

Decline in semi-arid reptile occurrence following habitat loss and fragmentation

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ABSTRACT

Context. Habitat loss and fragmentation are leading causes of biodiversity decline worldwide. In Australia, woodland habitat has been extensively cleared and fragmented yet there has been limited research on the effects of habitat loss and fragmentation on semi-arid reptiles, impeding conservation planning and recovery efforts. **Aims.** We aimed to investigate factors influencing the distribution and occurrence of habitat specialist and generalist reptile species on a large agricultural holding in south-eastern Australia that has experienced habitat loss and fragmentation. **Methods.** Reptiles were surveyed using pitfall and funnel traps and active searches across 20 sites stratified by land use and vegetation type. Twelve sites were established in remnant woodland patches embedded within an agricultural matrix and eight sites were established in a private conservation reserve on the same property. Generalised linear models were used to explore relationships between the occurrence of eight reptile species and predictor variables describing site, landscape and vegetation variables. **Key results.** Of the 31 reptile species that were detected, eight were modelled. The results revealed that four specialist species, the eastern mallee dragon (*Ctenophorus spinodomus*), nobbi dragon (*Diporiphora nobbi*), barred wedge-snouted ctenotus (*Ctenotus schomburgkii*) and shrubland pale-flecked morethia (*Morethia obscura*), were closely associated with the conservation reserve, and that the southern spinifex ctenotus (*Ctenotus atlas*) had a strong association with spinifex (*Triodia scariosa*) dominated vegetation community. **Conclusions.** Reptile habitat specialists are particularly sensitive to habitat loss and fragmentation and are at a higher risk of local extinction compared with habitat generalists. Reptile occurrence was reduced in remnant woodland patches, but remnant patches also supported a suite of habitat generalists. **Implications.** A suite of semi-arid reptile species are sensitive to the effects of habitat loss and fragmentation and are susceptible to localised extinction. However, the presence of habitat generalists within woodland remnants highlights the value of retaining representative habitat patches in agricultural landscapes. Conservation of semi-arid woodland reptiles will depend on the retention of large tracts of protected vegetation across a broad range of soil types to maintain habitat heterogeneity and reptile diversity.

Keywords: agricultural intensification, generalist, habitat fragmentation, habitat relationships, landscape modification, mallee, reptile occurrence, semi-arid woodland, specialist.

Introduction

Human activities are causing extinction rates to increase rapidly (Haddad et al. 2015; Maxwell et al. 2016; Garnett et al. 2022). Approximately 28% of all species assessed by the International Union for Conservation of Nature are currently threatened with extinction (IUCN 2022). Habitat loss and fragmentation due to agricultural development is a major threat to biodiversity globally (Levy et al. 2010; Youngentob et al. 2013; Maxwell et al. 2016; Cox et al. 2022). Habitat fragmentation occurs as a direct result of habitat loss, where continuous native vegetation is divided into multiple, smaller, isolated patches (Fahrig 2003; Haddad et al. 2015; Keinath et al. 2017).

Following habitat loss and fragmentation, ecological communities within remnant patches are faced with isolation and disturbances that place some species at greater risk

of local extinction (Haddad *et al.* 2015). Loss of connectivity between patches can limit species dispersal, resulting in reduced gene flow and genetic diversity (Gibbs 2001; Jules and Shahani 2003). Elevated levels of disturbance by livestock and stochastic events (e.g. fire) can result in further changes in species composition (Doherty *et al.* 2020). A species' ability to survive in a fragmented landscape can be influenced by ecological traits, habitat requirements, and factors such as the composition, size, and type of remnant vegetation (Haddad *et al.* 2015; Keinath *et al.* 2017).

Australia has one of the highest levels of reptile diversity worldwide, accounting for approximately 10% of reptile species globally (Uetz *et al.* 2022; Tan *et al.* 2023). Habitat loss and fragmentation are two of the main causes of reptile decline in Australia (Tingley *et al.* 2019). However, reptiles remain one of the most poorly studied taxonomic groups among vertebrates in Australia (Slatyer *et al.* 2007; Thompson *et al.* 2016; Triska *et al.* 2017; Tingley *et al.* 2019). Unlike other terrestrial vertebrates, basic knowledge on species distributions and habitat requirements, for even common and widespread reptile species, are limited (Meiri and Chapple 2016; Tingley *et al.* 2016). In particular, the order Squamata, which includes lizards and snakes, has received relatively little scientific attention (Tingley *et al.* 2019), impeding conservation efforts.

Habitat specialists are often more susceptible to habitat loss and fragmentation than habitat generalists (Devictor *et al.* 2008; Keinath *et al.* 2017; Yan *et al.* 2022). The loss of habitat specialists that often accompanies habitat fragmentation (Driscoll 2004) can result in an influx of generalist species, potentially masking the decline of specialists (Matthews *et al.* 2014). Keinath *et al.* (2017) found specialist reptile species were highly sensitive to habitat fragmentation and although data on reptile species are limited, Doherty *et al.* (2020) suggest that reduced mobility may limit some reptile species ability to move between patches of remnant vegetation. Small-bodied habitat specialists such as arboreal geckos are often restricted to patches and are sensitive to habitat fragmentation (Hansen *et al.* 2020) compared with terrestrial habitat generalists, such as many widespread skink species, which often persist in modified agricultural landscapes (Jellinek *et al.* 2014; Michael *et al.* 2016; Pulsford *et al.* 2017).

The impact of habitat fragmentation on less vagile species can be exacerbated by matrix type (the dominant land use surrounding habitat patches) (Franklin and Lindenmayer 2009; Pulsford *et al.* 2017). Disturbance incurred from cropping and grazing practices can negatively affect reptile abundance and occurrence patterns (Doherty *et al.* 2020). Agricultural matrices can limit animal movement and therefore reduce dispersal by acting as a barrier (Driscoll *et al.* 2013; Hansen *et al.* 2020), while also increasing species vulnerability to predation (Hansen *et al.* 2019). Other properties of the matrix may also influence movements patterns. For example, Kay *et al.* (2016) found homing ability and movement patterns in the southern marbled gecko (*Christinus marmoratus*) to

be influenced by crop orientation. Remnant woodland patches embedded within grazing matrices may be impacted by grazing pressure and disturbance, resulting in reduced habitat quality (Driscoll 2004). Understanding how matrix conditions (e.g. disturbance regimes, habitat structure) affect the distribution and abundance of reptiles within patches is therefore important for understanding community composition in fragmented landscapes (Mulhall *et al.* 2022).

In south-eastern Australia, semi-arid woodland vegetation communities, including mallee woodland, support relatively high levels of reptile diversity compared with temperate woodland or riparian vegetation communities (Menkhorst and Bennett 1990). High-diversity patterns may be maintained by the presence of specific plant species, coupled with habitat heterogeneity (Clarke *et al.* 2021). Spinifex (*Triodia* sp.) is a dominant hummock-forming grass species found throughout arid Australia, particularly mallee woodland vegetation communities on sandy soils, and is considered a foundation species (Verdon *et al.* 2020). A number of studies have found strong association between *Triodia* cover and lizard distribution patterns (Nimmo *et al.* 2013; Sadlier *et al.* 2019; Bell *et al.* 2021a). However, *Triodia* structure and abundance can be negatively affected by soil compaction and elevated soil nutrients caused by agricultural activities (Bell *et al.* 2021b).

In this study, we aimed to investigate factors influencing the distribution and abundance of mallee woodland reptiles in a fragmented agricultural landscape that was cleared recently (~20 years ago) in western New South Wales (NSW), Australia. We posed three specific questions:

1. Which mallee woodland reptile species are sensitive to habitat fragmentation? We predicted that habitat specialists will be more sensitive to habitat fragmentation than habitat generalists, and therefore, will be absent or in lower abundance in remnant patches compared with a conservation reserve (hereafter referred to as reserve) (Michael *et al.* 2015; Keinath *et al.* 2017).
2. How important is the matrix (land use type) in explaining species distribution patterns? We predicted that in comparison with sites within patches surrounded by a grazing matrix, patches surrounded by a cropping matrix will support fewer species, especially fossorial species, due to the barrier effects of cropping activities on soil-dwelling species (Ricketts 2001; Fischer *et al.* 2005; Franklin and Lindenmayer 2009).
3. How important is vegetation type in explaining species distribution patterns? Given variation in vegetation communities across small spatial scales can influence reptile community composition, we predicted that species dependant on *Triodia scariosa* (a foundation plant species) will be restricted in distribution, whereas habitat generalists would be widespread across the study area (Verdon *et al.* 2020; Bell *et al.* 2021a).

Material and methods

Study area

The study was conducted on a mixed-agricultural property 12 km north of Balranald in south-eastern Australia (34°32'13"S, 143°31'11"E). The study area was selected due to the spatial configuration of remnant habitat in two agricultural land use types (cropping and grazing) coupled with a private reserve. Historically, the entire property was grazed by sheep (*Ovis aries*). In 1975, a large fire burnt through the entire property leaving only a small number of unburnt trees and resulting in relatively even-aged stands of regrowth. In 1998, a 4000-ha reserve was established on the property to offset a 3-year phase of land clearing for agricultural purposes, whereby all livestock grazing in the reserve ceased. Between 1998 and 2001, a network of remnant mallee patches was retained. Grazing occurs across the eastern section of the property and in 2003, crops were established on approximately half of the cleared land and sown biennially. During the study period, the cropping areas remained fallow and stocking levels were 1000 head of sheep per 1500 ha. Pest control, including 1080 baiting and lethal destruction via shooting, was applied throughout the cropping and grazing areas, targeting European red foxes (*Vulpes vulpes*), feral cats (*Felis catus*) and European rabbits (*Oryctolagus cuniculus*). No pest control was conducted in the reserve during the study period.

The main vegetation communities in the study area include sandplain mallee woodland (hereafter referred to as sandplain mallee) and dune mallee woodland (hereafter referred to as dune mallee). Mallee woodlands are widespread throughout the arid zone and have experienced significant habitat loss and extensive clearing due to the expansion of agricultural enterprises (Clarke *et al.* 2021). Sandplain mallee is dominated by yorrell (*Eucalyptus gracilis*) and oil mallee (*E. oleosa*) overstorey, on fertile red-brown soils with a shrubby understorey of various chenopod and *Acacia* sp. species (OEH 2022). Dune mallee is dominated by white mallee (*E. dumosa*) and slender-leaved red mallee (*E. leptophylla*) overstorey, typically containing a low soil clay content with deep red sand dunes supporting *T. scariosa* hummocks (OEH 2022). The climate is classified as semi-arid, the average annual rainfall is 323 mm and the mean minimum and maximum temperature ranges from 16.6 to 33.1°C in summer and 3.5 to 15.7°C in winter (BOM 2022).

Study design

In total, 20 sites were selected in this study (Fig. 1), classified as either reserve or patch. Eight sites were established within the reserve to serve as reference sites and 12 sites were established within patches of remnant vegetation and ranged in size from three to 21 ha (mean = 14 ha). Each site was further stratified by vegetation type (sandplain mallee or dune mallee) and dominant land use (continuous vegetation,



Fig. 1. Location of the study area in New South Wales, south-eastern Australia.

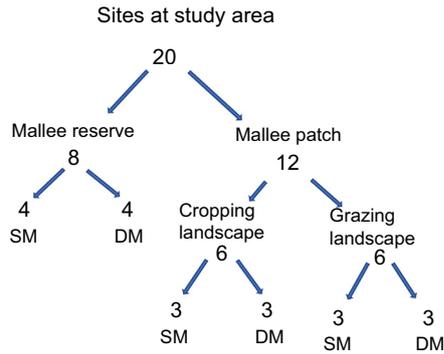


Fig. 2. Study design showing the spatial arrangement of the 20 survey sites stratified by site type. SM, sandplain mallee; DM, dune mallee.

cropland or grazing land) (Fig. 2). The distance between sites ranged from 900 m to 1510 m in the cropping landscape, 500 m to 1700 m in the grazing landscape and 400 m to 2400 m in the reserve, thus ensuring independence between sites and survey periods. Because we were primarily interested in sampling a wide variety of patches, area-controlled survey effort was not employed; instead, a single site was established within each patch. Time and budget constraints also prevented additional sites being established within the larger remnant patches. All sites were constrained to the same property to avoid confounding effects associated with potential differences in land management practices.

Survey protocol

At each site, reptiles were surveyed on three repeat occasions between November 2021 and February 2022 using pitfall and funnel traps (Baumgardt *et al.* 2021), with active searches of natural habitat constrained by time (1 h) and area (1 ha). Repeated surveying was conducted to minimise bias in species detection levels and account for potential issues associated with imperfect detection (MacKenzie *et al.* 2009). Active searches involved scanning the area for reptile activity (visual encounters), turning over and inspecting logs or debris, sifting through leaf litter and lifting loose bark on trees. Reptiles were captured by hand where possible, identified to species level using Wilson and Swan (2021) and released at their point of capture.

Trap arrays consisted of 3 × 20-L buckets spaced 15 m apart, connected by a 30-m drift fence (damp coarse), with two funnel traps (dimensions: 75 cm long × 18 cm wide × 18 cm high) placed either side at the 10-m and 20-m points along the fence. Funnel traps are a complementary method to pitfall traps because they often capture more snake species and larger-sized lizards (Thompson and Thompson 2007). In total, 25 trap nights were applied to each site during each of the three survey periods, amounting to 1500 trap nights (i.e. three buckets + two funnels × five nights × three surveys × 20 sites). Traps were checked each

morning and before sundown. In each bucket, a paper plate, sand and leaf litter were placed in the bottom to provide shelter to captured animals. Branches and leaf litter were placed on top of funnel traps to provide shade. A single trapping array was established at each site and positioned at least 50 m from the edge of the patches to avoid potential confounding associated with edge effects. Each individual reptile was weighed to the nearest g using a handheld spring scale (Persola) and calico bag, measured (total length and snout–vent–length) to the nearest mm using a ruler and sexed from external features when possible. Individuals were marked using a permanent marker pen to identify recaptures and released 5 m from their point of detection. Richgro® ant sand was applied around the pits and funnels, and all funnel traps were closed when temperatures were forecasted to exceed 33°C to minimise animal welfare issues.

Statistical analysis

Prior to modelling species occurrence, we investigated which species could be reliably detected at a site by using single season occupancy-detection models (MacKenzie *et al.* 2002), fit using the ‘unmarked’ package (Fiske and Chandler 2011). Species were considered at this stage if they occurred at >25% of sites and had a minimum of 10 detections. Occupancy–detectability models were fit to the repeated surveys ($n = 3$) with a single predictor variable for detectability indicating the survey method type: either pitfall/funnel trapping or active search. This generated a nightly detection probability for each of the two survey methods. Next, we calculated the cumulative probability of detecting each species, if present, across the 15 nights of pitfall/funnel trapping and the three active searches following Kéry (2002). To reduce the probability of false absences, we used a threshold adapted from Nimmo *et al.* (2014) where only species with >80% cumulative probability of being detected (if present) were included in subsequent modelling of presence/absence or abundance. Eight of the 10 species meeting the selection criterion met the cumulative detection probability threshold. All species were classified as either habitat generalists or specialists, specifically within the Murray–Darling Depression bioregion. Justification for the designation of species as habitat specialists or habitat generalists was based on the primary literature cited in Greer (2022), and macro and microhabitat accounts reported in Wilson and Swan (2021) and the Atlas of Living Australia (ALA) (2023) (see Supplementary Table S1). Thus, habitat specialists were species restricted to a specific type of vegetation community or microhabitat type within the specified bioregion.

Because we were interested in the influence of habitat loss and fragmentation on the presence/absence of reptile species, we fit a series of Generalised Linear Models (GLM) using logistic regression. The robust slider (*Lerista punctatovittata*) was present at 95% of sites, so models of presence/absence for

this species would not be informative. Instead, this species was modelled using abundance (count data) as the response variable, thus specifying a Poisson distribution. Patch size can influence species occurrence patterns; therefore, we first explored the relationship between patch area (ha) ($n = 12$) and species presence/absence. We then considered six additional GLMs for each species. The first model concatenated all categorical variables considered during the experimental design (site type \times vegetation type \times matrix type) to create a categorical variable with six levels. This model was supported if a species was sensitive to all three predictor variables. The second model included a four-level categorical variable that concatenated site type and vegetation type, the third model included a three-level categorical variable that captured the landscape matrix surrounding the site (i.e. continuous vegetation, cropland or grazing land), the fourth model included only vegetation type and the fifth model included only site type. The sixth model was a 'null' model and included only an intercept term and would be supported if the species did not respond significantly to any of the other predictor variables. Some models failed to converge due to complete separation and were therefore refit within a Bayesian framework using the `brglm` package (Kosmidis 2021).

Akaike's Information Criterion (AIC) was used to identify the best-performing model(s) for each species using the package 'AICcmodavg' (Mazerolle 2020). The AICc value was used to determine models with a considerable level of support. The AICc of candidate models were compared against the best model (lowest AICc) (Burnham and Anderson 2002). Models with AICc values < 2 were considered to have the greatest support in explaining species presence (and abundance for *L. punctatovittata*) (Burnham and Anderson 2002). The coefficient of determination (R^2) was calculated for each best fit model(s) to determine 'goodness of fit'. Model diagnostics were examined (QQ plots, residual vs predicted values) using DHARMAa package (Hartig 2022). Models with significant effects (P -value ≤ 0.05) were plotted using packages 'ggeffects' (Lüdtke 2018) and 'ggplot2' (Wickham 2016). All analysis was performed in R ver. 4.2.2 (R Core Team 2022).

Results

Summary statistics

In total, 480 individuals from 31 species and nine families were detected (Table 1). Acknowledging the uneven sampling effort between reserve and patch sites, we recorded a total of 332 individuals (69%) from 24 species in the eight reserve sites and 148 individuals from 12 sites in the remnant patches (17 species accounting for 73 individuals detected in the cropping matrix and 16 species with 75 individuals in the grazing matrix). The most abundant species was the eastern mallee dragon (*Ctenophorus spinodomus*), accounting for

114 observations (24% of total detections), followed by the eastern robust slider (*L. punctatovittata*; 70 observations) and dwarf three-toed slider (*Lerista timida*; 46 observations).

Nine species (29%) were recorded only in the reserve and accounted for 152 detections, whereas seven species (23%) were only found in patches and accounted for 18 detections. Species restricted to the reserve included *C. spinodomus*, nobbi dragon (*Diporiphora nobbi*), eastern stone gecko (*Diplodactylus vittatus*), eastern beaked gecko (*Rhynchoedura ormsbyi*), red-tailed worm-lizard (*Aprasia inaurita*), Mitchell's short-tailed snake (*Suta nigriceps*), royal ctenotus (*Ctenotus regius*), Bougainville's slider (*Lerista bougainvillii*) and the desert skink (*Liopholis inornata*). Species found exclusively in patches included the eastern thick-tailed gecko (*Underwoodisaurus milii*), eastern brown snake (*Pseudonaja textilis*), bandy bandy (*Vermicella annulata*), Bynoe's gecko (*Heteronotia binoei*), shingleback (*Tiliqua rugosa*), dark-spined blind snake (*Anilius bicolor*) and prong-snouted blind snake (*Anilius bituberculatus*). *L. punctatovittata* and *L. timida* were the only species detected across all treatments (see Fig. S1).

Detection probability by survey method

In total, 10 species met the criteria to be modelled, occurring at $> 25\%$ of sites with a minimum of 10 detections (Table 2). There was no significant difference in the probability of detection across survey methods for six species: barred wedge-snouted skink (*Ctenotus schomburgkii*); common dwarf skink (*Menetia greyii*); *L. punctatovittata*; sand goanna (*Varanus gouldii*); shrubland pale-flecked morethia (*Morethia obscura*); and the southern spinifex ctenotus (*C. atlas*). Four species, *D. nobbi*, *M. boulengeri*, *L. timida* and *C. spinodomus*, were significantly less likely to be detected using pitfall/funnel traps compared with active searches (see Table S2). The cumulative detection probability for the pitfall/funnel trap nights and three active searches revealed that eight of the 10 species satisfied the requirements of having a $> 80\%$ chance of being detected given their presence at a site (Table 2).

Model selection

We found no significant relationships between patch size ($n = 12$) and occurrence patterns for any species. Therefore, patch size was not included in subsequent model building. The model with site type (reserve or patch) was the best-fitting model for *C. spinodomus*, *D. nobbi*, *C. schomburgkii* and *M. obscura* (Table 3). All four species were more likely to occur in the reserve (probability of occurrence 75%+) compared with patches (Table 4, Fig. 3a–d). The landscape matrix model (continuous, cropping or grazing) was supported by *C. schomburgkii* and *M. obscura* (Table 3). Both species were more likely to be detected in continuous vegetation followed by patches in the grazing matrix (Table 4, Fig. 4a, b). The only

Table 1. Total number of observations for all reptile species classified according to site type (patch versus reserve) between November 2021 and February 2022.

| Common name | Scientific name | Agricultural patches | Conservation reserve | Total count |
|---------------------------------|--------------------------------|----------------------|----------------------|-------------|
| Agamidae | | | | |
| Eastern Mallee Dragon | <i>Ctenophorus spinodomus</i> | 0 | 113 | 113 |
| Nobbi Dragon | <i>Diporiphora nobbi</i> | 0 | 24 | 24 |
| Eastern Bearded Dragon | <i>Pogona barbata</i> | 3 | 2 | 5 |
| Carphodactylidae | | | | |
| Common Thick-tailed Gecko | <i>Underwoodisaurus milii</i> | 3 | 0 | 3 |
| Diplodactylidae | | | | |
| Eastern Stone Gecko | <i>Diplodactylus vittatus</i> | 0 | 6 | 6 |
| Beaded Gecko | <i>Lucasium damaeum</i> | 3 | 7 | 10 |
| Eastern Beaked Gecko | <i>Rhynchoedura ormsbyi</i> | 0 | 2 | 2 |
| Southern Spiny-tailed Gecko | <i>Strophurus intermedius</i> | 1 | 4 | 5 |
| Elapidae | | | | |
| Eastern Brown Snake | <i>Pseudonaja textilis</i> | 3 | 0 | 3 |
| Mitchell's Short-tailed Snake | <i>Suta nigriceps</i> | 0 | 1 | 1 |
| Common Bandy Bandy | <i>Vermicella annulata</i> | 1 | 0 | 1 |
| Gekkonidae | | | | |
| Variegated Dtella | <i>Gehyra versicolor</i> | 5 | 0 | 5 |
| Bynoe's Gecko | <i>Heteronotia binoei</i> | 2 | 4 | 6 |
| Pygopodidae | | | | |
| Red-tailed Worm-lizard | <i>Aprasia inaurita</i> | 0 | 2 | 2 |
| Spinifex Delma | <i>Delma butleri</i> | 1 | 1 | 2 |
| Burton's Legless Lizard | <i>Lialis burtonis</i> | 3 | 1 | 4 |
| Scincidae | | | | |
| Southern Spinifex Ctenotus | <i>Ctenotus atlas</i> | 14 | 12 | 26 |
| Short-clawed Ctenotus | <i>Ctenotus brachyonyx</i> | 1 | 10 | 11 |
| Royal Ctenotus | <i>Ctenotus regius</i> | 0 | 1 | 1 |
| Barred Wedge-snouted Ctenotus | <i>Ctenotus schomburgkii</i> | 1 | 12 | 13 |
| Bougainville's Slider | <i>Lerista bougainvillii</i> | 0 | 1 | 1 |
| Eastern Robust Slider | <i>Lerista punctatovittata</i> | 46 | 24 | 70 |
| Dwarf Three-toed Slider | <i>Lerista timida</i> | 25 | 21 | 46 |
| Desert Skink | <i>Liopholis inornata</i> | 0 | 1 | 1 |
| Common Dwarf Skink | <i>Menetia greyii</i> | 6 | 11 | 17 |
| Boulenger's Morethia | <i>Morethia boulengeri</i> | 3 | 10 | 13 |
| Shrubland Pale-flecked Morethia | <i>Morethia obscura</i> | 1 | 29 | 30 |
| Shingleback | <i>Tiliqua rugosa</i> | 1 | 0 | 1 |
| Typhlopidae | | | | |
| Dark-spined Blind Snake | <i>Anilius bicolor</i> | 1 | 0 | 1 |
| Prong-snouted Blind Snake | <i>Anilius bituberculatus</i> | 3 | 0 | 3 |
| Varanidae | | | | |
| Sand Goanna | <i>Varanus gouldii</i> | 16 | 4 | 20 |
| Total Records | | 148 | 332 | 480 |

Counts exclude recaptured animals and include data from both survey methods (active searches and pitfall/funnel trapping).

Table 2. Summary of detection probabilities for 10 reptile species by survey method.

| Species | Cumulative detection probability (%) | Trapping detection probability (%) | Active search detection probability (%) |
|--------------------------------|--------------------------------------|------------------------------------|---|
| <i>Ctenotus schomburgkii</i> | 92.9 | 15.5 | 3.9 |
| <i>Morethia boulengeri</i> | 59.4 | 2.3 | 17.0 |
| <i>Menetia greyii</i> | 53.4 | 4.3 | 3.6 |
| <i>Lerista timida</i> | 86.3 | 8.0 | 21.7 |
| <i>Ctenophorus spinodomus</i> | 100 | 31.1 | 72.2 |
| <i>Lerista punctatovittata</i> | 94.9 | 18.0 | 0.0 |
| <i>Diporiphora nobbi</i> | 96.0 | 12.8 | 32.0 |
| <i>Varanus gouldii</i> | 92.9 | 15.5 | 3.9 |
| <i>Morethia obscura</i> | 96.5 | 14.7 | 27.6 |
| <i>Ctenotus atlas</i> | 97.1 | 20.4 | 4.6 |

model with substantial support for *C. atlas* and *L. timida* was the vegetation-type model (sandplain mallee or dune mallee) (Table 3). *Ctenotus atlas* was significantly more likely to occur in dune mallee (Table 4, Fig. 4c), whereas *L. timida* was more likely to occur in sandplain mallee, although the difference was not significant (Table 4, Fig. 4d). The site and vegetation-type model had substantial support from *M. obscura* and *V. gouldii* (Table 3). *M. obscura* was most likely to occur in sandplain mallee reserve sites and was least likely to occur in sandplain mallee patches (Table 4, Fig. 4e). *Varanus gouldii* was most likely to occur in dune mallee vegetation patches (Table 4, Fig. 4f). The best-performing model that explained *L. punctatovittata* abundance included site type × vegetation type × matrix type (Table 3). *Lerista punctatovittata* was significantly more abundant in dune mallee patches surrounded

by cropland and sandplain mallee in the reserve (Table 4, Fig. 4g). Confidence intervals around these predictions are wide in many instances.

Discussion

Our study provides insight into which reptile species are potentially vulnerable to habitat loss and fragmentation in an arid zone landscape, with two species, *M. obscura* and *C. schomburgkii*, being rarely detected in remnant patches and *C. spinodomus* and *D. nobbi* being absent from remnant patches. We found support for our prediction that habitat loss and fragmentation would have greater impacts on habitat specialists, but less support for matrix or vegetation-type effects. Although habitat fragmentation can lead to a decline in habitat specialists, small remnant patches of mallee woodland provide important habitat for generalist reptile species.

Which species are sensitive to habitat fragmentation?

Reptiles are often highly sensitive to habitat loss and fragmentation (Keinath et al. 2017). Of the eight species we modelled, five species were classified as habitat specialists (*C. spinodomus*, *D. nobbi*, *C. schomburgkii*, *C. atlas* and *M. obscura*). Of these species, *C. spinodomus*, *D. nobbi*, *C. schomburgkii* and *M. obscura* were significantly associated with the reserve, with between 73% and 83% probability of occurring in the reserve and only 3–10% probability of occurring in patches. These results are consistent with previous studies on mallee reptiles in south-central NSW, where *D. nobbi* (syn. *Amphibolurus nobbi*), *M. obscura* and *C. schomburgkii* were found to be biased towards a mallee woodland reserve and *C. spinodomus* (syn. *Ctenophorus fordii*) was detected exclusively within a reserve (Driscoll 2004).

Table 3. Summary of the GLM results examining reptile presence (or abundance) and predictor variables.

| Species | Model | K | AICc | Δi | Modellik | wi | LL | Cumulative wi | R ² |
|--------------------------------|------------------------------------|---|--------|-------|----------|-------|---------|---------------|----------------|
| <i>Ctenophorus spinodomus</i> | Site type | 2 | 13.703 | 0.000 | 1.000 | 0.648 | -4.499 | 0.648 | 0.632 |
| <i>Diporiphora nobbi</i> | Site type | 2 | 10.734 | 0.000 | 1.000 | 0.727 | -3.014 | 0.727 | 0.767 |
| <i>Ctenotus schomburgkii</i> | Site type | 2 | 20.587 | 0.000 | 1.000 | 0.601 | -7.941 | 0.601 | 0.387 |
| <i>Ctenotus schomburgkii</i> | Matrix type | 3 | 21.904 | 1.317 | 0.518 | 0.311 | -7.202 | 0.912 | 0.444 |
| <i>Morethia obscura</i> | Site type | 2 | 20.587 | 0.000 | 1.000 | 0.419 | -7.941 | 0.419 | 0.387 |
| <i>Morethia obscura</i> | Matrix type | 3 | 21.904 | 1.317 | 0.518 | 0.217 | -7.202 | 0.887 | 0.444 |
| <i>Morethia obscura</i> | Site type × veg type | 4 | 21.619 | 1.031 | 0.597 | 0.250 | -5.476 | 0.670 | 0.577 |
| <i>Lerista timida</i> | Veg type | 2 | 16.923 | 0.000 | 1.000 | 0.655 | -6.109 | 0.655 | 0.277 |
| <i>Ctenotus atlas</i> | Veg type | 2 | 16.923 | 0.000 | 1.000 | 0.937 | -6.109 | 0.937 | 0.528 |
| <i>Varanus gouldii</i> | Site type × veg type | 4 | 27.025 | 0.000 | 1.000 | 0.516 | -8.179 | 0.516 | 0.392 |
| <i>Lerista punctatovittata</i> | Site type × veg type × matrix type | 6 | 83.000 | 0.000 | 1.000 | 0.946 | -32.297 | 0.946 | 0.812 |

The AICc and Δi outputs identify best-performing model(s) and models with substantial support (Δi < 2). The coefficient of determination is also represented as R².

Table 4. Summaries of the best-performing regression models predicting the probability of occurrence for eight reptile species.

| Species | Model | Variable | Estimate | s.e. | z-value | Pr(> z) |
|--------------------------------|--|---------------------------|----------|-------|---------|--------------|
| <i>Ctenophorus spinodomus</i> | Site type | (Intercept) | 0.956 | 0.789 | 1.211 | 0.226 |
| | | Patch | -4.174 | 1.696 | -2.461 | 0.014 |
| <i>Diporiphora nobbi</i> | Site type | (Intercept) | 1.609 | 0.949 | 1.696 | 0.090 |
| | | Patch | -4.828 | 1.776 | -2.719 | 0.007 |
| <i>Ctenotus schomburgkii</i> | Site type | (Intercept) | 1.099 | 0.817 | 1.346 | 0.178 |
| | | Patch | -3.497 | 1.326 | -2.637 | 0.008 |
| <i>Ctenotus schomburgkii</i> | Landscape matrix | (Intercept) | 0.956 | 0.789 | 1.211 | 0.226 |
| | | Cropping | -3.521 | 1.771 | -1.988 | 0.047 |
| | | Grazing | -2.255 | 1.270 | -1.775 | 0.076 |
| <i>Morethia obscura</i> | Site type | (Intercept) | 1.099 | 0.817 | 1.346 | 0.178 |
| | | Patch | -3.497 | 1.326 | -2.637 | 0.008 |
| <i>Morethia obscura</i> | Landscape matrix | (Intercept) | 0.956 | 0.789 | 1.211 | 0.226 |
| | | Cropping | -3.521 | 1.771 | -1.988 | 0.047 |
| | | Grazing | -2.255 | 1.270 | -1.775 | 0.076 |
| <i>Morethia obscura</i> | Site type × vegetation type | (Intercept) | 2.197 | 1.667 | 1.318 | 0.187 |
| | | Reserve dune mallee | -2.197 | 1.944 | -1.130 | 0.258 |
| | | Patch sandplain mallee | -4.762 | 2.300 | -2.070 | 0.038 |
| | | Patch dune mallee | -3.497 | 1.941 | -1.801 | 0.072 |
| <i>Lerista timida</i> | Vegetation type | (Intercept) | 3.045 | 1.518 | 2.005 | 0.045 |
| | | Dune mallee | -2.282 | 1.663 | -1.372 | 0.170 |
| <i>Ctenotus atlas</i> | Vegetation type | (Intercept) | -3.045 | 1.518 | -2.005 | 0.045 |
| | | Dune mallee | 3.807 | 1.663 | 2.289 | 0.022 |
| <i>Varanus gouldii</i> | Site type × vegetation type | (Intercept) | 0.000 | 1.000 | 0.000 | 1.000 |
| | | Reserve dune mallee | -2.197 | 1.944 | -1.130 | 0.258 |
| | | Patch sandplain mallee | -1.299 | 1.411 | -0.921 | 0.357 |
| | | Patch dune mallee | 1.299 | 1.411 | 0.921 | 0.357 |
| <i>Lerista punctatovittata</i> | Site type × vegetation type × landscape matrix | (Intercept) | 1.504 | 0.175 | 8.578 | 0.000 |
| | | Reserve dune mallee | -1.099 | 0.351 | -3.133 | 0.007 |
| | | Cropping dune mallee | 0.765 | 0.223 | 3.425 | 0.004 |
| | | Grazing dune mallee | -0.523 | 0.316 | -1.655 | 0.120 |
| | | Cropping sandplain mallee | -1.504 | 0.464 | -3.242 | 0.006 |
| | | Grazing sandplain mallee | -0.811 | 0.351 | -2.312 | 0.036 |

Bold values are significant at $P < 0.05$.

Driscoll (2004) concluded that *D. nobbi* and *C. spinodomus* are extremely sensitive to fragmentation, occurring in high abundances in the reserve while being absent from patches. By contrast, Driscoll and Hardy (2005) found genetic evidence indicating high dispersal and migration in *D. nobbi* from a reserve within a fragmented agricultural landscape to ungrazed linear remnants. It is possible that the patches in our study were too widely spaced (averaging 1000 m) between neighbouring patches, or the reserve, to enable sufficient dispersal and maintain viable populations within remnant patches, or that disturbance by livestock grazing (and trampling) influenced shelter and breeding site suitability.

The habitat specialist, *C. atlas*, was the only species that was not significantly associated with the reserve. This may be due to *C. atlas* having the ability to disperse through fragmented landscapes or because its requirements of mid to late post-fire successional stage *Triodia* cover were met within patches dominated by dune mallee (Smith et al. 2011; Verdon et al. 2020).

Three of the eight species modelled were classified as habitat generalists (*V. gouldii*, *L. timida* and *L. punctatovittata*). These three species were widespread across the study area. *L. punctatovittata* occurred at 100% of patches and *L. timida* and *V. gouldii* occurred at 83% and 50% respectively,

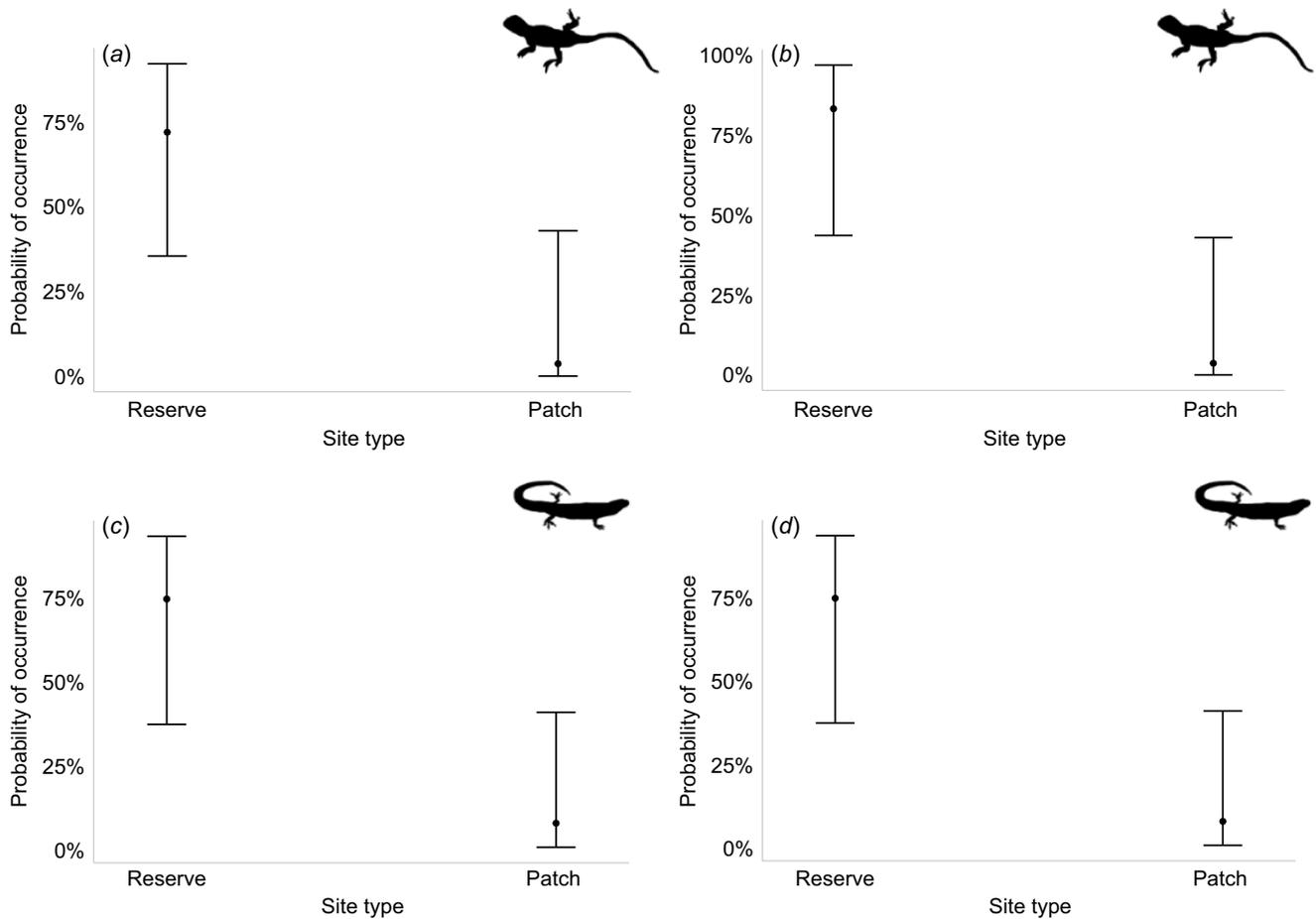


Fig. 3. The probability of occurrence of (a) *Ctenophorus spinodomus*, (b) *Diporiphora nobbi*, (c) *Ctenotus schomburgkii* and (d) *Morethia obscura* between reserve and patch sites. Error bars represent 95% confidence intervals.

suggesting these species are less vulnerable to processes associated with habitat loss and fragmentation. Furthermore, we found *L. punctatovittata* was significantly more abundant in dune mallee patches in the cropping landscape compared with any other site type. *L. punctatovittata* is a nocturnal, fossorial species associated with extensive leaf litter (Henle 1989). Driscoll (2004) found this species attained extremely high numbers along linear roadsides, conceivably due to increased nutrients and food resources. Cultivation around patches may act as a barrier to dispersal and reduced competition for resources with specialists could also explain the higher numbers observed. *Lerista punctatovittata* also responds positively to destocking (Neilly *et al.* 2021), so another plausible explanation is that this species has increased in response to the reduced level of grazing pressure across the property.

How important is the matrix?

The matrix can have a substantial influence on ecological communities and species distribution patterns (Michael *et al.* 2008; Munguia-Vega *et al.* 2013). Cropland in particular can

act as a barrier to reptiles and restrict movement among remnant vegetation (Kay *et al.* 2016; Hansen *et al.* 2020). We predicted that patches in the cropping matrix would have lower occurrence rates than continuous vegetation (reserve) or patches in the grazing matrix. However, we found little difference in species occurrence patterns in patches among matrix types. Matrix type only featured in the models for *C. schomburgkii* and *M. obscura*, where both species were more likely to occur in sites surrounded by continuous vegetation and therefore were more likely to occur in the reserve. The limited support for our prediction could be attributed to the relatively small sample size, lack of replication, relatively recent land clearing and potentially confounding influence of unmeasured disturbances. Structural similarities and the same time since clearing between cropping and grazing matrices may indicate similar ecological impacts on reptiles. Pulsford *et al.* (2017) found that the intensity of matrix use for agricultural purposes was more important than matrix type itself in predicting reptile distribution patterns in temperate woodland landscapes. Therefore, improving matrix quality and appropriately

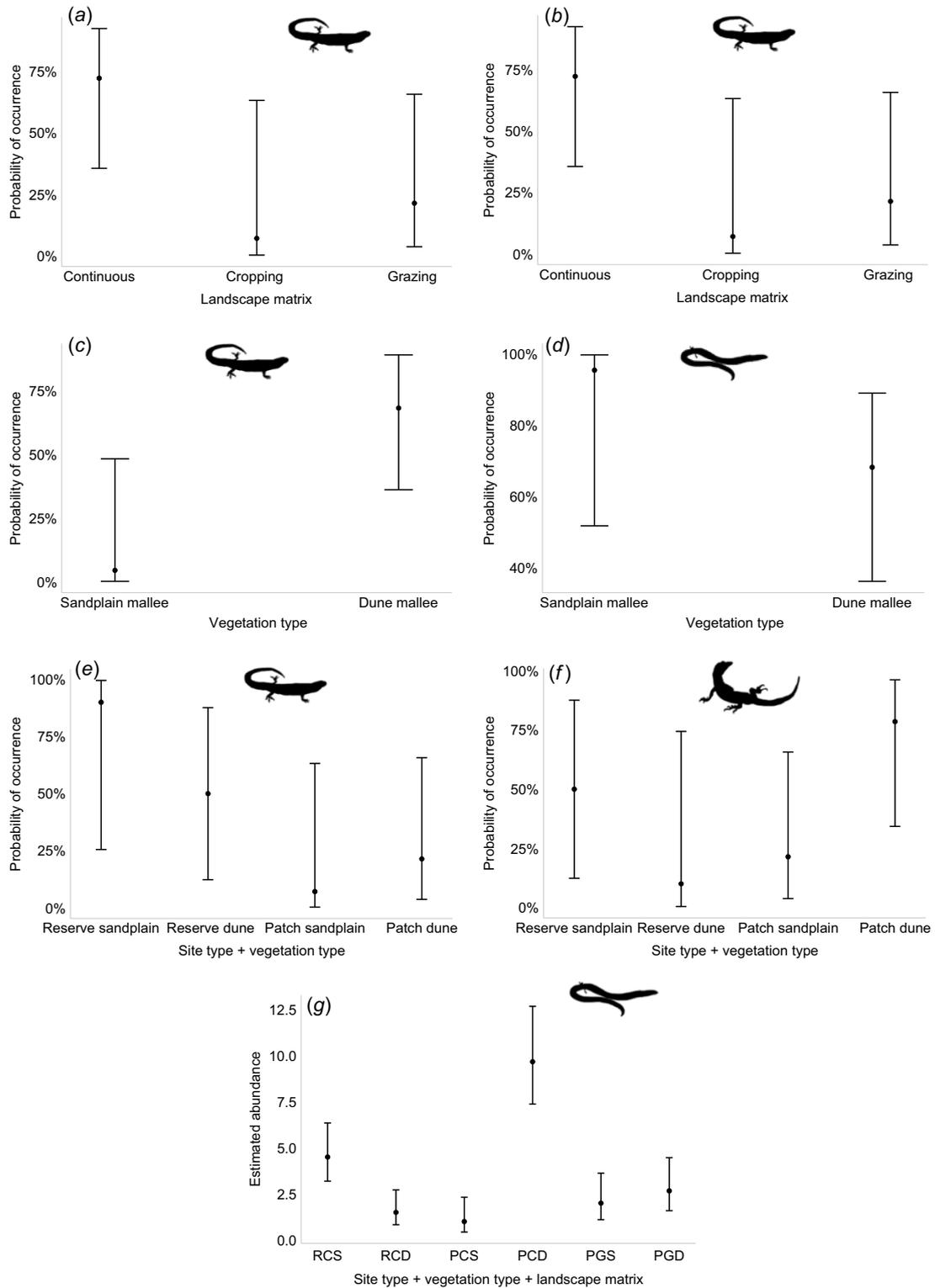


Fig. 4. The probability of occurrence of: (a) *C. schomburgkii* and (b) *M. obscura* on sites surrounded by continuous, cropping or grazing land use types; (c) *C. atlas* and (d) *L. timida* in sandplain mallee or dune mallee vegetation type; (e) *M. obscura* and (f) *V. gouldii* in site and vegetation type combinations; and (g) *L. punctatovittata* estimated abundance across treatments (RC, reserve continuous; PC, patch cropping; PG, patch grazing; S, sandplain; D, dune). Error bars represent 95% confidence intervals.

designed matrix improvements can help increase conservation outcomes in modified landscapes (Franklin and Lindenmayer 2009; Driscoll *et al.* 2013).

How important is vegetation type in explaining species distribution patterns?

At large spatial scales, reptile communities are strongly influenced by vegetation communities. Sass (2006) found that mallee sites supporting *Triodia* maintained higher abundance and diversity of reptile species than areas without *Triodia*. We predicted that habitat specialists would be restricted to dune mallee, due to the presence of *Triodia*, whereas habitat generalists would be distributed across vegetation types. We found support for this prediction for *C. atlas*, which was associated with dune mallee. This pattern is consistent with previous studies that found *Triodia* cover to be an important predictor of *C. atlas* occurrence (Verdon *et al.* 2020; Bell *et al.* 2021a). We found limited support for a vegetation type effect for *C. spinodomus*, a species reported to have affiliations with early–mid stage *Triodia* cover (Nimmo *et al.* 2012; Sadlier *et al.* 2019; Verdon *et al.* 2020). However, the lack of a vegetation type relationship in our study may be due to the species' complete absence from patches, including those with *Triodia*, hence the overriding effect of fragmentation. The only other species that exhibited a vegetation type effect was *M. obscura*, which was most likely to occur in sandplain mallee within the reserve. Preference for chenopod-dominated vegetation communities with open canopies and abundant leaf litter are consistent with documented habitat relationships for this species (Triska *et al.* 2016; Dundas *et al.* 2021).

Management implications

There are several broader management implications that stem from this study. First, offsetting habitat loss by establishing in-perpetuity conservation areas representative of the vegetation communities affected by agricultural intensification is an important factor in preserving reptile diversity on private land. Second, remnant patches within cleared areas could be better managed to improve habitat suitability for reptile specialists. Although we were unable to explain the mechanisms behind the decline in habitat specialists in this study, strong habitat affiliations with foundation species such as *Triodia* suggest that declining habitat condition and/or extent could be responsible. *Triodia* cover can be substantially altered due to agricultural activities, especially soil compaction and increased soil nutrients (Bell *et al.* 2021b). Fencing remnants to control livestock grazing pressure immediately following habitat fragmentation may help to preserve ground cover condition (Pulsford *et al.* 2017). Small-scale ecological burns could also be trialled to promote *Triodia* growth and post-fire seral stages. Third, improved matrix management through managing stocking levels and strategically orientating crops

(Kay *et al.* 2016) could reduce barrier effects between remnants. Lastly, future research could trial small-scale translocations (Watson and Watson 2015) to investigate the feasibility of recovering locally extinct species.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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