Using referential alarm signals to remotely quantify ‘landscapes of fear’ in fragmented woodland

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ABSTRACT

Land-use changes have greatly impacted biodiversity and led to new conservation challenges, including greater predation pressure, although this can be difficult to quantify. Here we directly monitor predator encounters in fragmented woodlands by using passive acoustic monitoring (PAM) and a semi-automated assessment protocol to detect functionally referential alarm vocalisations of the noisy miner *Manorina melanopephala*. We demonstrate that measuring changes in perceived predation pressure, the so-called ‘landscape of fear’, in a prey species across temporal (dawn, midday, dusk across multiple seasons) and spatial scales (small/large fragments and edge/centre locations within fragments) is achievable. Vocalisations linked with ground predator presence were rarer during midday recordings, but more commonly detected from the edge rather than centre of smaller fragments. While the probability of detecting aerial alarm calls directed at flying raptors also increased in edge habitat, aerial alarm detections declined from a dawn peak to a minimum during dusk recordings. These patterns did not simply reflect noisy miner occupancy or different sections of monitored patches, but highlighted higher perceived predation risk along edges, particularly for small patches, demonstrating the nuanced insights that PAM can offer when quantifying animal behaviour.

Introduction

Anthropogenic impacts leading to habitat change provide one of the biggest threats to maintaining biodiversity worldwide, potentially impacting large areas following changing climatic conditions (Bellard et al. 2012), through to rapid, direct habitat loss associated with land-use change (Fahrig 2017). The large impacts of the latter have been an area of concern for decades (Saunders et al. 1991), and at present truly untouched areas are extremely rare (Allan et al. 2017). Developing efficient monitoring tools to map and understand these changes is therefore critical to future conservation efforts.
New tools for monitoring biodiversity can be determined using well-established traditional surveys, and/or a range of passive options that are being increasingly deployed, such as the use of e-DNA, passive acoustic monitoring (PAM), or camera trapping (Fleming et al. 2014; Thomsen and Willerslev 2015; Marchal et al., 2021). Despite these advances, finer-scale information on changes in animal behaviour following habitat fragmentation remains difficult to obtain. Detailed data from tagged individuals is ideal for this purpose, but is often prohibitively expensive to deploy and entails the use of an invasive technique (Walker et al. 2011; Griffin et al. 2020). PAM offers a potentially more cost-effective and less invasive approach, particularly when animal vocalisations encode a rich variety of information.

One factor that can have profound impacts on biodiversity following habitat fragmentation is changes in predator behaviour. Predator presence and behaviour is a key influence across a range of ecosystem characteristics, including cryptic impacts on the physiology, movement and connectivity of prey species that are relevant when considering the impacts of fragmentation (Gaynor et al. 2019). Indeed, in an experimental setting, the potential threat of predation had a greater impact on populations than direct predation itself (Preisser et al. 2005; Smith et al. 2015; Grade et al. 2021). Collectively, these non-lethal, or non-consumptive impacts of predation have become known as the ecology or ‘landscape of fear’, where spatial variation in the perceived predation risk exists among prey (Brown et al. 1999; Gaynor et al. 2019). This landscape of fear is impacted by changes in predator behaviour, and therefore can vary markedly for a given location, either temporally or as a result of site-level changes, such as habitat fragmentation (Laundré et al. 2001; Whytock et al. 2020). Understanding and quantifying these predator–prey relationships is important, as considerable biodiversity impacts can occur as a result of fear, with prey potentially reducing the time that they devote to foraging, or moving into sub-optimal areas to minimise predation risks at the expense of short-term nutritional needs (Lima 2002; Cresswell 2008). For example, perceived threats of grey wolf (Canis lupus) predation can impact elk (Cervus canadensis) foraging to the point where measurable vegetation structure changes occur in the environment (Fortin et al. 2005). Indeed, even the acoustic simulation of predators, without visual confirmation, is enough to measurably impact the mean body mass of great tits (Parus major; Abbey-Lee et al. 2016). These examples highlight the importance of gaining a detailed appreciation of the landscape of fear to which animals are responding, as data on predation rates or the presence/absence of potential predatory taxa alone is not always sufficient to understand local biodiversity and habitat quality (Brown et al. 1999).

Understanding landscapes of fear is particularly important in modified landscapes, where predator activity is frequently suggested to be more focused on edge areas (Chalfoun et al. 2002; Lariviere 2003). Any targeting of specific habitat such as this following habitat modification may undermine the potential conservation value of remaining areas in fragmented landscapes, however a reliable means of quantifying landscapes of fear is not always apparent and new approaches are needed (Moll et al. 2017). Typically, experimental cues of predation, such as predator vocalisation playback, are used to stimulate fear, however this approach fails to include consumptive effects of predation, and is often conducted at unnaturally high levels that may yield atypical results (Peers et al. 2018). The use of PAM as an alternative to monitor predator–prey interactions in situ offers an approach that is both passive and also able to be deployed on
very large scales (Blumstein et al. 2011; Roe et al. 2021). As techniques to improve the analysis of large acoustic datasets become increasingly available (e.g. Sueur et al. 2014; Leseberg et al. 2020; Marchal et al., 2021), this approach offers great potential for monitoring landscapes of fear.

To achieve this, detailed information on the appropriate sounds to monitor is required. Instead of monitoring predators directly, listening for changes in the calling behaviour of potential prey offers a more effective acoustic assessment of predator–prey interactions, and this has been used successfully to monitor alarm vocalisations in woodland fragments within an agricultural landscape (Whytock et al. 2020). In species with multiple alarm calls, additional detailed information is often encoded in different signals, including predator distance from the caller (Dutour et al. 2021), or information on the type of predator (Cheney and Seyfarth 1990; Bugnyar et al. 2001) that PAM can also quantify to develop fine-scaled landscapes of fear.

In the woodlands of south-eastern Australia, the alarm vocalisations of a colonial, highly vocal bird provide a perfect species to examine the feasibility of this approach: the aptly named noisy miner (Manorina melanocephala). Noisy miners are an edge specialist that preferentially occupy fragmented habitats (Clarke and Oldland 2007; Barati et al. 2016), key landscapes that are likely impacted by changing predator behaviour shifts driven following habitat fragmentation. Miners are highly cooperative across a range of social contexts, with this behaviour being facilitated by a highly complex vocal repertoire (Holt et al. 2017) that includes regular chip contact calls that can be used to document their presence (Holt et al. 2017). Further, miners have functionally referential alarm vocalisations; predators on the ground such as quadrupedal mammals elicit chur calls, whilst aerial predators such as raptors stimulate aerial alarm vocalisations (Holt et al. 2017; Farrow et al. 2017). These call types are individually distinctive, readily identifiable, and have been experimentally demonstrated to be referential (Farrow et al. 2017; Cunningham and Magrath 2017). Further, miners reliably vocalise in the presence of predators, and share the same predator guild as many co-occurring taxa, allowing extrapolation from noisy miner perceived predation risks to those of other woodland birds. We therefore used these acoustic traits to remotely monitor perceived predator encounters by noisy miners across a fragmented habitat, where anthropogenic habitat changes had created numerous edges and patches of varying size. We aimed to explore the potential for PAM to extract detailed information on the vocal behaviour of miners, and by extension the landscape of fear within the sampled areas.

**Methods**

**Study site**

To assess differences in alarm calling behaviour of birds occupying different habitats, a total of 24 passive acoustic sensors (SM2+, Wildlife Acoustics, Maynard, USA) were deployed in the New England Tablelands region of north-eastern New South Wales, Australia (Table 1) between 25th May and 19 September 2014. Sensors were deployed in fragments of open woodland habitat of varying size, namely 12 ‘small’ and 12 ‘large’ fragments. Small fragments were remnants that were no more than 200 metres across at their widest point, whilst the large fragments were greater than this when measured using
Table 1. The 12 study sites used in the experiment, with an indication of whether the area was classified as either a small (200 m or less) versus large fragment (over 200 m at the widest point), and whether the passive bioacoustic recorder was placed at either the edge habitat (within 10 m of the edge trees of a fragment) or centre of fragments. The widest point of fragments is listed under size in kilometres.

| Site          | Fragment Site | Size Class | Size | PAM location   | GPS Location            |
|---------------|---------------|------------|------|----------------|-------------------------|
| 1             | Newholme      | Large      | >6 km| Centre         | 151.63201E; 30.41576S  |
| 2             | Newholme      | Large      | >6 km| Edge           | 151.63209E; 30.41699S  |
| 3             | Newholme      | Small      | 100 m| Centre         | 151.63112E; 30.422945  |
| 4             | Newholme      | Small      | 100 m| Edge           | 151.63057E; 30.422465  |
| 5             | Newholme      | Large      | >6 km| Centre         | 151.64537E; 30.417705  |
| 6             | Newholme      | Large      | >6 km| Edge           | 151.64589E; 30.419265  |
| 7             | Newholme      | Small      | 75 m | Centre         | 151.64666E; 30.42110S  |
| 8             | Newholme      | Small      | 75 m | Edge           | 151.64617E; 30.42152S  |
| 9             | Newholme      | Large      | >6 km| Centre         | 151.65012E; 30.41547S  |
| 10            | Newholme      | Large      | >6 km| Edge           | 151.65141E; 30.41682S  |
| 11            | Newholme      | Small      | 100 m| Centre         | 151.65609E; 30.41953S  |
| 12            | Newholme      | Small      | 100 m| Edge           | 151.65631E; 30.42009S  |
| 13            | Hillgrove     | Large      | 2 km | Centre         | 151.88272E; 30.52810S  |
| 14            | Hillgrove     | Large      | 2 km | Edge           | 151.88034E; 30.53087S  |
| 15            | Hillgrove     | Small      | 100 m| Centre         | 151.87987E; 30.53462S  |
| 16            | Hillgrove     | Small      | 100 m| Edge           | 151.88089E; 30.53425S  |
| 17            | Hillgrove     | Large      | 2 km | Centre         | 151.88549E; 30.52923S  |
| 18            | Hillgrove     | Large      | 2 km | Edge           | 151.88756E; 30.52784S  |
| 19            | Hillgrove     | Small      | 50 m | Centre         | 151.89394E; 30.52841S  |
| 20            | Hillgrove     | Small      | 50 m | Edge           | 151.89264E; 30.52866S  |
| 21            | Dumaresq Dam  | Large      | 1 km | Centre         | 151.59772E; 30.42462S  |
| 22            | Dumaresq Dam  | Large      | 1 km | Edge           | 151.59851E; 30.42601S  |
| 23            | Dumaresq Dam  | Small      | 75 m | Centre         | 151.59606E; 30.42261S  |
| 24            | Dumaresq Dam  | Small      | 75 m | Edge           | 151.59677E; 30.42285S  |

Google Earth satellite imagery. Remnant vegetation in all patches was dry, open woodland, with a lightly vegetated understory and a canopy dominated by New England peppermint (*Eucalyptus nova-anglica*).

**Passive acoustic monitoring protocol**

Sensors were deployed in pairs within each fragment, with sampled fragments located at least 1 kilometre apart to ensure independence of recordings. One sensor was placed on the ‘edge’ of fragments, another in the ‘centre’. Fragment edge was defined as within 10 metres of the outermost canopy trees of the patch, while the centre of smaller fragments was identified using satellite imagery. In large fragments, the centre location was limited to a point 200 metres from the edge, as many larger fragments in this area were extensive and did not always contain suitable noisy miner habitat beyond this distance. Noisy miner vocalisations are sufficiently loud that they can be detected from approximately 100 m away with our equipment and this, along with the relatively small activity spaces of miners (ca.100 m radius; Dow 1979), allowed us to be confident that the vast majority of recorded calls originated in the focal woodland patch. Sensors were placed approximately 2.4 metres above ground using a metal bracket and secured with a python lock (Faunatech, Australia). Each was fitted with a SMX-II microphone (Wildlife Acoustics) and configured to record 6 hours of audio each day in the form of three sets of 2 hr recording periods centred on civil sunrise, midday, and civil sunset, respectively. Recordings were in 16-bit WAV format and at 16 kHz, with a new file being initiated every 30 minutes, so that a 2 hr sampling block
consisted of four consecutive 30-min files. Recordings were collected on 14 consecutive days during three distinct periods: the end of Autumn (24/05/2014 – 31/05/2014), Winter (1/06/2014 – 31/08/2014), and during the onset of breeding activities in the first half of Spring (1/09/2014 – 19/09/2014). The first complete day of recordings without precipitation or strong winds was analysed for each location, so that for each of the 12 different fragments six hours of recording was obtained from the edge and centre, respectively, yielding a total of 432 hrs of audio analysed herein.

**Kaleidoscope pro accuracy in comparison to manual screening of files**

To determine the ability of automated software to correctly extract sounds of interest, we first used RavenPro (v1.5, Charif et al. 2010) to manually screen 33 randomly selected 30-min files. We identified three different noisy miner vocalisations of interest: Chip, Chur, and Aerial Alarm vocalisations (as defined by Holt et al. 2017). These calls are highly context specific and, in the case of Chur and Aerial Alarms, are also functionally referential (Holt et al. 2017; Farrow et al. 2017). This manually scored test data allowed us to identify both whether or not at least one call of each type was present within a 30-min recording, but also the total amount of time (nearest second) devoted to a given call type within that file.

Kaleidoscope Pro (v4.5 Wildlife Acoustics, Maynard, USA) was used to automate the assessment of sound recordings for each of the three call types of interest. Initially, an optimisation protocol assessed the manually screened files to maximise detections, with the optimal signal parameters for this dataset being detection of signals between 1500 and 5000 Hz, a syllable length between 0.01 and 10 seconds, and a maximum inter-syllable gap of 0.01 seconds. We then used Kaleidoscope Pro to assess the 432 hrs of audio, and carried out a cluster analysis on detected signals (maximum distance from a cluster = 2.0, maximum states = 12, maximum distance from cluster centre = 0.5, maximum of 800 clusters). Numerous false positives were returned, so detections were then manually screened, with only those containing one of the three call types of interest included in analyses.

**Statistical analysis**

To ensure call detections by Kaleidoscope Pro were a reliable proxy of signals contained within the audio, both the total number of bouts and also the total duration of each call type manually detected on a file were compared with Kaleidoscope Pro data using linear regression models in the base R environment (R Core Team 2021).

Following validation of the semi-automated detection protocol, all 30-min files were then assessed for each of the three call types of interest to determine if a) a given 30-min file had at least one occurrence and, if so, b) the total number of occurrences of that vocalisation type within a 30-min file. These two metrics were then used to determine the factors that most reliably explained both the detection of a particular call within a 30-min recording, and subsequently the intensity or number of hits for that call within a recording. First, the detection of a calling bout within a given 30-min file was achieved through running a series of generalised linear mixed models (GLMMs) with a binomial loglink function, comparing results for each of the three call types separately. The dependent variable was measured as the total number of the four 30-min files collected over each 2 hr recording period with at least one call of interest (values therefore ranged...
from 0 to the maximum value possible of 4). The overdispersion parameter ($\hat{\gamma}$) was estimated from the global model (Burnham and Anderson 2002), using the \textit{AICmodavg} package (Mazerolle 2019). In our analyses $\hat{\gamma}$ values were all indicative of overdispersion not being an issue, so model fit was assessed using the Akaike Information Criterion accounting for small sample bias (AICc). Analyses were carried out in R (R Core Team 2021) using the \textit{lme4} package (Bates et al. 2015). Second, the factors that best described calling intensity, that is the number of 30-min files with at least one exemplar of a call type, were assessed with a Gaussian family loglink function, again with the package \textit{lme4} (Bates et al. 2015) within R.

For both analyses, a total of 8 different biologically plausible model types were assessed for fit based on current known data (Table 2). A unique number was assigned to each of the 12 locations where a sensor pair was deployed, and this ‘Site’ variable was used as a random term in each model. Other factors assessed in models included the Time of day samples were recorded (Dawn, Midday, Dusk), the Position of sensors within a fragment (Edge, Centre), the Size of a given fragment (Small, Large), the Period of sampling (Autumn – Early, Winter – Mid, or Spring – Late), and biologically relevant two-way interactions (Table 2). For each type of vocalisation, the model with the lowest AICc value was considered the most parsimonious (Burnham and Anderson 2002). Models within $\Delta$2 AIC units of each other were considered to have similar levels of support. In the event that numerous models were considered parsimonious, the models were averaged using the \textit{MuMIn} package (Bartoń 2019). This distributed the Akaike weights ($w_i$) between them, eliminating models with little or no $w_i$, creating an average model estimate for the impact of each retained model.

**Results**

*Do semi-automated assessment methods provide similar results to manual screening?*

The results from manually screening a subset of 33 randomly selected 30-min audio files for both the number, and total time of the recording devoted to each of the three signal types of interest (social: chip calls, ground predators: chir calls, aerial

| Model | Fragment Site |
|-------|---------------|
| Null  | Intercept only|
| Time  | Time only     |
| Position | Position only |
| Size  | Size only     |
| Season | Sampling period only |
| Temporal | Time + Sampling period + Time:Sampling period |
| Habitat | Position + Size + Position:Size |
| Global | Time + Position + Size + Sampling period + Time:Sampling period + Position:Size + Time:Size |
predators: aerial alarm calls) were comparable to those obtained using Kaleidoscope Pro to identify potential detections. There was a significant positive relationship between the number of calling bouts detected manually and the number of call detections identified by Kaleidoscope Pro ($F_{1,97} = 154.32, p< 0.005$, Adjusted $R^2 = 0.61$), as well as the total time of each file in which noisy miner vocalisations were detected if at least one detection had been noted ($F_{1,50} = 75.42, p< 0.005$, Adjusted $R^2 = 0.59$). For brevity, the results for each individual call type are not shown, but all returned statistically significant, positive correlations between data obtained across the two methods (Adjusted $R^2$ ranged from 0.22 to 0.66). Given this, we used a semi-automated assessment as a sufficient proxy of manual scoring to assess all 432 hrs of recordings.

**Impact of fragment characteristics and time of sampling on call detection**

For each two-hour recording period at either Dawn, Midday, or Dusk, we assessed which factors were the most parsimonious in explaining the likelihood of at least one of each of the three different types of noisy miner vocalisations being detected in a given 30-min file. We fitted the eight models outlined above for Chip calls (social, unrelated to predator presence), Chur calls (ground predator alarms) and Aerial alarms (airborne predator).

**Chip call detection** – The Global model had the most support in analyses assessing whether or not at least one chip call had been detected in a 30-min audio file, being more than 9 AICc points higher than the next best model (Table 3). Despite this, estimates of effect sizes were low and, with standard error variance applied, most either overlapped with or were very close to 0 (Appendix S1). The exceptions were the importance of fragment size and sensor position. Within smaller fragments, on average $2.6 \pm 0.10$ SE files (95%CI: 2.40–2.80) out of a possible 4 contained chip calls, a higher detection rate than in larger fragments ($1.5 \pm 0.12$SE; CI: 1.26–1.74; Appendix S1). Likewise, sensors placed on the edge of fragments ($2.3 \pm 0.12$SE files; 95%CI: 2.06–2.54) were more likely to detect chip calls than those in the Centre ($1.8 \pm 0.13$SE; 95%CI: 1.55–2.05; Appendix S1).

Further, time of day that recordings were taken also influenced results, with few detections during dusk recordings (Figure 1(a)). These results suggest that smaller fragments and along the edges of fragments were the preferred habitat of noisy miners, and that activity peaked during earlier parts of the day.

**Number of Chip calls detected** – The same model set was then used to examine which factors impacted the number of a given call type detected in each 30-min file, restricting analyses to only those audio recordings in which at least one noisy miner call had been detected above. In contrast to the detection data, there was clear support for the ‘Time’ and ‘Temporal’ models in best explaining the number of chip calls detected, with considerably less support was found for the next best fit model of ‘Position’ (Table 3). Model averaging was then undertaken, combining the two best supported models to generate model estimate parameters (Appendix S2). Relative to Dawn sampling periods, there were fewer chip calls at Dusk and Midday (Figure 1(b)), however the effect size of other factors following model
averaging were all minor and overlapped with zero when standard errors were taken into account (Appendix S2). Taken together, these indicate a general peak of noisy miner social calling activity in the Dawn sampling period as expected.

**Chur call detection** – As with chip calls, the probability of at least one chur call occurring in response to a ground predator in a 30-min audio file was best explained by the Global model (Table 4). When effect sizes were assessed (Appendix S3), the primary impacts on chur call occurrence were the Time of day, with calls being more likely in the Dawn period, and the interaction between fragment size and sensor position, with fewer chur calls occurring in the centre of large fragments (Figure 2(a,b)).

**Number of Chur calls detected** – ‘Time’ was the most parsimonious model in explaining the number of chur calls detected in 30-min files with at least one chur call (Table 4). There was a clear drop in the number of chur calls that were recorded during Midday as opposed to both the Dawn and Dusk recording period (Figure 2(c)).

**Aerial call detection** – The Global model was the best model in explaining the probability of at least one aerial alarm call being detected within a given 30-min file (Table 5). This model was more than 10 AICc points clear of the next best. When model estimates were examined, factors with biologically relevant effect sizes supported evidence for a reduction in aerial alarm call occurrence over Midday and Dusk periods in comparison to Dawn, and an increased number of files with at least one aerial call from sensors placed on the Edge of fragments was found (Figure 3; Appendix S4).

**Number of Aerial Alarm calls detected** – The Null model was among those that received the highest level of support when the number of aerial alarm calls recorded was examined (Table 5), indicating that none of the fitted models were explaining biologically relevant patterns.
Figure 1. Number of (a) four 30-min audio files where at least one chip call (a general social contact call) was detected, and (b) the total number of chip calls detected within 30-min files with at least one chip call according to the time of day that samples were collected. Dot points indicate raw data (with jitter applied for clarity), while error bars and means indicate means ± 1SE for data.
Table 4. Model fit output assessing candidate model set against a) number of four 30-min audio files where at least one chur call (indicating potential ground predator presence) was detected, and b) total number of chur calls detected within 30-min files for those with at least one chur call. Models considered to have higher levels of support are presented in bold.

| Model                  | K  | AICc  | ΔAICc | AICcWt | Cum.Wt | Loglik |
|------------------------|----|-------|-------|--------|--------|--------|
| **Chur vocalisation – occurrence** |    |       |       |        |        |        |
| Global                 | 15 | 598.04| 0     | 0.98   | 0.98   | −282.82|
| Time                   | 4  | 606.02| 7.97  | 0.02   | 0.99   | −298.91|
| Temporal               | 10 | 608.39| 10.35 | 0.01   | 1      | −293.66|
| Habitat                | 5  | 614.11| 16.07 | 0.0003 | 1      | −301.91|
| Position               | 3  | 623.06| 25.02 | <0.0005| 1      | −308.47|
| Season                 | 4  | 625.97| 27.93 | <0.0005| 1      | −308.89|
| Size                   | 3  | 627.44| 29.40 | <0.0005| 1      | −310.66|
| Null                   | 2  | 627.67| 29.63 | <0.0005| 1      | −311.81|
| **Chur vocalisation – number detected** |    |       |       |        |        |        |
| Time                   | 5  | 2290.78| 0     | 0.99   | 0.99   | −1140.22|
| Temporal               | 11 | 2300.70| 9.91  | 0.01   | 1      | −1138.57|
| Global                 | 16 | 2308.99| 18.20 | 0.0001 | 1      | −1136.84|
| Null                   | 3  | 2332.87| 42.09 | <0.0005| 1      | −1163.37|
| Size                   | 4  | 2334.72| 43.93 | <0.0005| 1      | −1163.24|
| Position               | 4  | 2334.74| 43.95 | <0.0005| 1      | −1163.26|
| Season                 | 5  | 2334.89| 44.10 | <0.0005| 1      | −1162.27|
| Habitat                | 6  | 2337.92| 47.13 | <0.0005| 1      | −1162.72|

**Discussion**

Understanding how land-use changes impact taxa is critical to ongoing biodiversity conservation (Bellard et al. 2012; Allan et al. 2017). However, given the nuanced behavioural decisions that can impact how different species utilise habitats, simply documenting presence/absence may not be sufficient to fully understand fragmentation impacts on biodiversity. One facet that can have profound impacts on prey species is the so-called ‘landscape of fear’, however this has often proven difficult to quantify. Here we take advantage of a functionally referential signalling system in a high vocal bird to examine perceived predation risk in a fragmented landscape using passive acoustic monitoring (PAM). Social vocalisations unrelated to predation pressure followed the anticipated peaks in calling activity for this species using this method, being more often detected along fragment edges, particularly smaller fragments as fits the species preferred habitat (Clarke and Oldland 2007; Barati et al. 2016), confirming the validity of the general monitoring process.

When alarm call vocalisations were examined to quantify predation risk, signals given in response to ground predators (chur calls) were detected more often during both dawn and dusk recordings, a pattern that did not simply mirror noisy miner activity. Whether or not a single chur call was detected in a file was further linked to fragment size, with chur calls less likely to be heard in the centre of larger fragments. In contrast, aerial predator alarm vocalisations (aerial alarms) did not vary in their number according to any of the assessed factors, however at least one bout of aerial alarm calling was more likely to be detected along fragment edges, regardless of patch size. Further, aerial alarm call bout detections declined steadily throughout the day, from a peak at dawn through to their lowest detection rate at dusk. Together, these data suggest that the perceived risk of predation experienced by noisy miners is impacted by fragmentation, with a landscape of fear characterised by increased encounters with aerial and ground predators on the edges.
of fragments, and further by fragment size, with miners occupying smaller patches being more likely to encounter predators. Changes in different call types over the course of a day, but not season, indicate within day temporal effects on fear levels were also apparent.

**The use of semi-automated analysis to enhance data acquisition**

While the use of Kaleidoscope Pro was faster than manual scoring when assessing our audio data, software accuracy did not allow the use of automated output without verification. Instead, we used a hybrid model to automate the finding of potential signals of interest, before manually classifying these, a common limitation in this field (Marchal et al., 2021). As automated analysis techniques continue to improve in both speed and accuracy, this manual step may become unnecessary; however, for now careful assessment of any automated output remains an essential part of PAM workflows.
Table 5. Model fit output assessing candidate model set against a) number of four 30-min audio files where at least one aerial alarm call (indicating potential raptor in flight) was detected, and b) total number of aerial alarm calls detected within 30-min files for those with at least one aerial alarm call. Models considered to have higher levels of support are presented in bold.

| Model                        | K  | AICc | ΔAICc | AICcWt | Cum.Wt | Loglik |
|------------------------------|----|------|-------|--------|--------|--------|
| Aerial vocalisation – occurrence a | 15 | 548.87 | 0     | 0.99   | 0.99   | −258.23|
| Global                       | 4  | 559.57 | 10.70 | 0.005  | 1      | −275.69|
| Time                         | 10 | 560.90 | 12.03 | 0.002  | 1      | −269.91|
| Temporal                     | 5  | 603.34 | 54.47 | <0.0005| 1      | −296.52|
| Habitat                      | 3  | 605.08 | 56.21 | <0.0005| 1      | −299.48|
| Position                     | 4  | 615.15 | 66.28 | <0.0005| 1      | −303.48|
| Season                       | 2  | 617.10 | 68.23 | <0.0005| 1      | −306.52|
| Null                         | 3  | 618.08 | 69.21 | <0.0005| 1      | −305.98|
| Aerial vocalisation – number detected b | 5  | 1259.39 | 0     | 0.29   | 0.29   | −624.46|
| Time                         | 5  | 1259.54 | 0.15  | 0.27   | 0.56   | −624.53|
| Season                       | 3  | 1259.76 | 0.38  | 0.24   | 0.80   | −626.79|
| Null                         | 4  | 1261.84 | 2.45  | 0.09   | 0.89   | −626.76|
| Size                         | 4  | 1261.89 | 2.50  | 0.08   | 0.97   | −626.79|
| Position                     | 11 | 1264.66 | 5.27  | 0.02   | 0.99   | −620.24|
| Temporal                     | 6  | 1266.19 | 6.80  | 0.01   | 1      | −626.76|
| Habitat                      | 16 | 1272.80 | 13.41 | 0.0004 | 1      | −618.05|

Noisy miner presence and activity

The complex acoustic repertoire of noisy miners enabled an assessment of PAM efficiency in detecting the presence of miners, so in this context our results matched the expected peaks in miner activity during the dawn chorus period and along fragment edges, particularly in smaller patches (Clarke and Oldland 2007; Thomson et al. 2015). While it was beyond the scope of this study, vocal features such as call rate may well be useful in determining miner density as has been found for its close relative the bell miner (M. melanocephala; Lambert and McDonald 2014). Regardless, the subtle differences in the likelihood and number of detections between social calls and the two alarm vocalisations indicate that PAM was able to detect differences in the bird’s response to stimuli in the environment, providing a nuanced insight into perceived predation risk.

Perceived ground predator pressure

The most important factors that impacted the likelihood of a chur or ground predator alarm call being detected were location within fragments and the time of recordings, with miners more likely to encounter ground predators at dawn on the edge of fragments. Noisy miners give chur calls to a range of potential threats in their environment, including perched raptors, but most often these are directed towards diurnal mammalian predators such as cats (Felis catus), red foxes (Vulpes vulpes) and canines (Holt et al. 2017). As detected peaks of chur call activity match the known periods of hunting activity for these introduced mammalian predators in Australian ecosystems (Gil-Fernández et al. 2020), these data are highly likely to reflect greater encounter rates between noisy miners and these predators.

From a conservation perspective, this increased encounter rate at the edges of fragments, particularly small fragments, suggests increased predation pressure, or at least a higher perceived risk of predation by potential prey. This has been suggested in a range of studies, for example, extensive literature looking at artificial nest predation rates along fragment
Figure 3. Number of four 30-min audio files where at least one aerial alarm call (indicating potential raptor in flight) was detected relative to (a) the time of day that samples were collected, and (b) the position of sensors within fragments. Dot points indicate raw data (with jitter applied for clarity), while error bars and means indicate means ± 1SE for data.
edges (e.g. Chalfoun et al. 2002). While smaller fragments do provide significant conservation value (Wintle et al. 2019), our results indicate that animals occupying these smaller habitats are likely to experience additional physiological stress associated with increased predator encounters (Zanette et al. 2019).

**Perceived aerial predator pressure**

In contrast to both chip and chur vocalisations, the detection and number of aerial alarm calls in the dataset showed less distinctive patterns of occurrence, suggesting a more random encounter rate with raptors, the typical predators that stimulate this call from miners (Holt et al. 2017). This response aligns with those of other predator-prey systems, where the more unpredictable nature of encounters with aerial predators does not impact habitat use (Willems and Hill 2009). There was some evidence of aerial predator encounters becoming rarer throughout the day, and further that recorders placed near edges were more frequently recording aerial predator encounters. These differences may reflect the hunting strategy of the most common raptor species in the area, with Accipitridae species typically moving rapidly along fragment edges searching for prey in the area. Further, with well-known peaks in avian activity at dawn, a matched response by predators targeting those avian prey is not surprising.

**Using PAM to quantify landscapes of fear**

Together, these results offer direct insight into the nuanced predator/prey relationships between noisy miners and their suite of potential predators in fragmented environments. Similar results have been obtained in another agricultural system, where alarm calls of a woodland bird were more often detected in woodland patches with a greater amount of agricultural land in the vicinity (Whytock et al. 2020). Here, we have further documented changes in predation risk according to fragment size, position within these fragments and predator type by monitoring referential alarm vocalisations. Edges of smaller fragments had the greatest perceived predation risk overall, with short-term temporal changes also seeing predator encounters peak during dawn observations.

For these woodland areas, predators that elicit an alarm call response in noisy miners also predate a range of other small passerines occupying the same environment and experiencing the same predation risk, many of which are of conservation significance (Thomson et al. 2015). While the use of PAM does not allow confirmation of predator presence, recognition errors made by miners vocalising towards non-predatory species still elicit anti-predator responses in conspecifics (Farrow et al. 2017) and likely other taxa (Magrath and Bennett 2012), such that these results likely reflect true landscapes of fear in this system.

PAM can clearly yield information beyond survey presence/absence, and can further offer detailed information on nuanced use of habitats via a non-invasive data collection method. As acoustic analysis software is further refined, this approach will only become more efficient, offering a highly informative means to directly monitor animal behaviour. This is particularly true for predation pressure and landscapes of fear, with a range of potential focal species that can be monitored in this way, thereby generating important insight for habitat management and conservation.
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Data availability statement

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Ethical statement

This study followed the institutional and national ethical guidelines for scientific research in Australia.

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