grasses). To examine how harvesting influenced predation risk, we deployed a new set of models before and after crops were harvested (“harvesting”). We placed a single camera trap (Scout Guard SG560K-8mHD; Gotcha Traps Pty Ltd) at each plot (i.e., 0 m, 20 m, and 200 m into a remnant patch, 20 m and 200 m into a paddock; Figure 1d) to identify species of predators near the models over a 4-day period. Access constraints prevented one pasture treatment at one location from being surveyed.

We considered a predation attempt to be the displacement of the model from its original position, complete removal, or visible signs of attack (bite, claw, or scratch marks; see Supporting information Figure S1b,c in Appendix S1). We also considered investigation of a model by a reptile predator, captured by camera footage, as a predation attempt. For each model, we recorded: whether the model had been attacked, the evidence for predation (visible signs, attached hairs, displacement), where on the model the visible signs of attack were located, and the type of predator attacking the model.

2.5 | Statistical analysis

We examined the effect of changes within the matrix environment on predation risk by fitting (GLMM; Bolker et al., 2009) assuming a binomial distribution with a logit-link function. We included the condition of the plasticine models (attacked vs. not attacked) as the response variable, fitting separate GLMMs for three groups of predators: all predators, mammal predators, and bird predators. We modelled the interaction of treatment (four farmland types: planting, pasture, woody debris, and crop), harvesting period (before and after harvesting) and habitat (remnant, edge, and matrix) as fixed effects. Physical structure of the 20 m and 200 m points were not found to substantially differ and were pooled into each respective habitat types (remnant and matrix) for analysis. We included model type (scented and unscented) as an additive fixed effect. 'Camera trap number' was nested within location (sites were clustered into east and west) as random effects to account for regional variation across the geographical gradient of sites, repeated sampling units, and camera trap differences within the data. To examine if scent influenced predation attempts between predators, we fitted separate GLMMs with the plasticine models (scented vs. unscented) as the response variable and all predators and predator groups as fixed effects.

We calculated *p*-values using the 'ANOVA' function in the 'lme4' package to reveal significant effects and interactions of the model (Bates et al., 2013). We conducted a post hoc analysis of significant interactions using the 'lsmeans' function (Lenth, 2016).

We conducted all analyses using R 3.4.0 (R Core Team, 2017).

3 | RESULTS

Of the 540 models we deployed, 186 models were attacked and investigated by 21 species, 15 of which are considered potential gecko predators (Table 1, Figure 2). We identified predation attempts by model attacks (30%; *n* = 55), camera identification (41%; *n* = 77, Figure 2), or both (29%; *n* = 54). Animals investigating or attacking the models included birds (55.1% of attacks; *n* = 114), mammals (41.1% of attacks; *n* = 85), reptiles (3.4% of attacks; *n* = 7), and invertebrates (0.5% of attacks; *n* = 1). Three species dominated the predation events: White-winged Chough *Corcorax melanorhamphos* (*n* = 61 predation events), Red Fox

Vulpes vulpes (*n* = 28 predation events), and Australian Magpie *Cracticus tibicen* (*n* = 20 predation events) (Table 1). Predation markings from bird and mammals were predominantly located on the head, tail, or hind limbs, suggesting that the predators perceived models as potential prey (Daly et al., 2008; Sato et al., 2014). Nearly all the predator species were native (86.7% of attacks, *n* = 13) with the remainder exotic (13.3% of attacks, *n* = 2) (Table 1).

3.1 | Effect of farmland type on predation risk in contrast to the adjacent edge ecotone and remnant patch

We did not find significant interactive effects of 'treatment', 'habitat', and 'harvesting' on predation risk of lizard models (*p* = 0.08) (Table 2). We did not detect any significant differences in total predation attempts (*p* = 0.33), or predation of models by birds (*p* = 0.61) or mammals (*p* = 0.18) between farmland types (Table 2).

Instead, we found models located in edge habitats had higher predation (all predators) than in the matrix or remnant patches (*p* = 0.02) (Table 2; Figure 3a). Avian predation attempts were similarly highest at the edge (36% of attacks; mean 6.43 ± 1.09 SE attacked models) compared to matrix (30% of attacks; mean 5.29 ± 1.02 SE attacked models) and remnant patches (34% of attacks; mean attacked models 6.00 ± 1.40 SE) (*p* < 0.01) (Table 2; Figure 3b). Predation attempts by mammals were similar across habitat types, with 40% of attacks in remnant patches (mean attacked models = 4.43 ± 0.92 SE), 29% of attacks in edge habitat (mean attacked models = 3.29 ± 0.48 SE), and 31% of attacks (mean attacked models = 3.43 ± 0.84 SE) in matrix habitats (*p* = 0.23) (Table 2 and Appendix S1).

3.2 | Effect of crop harvest on predation risk

We found no three-way interactive effect of 'treatment', 'habitat', and 'harvest', suggesting removal of crops did not increase predation attempts by predators or between groups of predators within crop paddocks (*p* = 0.08) (Table 2).

Instead, we found predation attempts by (all) predators were significantly lower along the crop transect after harvesting, compared to the woody debris transect (*p* = 0.02) (Figure 4). Predation by birds was highest at the edge prior to harvesting compared to the remnant patches and matrix (*p* = 0.04) (Table 2 and Appendix S1; Figure 5a). Similarly, predation attempts by mammals were higher at the edge prior to crop harvesting, compared to the matrix (*p* < 0.01) (Figure 5b). However, we found no significant contrasts after harvesting (see Supporting Information Table S1; Figure 5b).

3.3 | Other responses

Scented models were attacked in higher numbers (60% of total attacks; *n* = 50) by mammal predators compared to unscented models



FIGURE 2 Examples of predation on gecko models from camera footage. From top left to right clockwise: Australian Magpie *Cracticus tibicen*, Laughing Kookaburra *Dacelo novaeguineae*, Wedge-tailed Eagle *Aquila audax*, Grey Butcherbird *Cracticus torquatus*, Red Fox *Vulpes vulpes*, and Lace monitor *Varanus varius*

(40% of total attacks; $n = 33$) ($p = 0.05$) (Supporting Information Figure S2). Predation attempts by both predators (all predators) and bird predators were not influenced by scent (all predators: $p = 0.10$ birds: $p = 0.17$ respectively). Sample sizes of reptile predator attacks on models were too small to analyse ($n = 7$ scented; $n = 3$ unscented).

4 | DISCUSSION

We evaluated how farm management practices influence predation risk and developed new insights into the avoidance of particular farmland types by reptiles. Our findings reveal remnant patches, edge and farmland, and harvesting period were important factors influencing predation risk, with highest frequency of predation attempts at habitat edges, particularly prior to harvesting. We also found the harvesting of crops did not result in significantly increased predation attempts in the crop fields, or other farmland types. Predation risk within edge habitats may act as a potential barrier to movement of lizards into the matrix, and we argue that it may contribute to the

observed decline in reptile abundance from edges into some farmland habitats (Hansen, 2018). Based on this information, we can improve the capacity for managing predation risk and enhance reptile conservation in agroecosystems.

4.1 | The influence of farmland type, in contrast to the edge and remnant patches, on predation risk

A key finding of this study was that edge habitats are “riskier” than the matrix for lizards, with both mammal and bird predators contributing to predator attacks along edges. We found elevated predation risk at the edge, irrespective of adjacent farmland type. Further, both matrix-generalist predators, such as the Red Fox *Vulpes vulpes*, and the Australian Raven *Corvus coronoides*, and forest-specialist predator species such as Yellow-footed antechinus *Antechinus flavipes* contributed to predation attempts at the edge (Table 1).

Our findings are partially congruent with our prediction that edges would result in higher predation risk (Introduction, question 1). This is consistent with previous studies showing increased

TABLE 2 GLMM results for harvest (preharvesting vs. postharvesting), treatment (four farmland types: planting, pasture, woody debris, and crop) and habitat (remnant native vegetation, edge, and matrix) on predation rates on gecko models

Response	Model terms	χ^2	df	p
All predator	treatment*habitat*harvest + model.type + (1 location/camera trap number)			
	treatment	3.79	3	0.29
	habitat	8.09	2	0.02
	harvest	0.62	1	0.43
	model.type	2.51	1	0.11
	treatment:habitat	6.86	6	0.33
	treatment:harvest	9.88	3	0.02
	habitat:harvest	0.55	2	0.76
	treatment:habitat:harvest	11.26	6	0.08
Bird predator	treatment + habitat + harvest + treatment:habitat + treatment:harvest + harvest:habitat + (1 location/camera trap number)			
	treatment	5.35	3	0.15
	habitat	19.20	2	<0.01
	harvest	3.22	1	0.07
	treatment:habitat	4.50	6	0.61
	treatment:harvest	6.74	3	0.08
	habitat:harvest	6.38	2	0.04
Mammal predator	treatment + habitat + harvest + model.type + treatment:harvest + harvest:habitat + treatment:habitat + (1 location/camera trap number)			
	treatment	0.91	3	0.82
	habitat	2.94	2	0.23
	harvest	1.65	1	0.20
	treatment:harvest	4.40	3	0.22
	habitat:harvest	9.17	2	0.01
	treatment:habitat	8.93	6	0.18

Note. Model type = scented vs. unscented.

Darker grey shadow denotes significant values e.g. <0.05. Lighter grey highlights near significant values.

predation in edge habitat, particularly by mammalian and avian predators (Keyser, Hill, & Soehren, 1998; Šálek, Kreisinger, Sedláček, & Albrecht, 2010). Higher rates of predation at edges could be due to a combination of predators using edges as movement corridors between landscape elements (consuming prey along the way; Anderson & Burgin, 2008; Piper, Catterall, & Olsen, 2002; Storch et al., 2005), generalist predators crossing edge habitat when penetrating patches from adjacent modified habitats (Andrén, 1995; Thompson, Warkentin, & Flemming, 2008) and forest-specialist predators spilling over opportunistically from patch into edge habitats (Storch et al., 2005). Higher diversity of forest-specialist and farmland generalist predators at edges may increase predation risk because a greater variety of predators are present (Andrén, 1995; Piper et al., 2002), resulting in more models being found. In our study area, reptile models were likely more exposed in open, edge

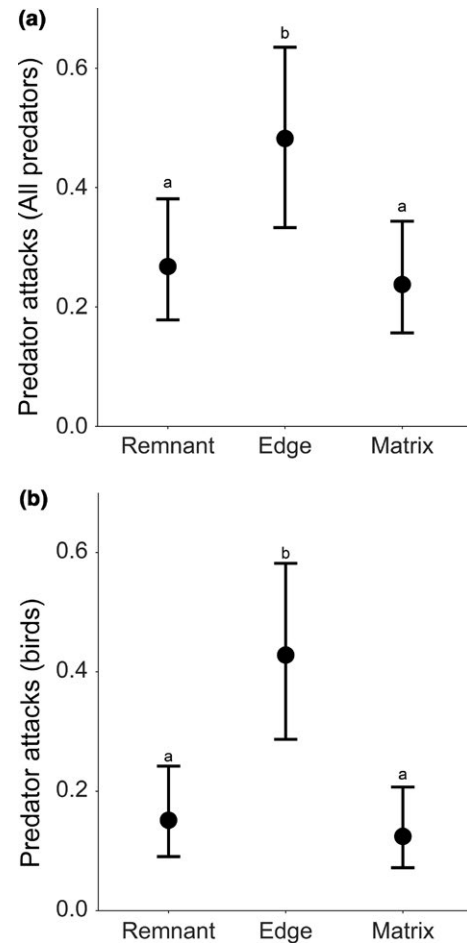


FIGURE 3 Significant interaction between habitat types and (a) all predators and (b) bird predators. Letters indicate post hoc pairwise contrasts. Different letters symbolize when contrasts are significantly different and error bars indicate 95% confidence intervals with fitted estimates plotted on the x-axis

habitats which were cleared dirt tracks and fence lines and subsequently more visible to predators compared to farmland and remnant patches.

Some of the bird species observed within our study (e.g., Laughing Kookaburra *Dacelo novaeguineae*, Australian Ravens *Corvus coronoides*, Pied Butcherbirds *Cracticus nigrogularis*, Australian Magpies *Cracticus tibicen*; Table 1) are known to take advantage of the elevated perching opportunities associated with human-made structures like fence posts at edges (Anderson & Burgin, 2008; Sewell & Catterall, 1998; Vander Haegen, Schroeder, & DeGraaf, 2002) and forage in both remnant patches and adjacent modified areas (Anderson & Burgin, 2008). Mammalian predators may take advantage of the concealment provided by adjacent woodland habitat, using edges as travel corridors (Andren, 1992; Bergin, Best, Freemark, & Koehler, 2000). Previous studies also have suggested some mammalian predators (e.g., Red Foxes *Vulpes vulpes*, mustelids; Table 1) show a preference for habitat edges compared to forest and farmland interiors (Šálek, Kreisinger, Sedláček, & Albrecht, 2009; Šálek et al., 2010). Our findings demonstrate predation risk is present in both the matrix and in

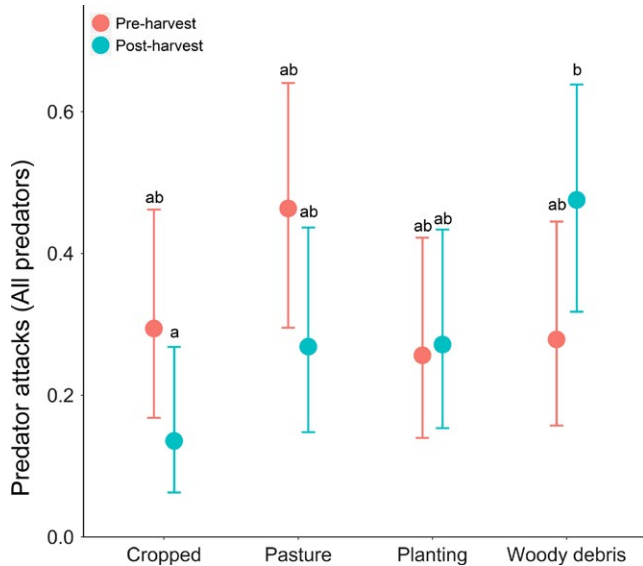


FIGURE 4 Significant relationships between habitat (a), harvesting and treatment (b), and the three-way interaction between treatment, habitat, and harvesting for predation attempts by all predators on plasticine models. Letters indicate post hoc pairwise contrasts. Different letters symbolize when contrasts are significantly different and error bars indicate 95% confidence intervals with fitted estimates plotted on the x-axis

remnant patches. These results likely reflect the foraging strategies of the generalist predator species observed and the degree of disturbance throughout the remnant patches within our study area. Remnant patches close to farmland edges are vulnerable to spillover of associated predator communities benefiting from crop systems (Andren, 1992; Rand et al., 2006; Vander Haegen et al., 2002) and is a process identified as a key driver of species decline within remnants (Matthews, Dickman, & Major, 1999; Saunders, Hobbs, & Margules, 1991). Surprisingly, we could not find published studies on the implications of spillover of predators from farmland on reptiles using patches, or adjacent matrix and suggests this is an area of fragmentation research that warrants critical attention.

4.2 | The influence of crop harvest on predation risk?

There are strong ecological reasons (Introduction, question 2) to expect harvesting of crops to increase predation attempts on models within crop fields (Cosentino et al., 2011; Purger et al., 2008; Thorbek & Bilde, 2004) and adjacent habitats (Schneider et al., 2013). We observed a trend for a decline in predation attempts after harvesting along the crop transect and an increase in the woody debris transect, leading to a significant difference between crops and woody debris after harvest (Figure 4). There may have been a transitory shift of predator populations into nearby woody mulch and remnant areas due to the rapid removal of resources in the crop paddock.

We found both mammalian and bird predators contributed to the high number of predation attempts on models in edge habitats prior

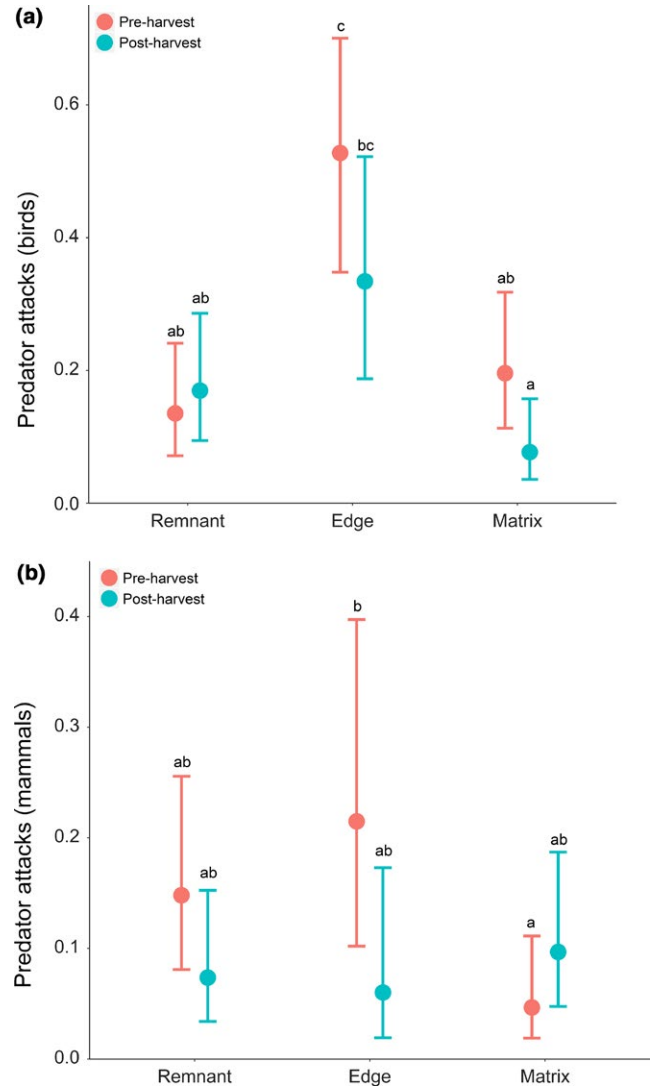


FIGURE 5 Significant interaction of habitat and harvesting from (a) bird predators and (b) mammal predators on gecko models. Letters indicate post hoc contrasts and error bars indicate 95% confidence intervals with fitted estimates plotted on the x-axis

to harvesting compared to the matrix, and compared to the lower attacks on models in the matrix and remnant patches after harvesting (bird predators only). We suggest predator breeding season—particularly for bird predators—may have intensified predation on lizard models within and nearby the agricultural matrix before harvesting. Our preharvesting surveys corresponded with the breeding period for many passerines within Australia (September–January; Howe, 1984). Previous studies attribute increased predation by birds on reptiles to the high density and opportunistic foraging behaviour of adults during the breeding season which may lead to reduced rates of predation when the breeding season ends and individuals move to other areas in the landscape (Castilla & Labra, 1998; Padilla, Nogales, & Marrero, 2007). We are unaware of any studies that causally link increased predation risk in edge habitat with avian breeding season, or if predator young of predators produced during the year contribute to observed trends, and suggest the mechanisms behind avian predatory

responses to changes in edge-farmland composition and landscape structure need to be further tested. However, the patterns of mammalian predator activity in modified landscapes are more likely related to abundances and distribution of main prey, rather than breeding season (Miller, Grand, Fondell, & Anthony, 2006; Šálek et al., 2010).

4.3 | Other responses: Use of scent on predators of replica models

The use of replica models is an important method for understanding potential risk of predation as treatments and sample size can be standardized, without compromising live specimens (Daly et al., 2008; Thompson et al., 2008). However, the detectability of plasticine models, particularly by mammals that rely on olfactory cues or those with a nocturnal foraging strategy, may be reduced because of their unnatural scent, or lack of scent (Bayne & Hobson, 1999; Major & Kendal, 1996). We attempted to counteract this possible bias by applying a natural gecko scent to a proportion of models, and testing whether an increase in the variety of predators could be detected. Our findings suggest the application of a natural gecko scent increases the detectability of plasticine models for olfactory-searching predators, including nocturnal foraging species such as the Yellow-footed Antechinus *Antechinus flavipes* and the Common Dunnart *Sminthopsis murina*. Both species were observed on camera footage, and attacked only the scented models. The scent likely increased the detectability of the model. However, some mammals are also neophilic and attracted to new or unusual scents (Bytheway, Price, & Banks, 2016; O'Connor, Morriss, & Murphy, 2005). Determining whether the responses we observed were a realistic predatory response to natural prey, or to a novel object would be a necessary next step to understanding the methodological accuracy for estimating predation risk.

4.4 | Management implications and future research

Understanding mechanisms underpinning the avoidance of particular habitat by reptiles can help identify habitats that may influence dispersal efficiency or movement (Driscoll et al., 2013; Whittingham & Evans, 2004) and inform management decisions to facilitate the persistence of reptiles in fragmented agricultural landscapes (Barton et al., 2015; Kay et al., 2016). Our study suggests predation risk—a key ecological driver of reptile movement (Daly et al., 2008; Sato et al., 2014)—can be significantly influenced by anthropogenic land use changes. Predation risk may further reduce the suitability of habitat for reptiles in agricultural areas (Driscoll et al., 2013; Sato et al., 2014). Our results show predation, from multiple predators, is highest at edges. These areas are already subject to extreme simplification and provide limited shelter from predators. Thus, reptiles may perceive these areas as high-risk, low-quality habitat and avoid them, or removal of individuals may reduce patch occupancy (Gehring & Swihart, 2003; Pita et al., 2007). Therefore, targeted management of edge habitats could influence species movements and potentially increase connectivity for some reptiles within agricultural areas. In a

previous study, we found reptile abundances to be highest in some of these edge habitats, and lowest within the adjacent farmland (N. A. Hansen, unpublished data). Based on this information, if reptiles accumulate at edges, and higher predation risk at edges may result in a population sink, then actions to reduce mortality risk within farmland may be important.

Vulnerability to predation may be increased by a lack of shelter within edge habitats increasing visibility of reptiles to predators (Anderson & Burgin, 2008; Sato et al., 2014). Reducing the hostility of edges by providing shelter (rocks, logs litter, and grasses) will offer refuge and provide stepping stones for reptiles between remnant patches and farmland (Manning et al., 2013; Michael, Cunningham, & Lindenmayer, 2011). Other studies have found that the lower stratum vegetation cover can provide shelter for reptiles from predators (Fischer, Lindenmayer, & Cowling, 2003; Michael et al., 2015). We also suggest increasing the ratio of interior area to edge in areas where dispersal might be important (e.g., by widening linear plantings) could reduce penetration of predators and improve the occurrence of reptiles within farmland (Graham, Maron, & McAlpine, 2013; Laurance & Yensen, 1991).

By providing new insights into why a target species might avoid a particular matrix type, our findings highlight important future research priorities. Dispersal and movement of a patch-dependent species between habitat patches may be altered by perceived predation risk in the matrix (Driscoll et al., 2013; Sato et al., 2014). A necessary next step is to examine if perceived predation risk influences an animal's willingness to move between patches or opportunistically utilize the matrix (Ewers & Didham, 2006; Rotem et al., 2013). Further, if lizards are attracted to edges because of basking opportunities and supplementary prey food resources from the adjacent farmland (Anderson & Burgin, 2008; Rotem et al., 2013), and as a result, are exposed to increased predation pressure, could edges act as a sinks and influence movement from patches.

Additionally, we are not aware of any studies specifically investigating the use of edges by predators and the consequences reptile populations in agroecosystems. We therefore suggest an important area of research is the need to establish the relative impacts of both native and exotic predators on reptile use of agricultural landscapes. For example, what is the impact of predation risk on reptile survival? Do mitigation measures to reduce predation risk in edge habitat (e.g., pest control of feral predators, or additional cover) improve reptile abundance in farmland? How far do predator's forage from edges (patch vs. farmland)? Is the effectiveness of plantings as habitat and for movement and the quality of remnant patches reduced due to predation risk at edges? Answering these questions will have consequences for the size and design of restoration areas and the management of remnant patches in croplands.

5 | CONCLUSIONS

Habitat fragmentation and loss has contributed to the decline of many reptile species world-wide. Our study demonstrates that edge

habitats are potentially “risky” for lizards, more so than the matrix. We suggest increasing shelter opportunities for lizards and to reducing the size of edges particularly where dispersal may be important (such as between remnants and linear plantings).

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AUTHORS' CONTRIBUTIONS

N.A.H. designed the study and methodology, collected the data, performed the lead writing and analysis. C.F.S. designed the study and edited. D.R.M. and D.B.L. edited. D.A.D. designed the study, assisted with the analysis, and edited. All authors confirm their approval for final publication of the manuscript.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.2f5v427> (Hansen, Sato, Michael, Lindenmayer, & Driscoll, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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