

1 **Life history characteristics and alarm calling in Australian arid-zone birds**

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Abstract

In prey species, it is often the case that individuals give alarms when they are threatened. In birds, such signals are frequently vocal signals which alert conspecifics to the presence of a threat. The responses to these calls by receivers may include fleeing to cover or approaching to mob the predator. Although most birds do give alarm calls when threatened, not all species do. We used Australian arid-zone bird species ($n = 171$) to test the hypothesis that alarm calling behaviour is determined by ecological, behavioural, and morphological characteristics. Eighty-nine percent of birds analysed possessed an alarm call, highlighting the prevalence of this behaviour. Our study found three variables – number of food types eaten, mobility, and breeding system – that were associated with predicting alarm calling behaviour in these species. The correspondence of alarm calling with these key life history attributes provides insight into benefits of having alarm calls and the evolutionary processes that have given rise to this behaviour.

Keywords

Alarm calling, Australian birds, arid zone, life history traits, predictor variables

Introduction

The use of vocalisations to warn of a nearby threat is common in birds (Marler 1955; Magrath et al. 2015). Such alarm calls function to alert conspecifics to the presence of danger, and encourage flight (termed ‘flee alarm calls’) or recruit help to harass the predator (‘mobbing alarm calls’; Klump and Shalter 1984; Magrath et al. 2015; Carlson and Griesser 2021). The calls produced may be acoustically distinct sounds only used in alarm contexts, such as the flee alarm calls of White-browed Scrubwrens (*Sericornis frontalis*; Leavesley and Magrath 2005), Superb Fairy-wrens (*Malurus cyaneus*; Magrath et al. 2007), and several other Australian passerines (Jurisevic and Sanderson 1994). Calls may also be multi-functional and used for contacting group members or during territorial disputes (Wheatcroft 2015). In some species, calls have been identified as functionally referent, such as the different vocalisations given by Pale-winged Trumpeters (*Psophia leucoptera*; Seddon et al. 2002) and Siberian Jays (*Perisoreus infaustus*; Griesser 2008) in response to predator behaviour or location. Noisy Miners (*Manorina melanocephala*) give a ‘chur’ call to perched predators and an aerial alarm call to flying predators (Holt et al. 2017).

Flee and mobbing signals can differ in their function, intended receivers, and acoustic structure. Flee alarm calls are usually in response to aerial predators (reviewed in Magrath et al. 2015) and are high-pitched with gradual on- and offset, making the caller difficult to locate (Marler 1955). These calls communicate to nearby conspecifics that a predator has been sighted and elicit escape or freezing (Klump and Shalter 1984). Mobbing signals are typically given to stationary or terrestrial predators (reviewed in Magrath et al. 2015), are low-pitched and harsh-sounding, and the caller is easier to locate. Mobbing calls may have multiple functions (reviewed in Carlson and Griesser 2021), with two key purposes being to communicate detection to the predator, and to recruit conspecifics to harass it (Klump and Shalter 1984). Alarm calling among adult conspecifics has received much attention, but less

is known about parent-offspring alarm communication (Kleindorfer et al. 1996; Colombelli-Négrel et al. 2010; Suzuki 2011). The begging calls of nestlings can be loud and may attract predators, and parents may alarm call to their young to provoke silence (e.g. White-browed Scrubwrens; Platzen and Magrath 2004).

Although alarm calling is widespread among birds, not all species give alarm calls (Goodale and Kotagama 2005; Griffin et al. 2005; Butler et al. 2017). Despite the widespread occurrence of alarm calls, it is not known whether there are ecological or behavioural traits that predict whether a species would or would not give alarm calls. To our knowledge, whether life history traits can be used to predict the likelihood of possessing an alarm vocalisation has not been investigated. This study presents a first look for evidence of these potential processes. It has previously been demonstrated that individuals or species may be more likely to produce a warning vocalisation in certain situations, such as when kin are nearby (e.g. Siberian Jays; Griesser and Ekman 2004) or in particular habitats (e.g. Common Starlings *Sturnus vulgaris*; Devereux et al. 2008). A species' morphology and other traits may impact their vulnerability to predation and could be an indicator of alarm calling behaviour.

Interactions between life history traits and vulnerability to predation are complex as possessing a certain trait can both increase and decrease predation risk (Caro 2005). The influence of individual morphology is particularly strong. Predators tend to feed on prey animals that are smaller than them (Cohen et al. 1993) and prey animals with a bigger body size have a lower risk of predation (Götmark and Post 1996). Smaller species therefore suffer a higher predation risk, however, there is a trade-off to consider here as smaller prey may be more difficult for predators to detect, harder to catch, and be less profitable (Götmark and Post 1996; Roth and Lima 2003). Animals living in groups face similar trade-offs. Here, ease of detection is a factor as larger groups of animals may be easier to find (Jackson et al.

2005), however they also confer a higher degree of protection than smaller groups. More group members increase the overall level of vigilance (the ‘many-eyes hypothesis’; Caraco et al. 1980) and decrease the probability of any one individual being eaten (the ‘dilution effect’; Foster and Treherne 1981). Groups are more successful at defending against predators (Kruuk 1964), and group cohesion can cause confusion (Neill and Cullen 1974). Cooperatively-breeding animals live in social groups of genetically related individuals (Emlen 1991). Enhanced survivorship is one hypothesis for the evolution of cooperative breeding (Emlen 1991). If nest helpers increase the overall group size, this in turn may increase aforementioned anti-predator benefits and enhance the helper’s own survivorship (Doerr and Doerr 2006).

Detection by predators is also impacted by habitat. Prey animals are easier to sight in open habitats compared to closed, thus predation risk is greater when individuals are more exposed (Caro 2005). However, predators also become easier to identify in open habitats, allowing animals more time to utilise defences (Devereux et al. 2006). Flight initiation distance (FID), the distance at which animals commence anti-predator behaviours when approached, is a life history trait (Weston et al. 2012), however, this can be affected by numerous factors including habitat and group size (Fernández-Juricic et al. 2002; Caro 2005), as well as individual characteristics such as sex, age, and quality (Weston et al. 2012). Blumstein (2006) reported a positive correlation between FID and body size, however studies on brain size have given conflicting results (Guay et al. 2013; Møller and Erritzøe 2014), thus the link here is unclear. In general, species that allow predators to get closer before escaping have a higher predation risk, as they may leave escape too late (Weston et al. 2012).

In the present study we focused on birds of the Australian arid zone (Fig. 1), which is typically defined as the area in which mean annual rainfall divided by evaporation (the moisture index) is less than 0.4 (Byrne et al. 2008). This area is home to approximately 230

bird species (Reid and Fleming 1992). The two main vegetation types in the arid zone are spinifex grassland and *Acacia* shrubland (Morton et al. 2011). Desert habitats are characterised by variable rainfall and low soil fertility resulting in periods of drought and a lack of nutrients (Morton et al. 2011), which make survival in this climate difficult. Predators of birds in the arid zone are common and include, among others, numerous species of raptors (family Acciptridae and Falconidae), owls (family Strigidae and Tytonidae), snakes (suborder Serpentes), goannas (*Varanus* spp.), and Dingoes (*Canis lupus dingo*), as well as feral Cats (*Felis catus*) and Red Foxes (*Vulpes vulpes*), both of whom are introduced (Letnic et al. 2005; Moseby et al. 2009).

Arid-zone birds form a useful starting point for the current type of research. The arid zone is the largest biome in Australia (Byrne et al. 2008), thus any species with a distribution falling within this large proportion of the country had the potential to be included in the analysis. Most of the species included in the analysis do not occur exclusively within the arid zone, however, it is assumed that their alarm calling behaviour (cf. call structure) would be the same regardless of their geographic location. Our objective was to determine if alarm calling and, in particular, use of a distinct alarm call to communicate with adult conspecifics, was more prevalent in species demonstrating certain characteristics related to morphology, habitat, diet, breeding, and migration.

Methods

Data collection

Species list

The Atlas of Living Australia (<https://spatial.ala.org.au>) was used to obtain the list of species included in this analysis. The Köppen climate classification (all classes) layer was added to the map of Australia, and the four desert regions selected (Fig. 1). The *area report* function

generated a list of all records of species found in this defined region and the bird list was exported. Records with a taxon rank other than species or subspecies were removed as these records were not specific enough to provide useable data. All raptors, nocturnal birds, waders and seabirds were removed from the dataset (Table S1). Records at the taxon level of subspecies were added to the corresponding species data to obtain a total number of records per species. Species with 100 or more records in the entire desert area were included in the analysis, resulting in a list of 171 species spanning 49 families across 10 orders (Table S2).

Predictor variables

Predictor variables used in the analysis were obtained from an online database of life history traits of Australian birds (<https://dx.doi.org/10.6084/m9.figshare.1499292>; Garnett et al. 2015). This extensive database of all Australian bird species and subspecies contains comprehensive information on a wide variety of life history traits, as well as details on taxonomy, distribution and conservation. There are 15 broad categories included in the database, eight of which (phylogeny, Australian population status, conservation status, legal status, distribution, climate metrics, and two categories used for organising the list) are not relevant to our investigation. Variables related to the remaining seven categories (taxonomy, morphology, habitat, food, behaviour, breeding, and mobility) have been included in this study. Eleven traits were selected for the present analysis and are described in Table 1. Six of these came directly from Garnett et al. (2015), while two new categories were created by combining information contained within the database: feeding gregariousness and mobility. The information for the final three categories - number of feeding habitats, number of breeding habitats, and number of food types - was obtained by counting the habitats and food types listed in the dataset as being utilised by each individual species. Data relating to the entry at species level were used for all variables. These twelve variables were chosen as they could each potentially contribute to the likelihood of alarm calling. Following the procedure

described below, we considered our dataset with all variables and omitted species with missing data from our analysis. Flight initiation distance (FID) was considered relevant during pilot work, but it was also the most limiting variable resulting in a substantial reduction in species included in our analysis (N=63). We repeated our analytical approach after excluding FID in order to consider a more complete dataset (N=144), and we report on this analysis.

Vocal alarm information

Information on alarm calling behaviour was obtained from the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB; see Table S2 for complete reference list). For each species, the sections on social behaviour and vocalisations were examined for mention of anti-predator responses. Species were first grouped into two broad categories: those recorded as possessing a vocal alarm signal and those with no mention of a vocal signal used in alarm communication. Our criterion for inclusion was a published account of calls given in alarm contexts. For the latter group (N=18), a literature search was undertaken to rule out false negatives. Given that some of these species are understudied, we stipulate that our characterisation reflects reported accounts rather than definitive statements of alarm calling behaviour. Sounds made only during distraction displays, or only during distress (i.e., capture or handling) were not considered vocal alarm signals. For each species, vocalisations were further classed according to the context in which these signals are used. A summary of the alarm call categories used in the present study is given in Table 1. For distinct alarm calls, it was also noted if the vocalisation was intended for conspecific adults or offspring.

Data analysis

We modelled separately whether the occurrence of a vocal alarm call, a functionally distinct alarm call, or a distinct alarm call directed to adults, was related to our set of predictor variables (Table 1). We used a time-calibrated phylogeny of extant bird species (Jetz et al.

2012) from the site <https://birdtree.org>, which utilise the genome-based phylogenies of Hackett et al. (2008). We limited the phylogenies to the 144 species in our final dataset and extracted a single random tree for use in our analyses (Fig. 2). Prior to each regression analysis, we considered the extent of multi-collinearity among the predictor variables using the *vif* function in the *car* package (Fox and Weisberg 2011) in the R statistical environment (R Core Team 2020). The *vif* function estimates the variance inflation factor and facilitates the determination of multi-collinearity in our predictor variable. We inspected the GVIF values adjusted for the number of coefficients in the model. Based on this, we removed body length from our set of predictor variables in all analyses. Continuous predictor variables were centred, scaled, and transformed to ensure they met the assumption of normality. We ran separate phylogenetic generalised mixed models for binary data using the *phylglm* function from the *phylolm* package (Ho and Ane 2014). We report results for the α parameter as an estimate for phylogenetic signal (Ives and Garland 2010), whereby small values indicate an effect of shared ancestry. The significance of predictor variables was determined through inspection of model coefficients and associated z-scores and p-values. The effects of significant continuous variables were explored graphically by plotting their effect on the occurrence of the category of alarm calling under investigation, fitting a logistic regression curve in each case. For categorical variables, we present the relative proportion of species performing the relevant category of alarm call by level of the categorical variable.

Results

Vocal alarm signalling

Around ninety percent (89.5%) of bird species used in this analysis possessed a vocalisation to signal alarm to conspecifics (Fig. 3a). Of those species, three-quarters (74.5%) had a vocal signal only used in alarm communication and not in any other contexts ('distinct' plus 'both';

Fig. 3b), and 88.6% of these birds are known to have a call used specifically to communicate with adult conspecifics (Fig. 3c).

Regression analysis

We first considered the presence of a *vocal alarm* call as the dependent variable (Fig. 3a). The results of phylogenetic generalised linear regression are summarised in Table 2 and indicate an effect of the number of food types and mobility. Although starting from a high proportion, the data suggest that vocal alarms are more likely as the number of food types increases (Fig. 4a), while a higher proportion of the more mobile species possess an alarm call than local dispersers and partial migrants (Fig. 5a). Our second analysis used the occurrence of a *distinct alarm call* as the dependent variable (Fig. 3b), with results of the phylogenetic generalised linear regression summarised in Table 3. Here, breeding system was the only significant predictor and indicates that a higher proportion of cooperative breeders use a distinct alarm call than non-cooperative breeders (Fig. 5b). Our final analysis used the occurrence of a *distinct alarm call directed to adults* as the dependent variable (Fig. 3c), with results of the phylogenetic generalised linear regression summarised in Table 4. The probability of species possessing a distinct alarm call directed to adults increases as species consume a greater number of food types (Fig. 4b), while a significant relationship due to breeding system suggests that cooperative breeders are more likely to possess a distinct alarm call to adults than non-cooperative breeders (Fig. 5c). Estimates of phylogenetic signal from the models (using the parameter α) were close to zero and suggest correlations in trait values between species (Tables 2-4).

Discussion

Our analysis found that most species were known to possess a vocal alarm signal, and most of these species had at least one vocalisation used only in alarm contexts. Overall, these

distinct calls were used to communicate with conspecific adults, with few species possessing distinct calls for parent-offspring alarm communication. Alarm calling was prevalent among a diverse group of species, indicating that it is intrinsically valuable. Although ancestral state reconstruction was not our goal, we speculate that alarm calling is ancestral and has been lost sporadically. Exploration of the data occurred in the context of phylogenetic relatedness and at three levels: presence of a vocal alarm call, presence of a call used only in alarm contexts (regardless of intended receiver), and possession of a distinct alarm call specifically directed at adult conspecifics. The number of food types and mobility were identified as predictors of the occurrence of a vocal alarm (level 1). Body size approached significance and should be considered in future work. Analyses at the second level showed that only breeding system could be used to predict the presence of a distinct alarm call, while at the third level, number of food types and breeding system showed significance.

Species eating more diverse food types were more likely to have a vocal alarm call and a distinct alarm call directed specifically to adults. In contrast, another diet-related variable that we analysed (number of feeding habitats) was not a significant predictor of alarm calling. Research linking diet and anti-predator behaviour is uncommon, however it is known from other studies that predator risk varies based on foraging location. The risk of predation by Eurasian Sparrowhawks (*Accipiter nisus*) is known to decrease with increasing foraging height (Götmark and Post 1996), and Selås (1993) reports that ground-foraging species were more vulnerable than those that foraged among vegetation. Our analysis implies no relationship between number of feeding habitats utilised and number of food types eaten. Data from Garnett et al. (2015) include species at both ends of this spectrum – dietary specialists foraging in numerous habitat types, and generalists foraging in few. Therefore, we suggest future work on the influence of diet should change the focus from where birds eat, to instead investigate what they eat and the behaviours they exhibit while eating. The literature

linking foraging habitat, group size and foraging efficiency of birds to predation risk is extensive (e.g. Thiollay and Jullien 1998; Elchuk and Wiebe 2002; Dias 2006; McCabe and Olsen 2015). However, no research connecting only diet type and vulnerability to predators could be found, thus it is unclear why birds with a generalist diet are more likely to possess a distinct alarm call than dietary specialists. Behaviour displayed while foraging is one potential answer as different food types must be collected using different methods, e.g. sallying for insects compared to head-down pecking. Our analysis has not considered the individual food items eaten by arid-zone birds and has instead used a simple summation of the total number of food types eaten by each species as listed in Garnett et al. (2015), with the maximum possible number being ten. If in future studies the specific type of food, diversity of foraging behaviour exhibited, and subsequent foraging location were analysed, this would undoubtedly provide more information on the link between food types and alarm calling (Götmark and Post 1996).

Our analysis suggested that nomadic species are more likely to possess an alarm call than both sedentary species (local dispersers) or partially nomadic species (some individuals leave the breeding area). It is difficult to predict how different levels of mobility can affect predation risk. Studies on this interaction focus mainly on migratory ungulates, such as Elk (*Cervus elaphus*; e.g. Hebblewhite and Merrill 2007) and Moose (*Alces alces*; e.g. Singh et al. 2012). Populations that undergo such large-scale migrations tend to experience a lower predation risk than residents, however, other factors such as human presence and habitat structure also have a considerable influence (Hebblewhite and Merrill 2007; Robinson et al. 2010). Contradictory evidence suggests that dispersing populations suffer higher predation levels as they are unfamiliar with the terrain, and this can hinder escape (Nelson and Mech 1991). Perhaps it is unfamiliarity with the local environment that prompts nomadic bird species to be more likely to possess an alarm call. We consider the link between alarm call

behaviour and mobility to be worthy of further research. For convenience, we collapsed information about national movements from Garnett et al. (2015) into a single categorical variable. However, many species exhibited movement in more than one category, and a key factor determining movement strategies within and between species is likely to be the availability of resources. These lead to the interesting possibility of population differences in the use of alarm calls.

The relationship between body mass and giving a distinct call to adults approached significance. Nonetheless, we consider it worthy of further consideration. The results show an expected negative relationship which suggests that larger birds are less likely to possess these calls. Larger animals are preyed on by fewer predator species and experience fewer predation attempts, thus their overall predation risk is much reduced compared to smaller species (Caro 2005; Valcu et al. 2014) and we therefore predict less of a need to develop an alarm call to warn adult conspecifics. Large prey animals suffer less predation due in part to a limitation on predator size and ability, and because larger animals are better able to defend themselves physically (Cohen et al. 1993; Caro 2005). Götmark and Post (1996) report a clear link between predation risk and body size whereby predation risk increased with body mass until about 40g, then declined as mass increased above this point. The smallest species experienced a lower risk than slightly larger species because they were harder to catch and less profitable. This does not appear to be a factor in our results, as the smallest species have the highest probability of alarm calling to adults.

Birds that breed cooperatively were more likely to have a distinct vocal alarm call, and more likely to have an alarm call directed to adults. Research into cooperative breeding has a long history, and the behaviour is well-studied in birds (e.g. Stacey and Koenig 1990; Koenig and Dickinson 2004). Leighton (2017) analysed connections between vocal repertoire and social system in avian species and found that cooperative breeding was a

significant predictor of repertoire size. Importantly, cooperative breeders possessed significantly more alarm calls than non-cooperative breeders. Cooperative breeders live in social groups where helpers are often genetically related to the breeding individuals they are assisting (Emlen 1991). Although bonds or kinship are clearly not necessary precursors for signalling predator presence to others (Smith 1986), in the majority of cooperatively breeding avian species, nearby conspecifics are likely to be relatives (Emlen 1991; Griesser et al. 2017) which could be an extra force driving the prevalence of distinct alarm calls intended for adults in this group. An additional aspect to consider is whether species live in kin groups outside of the breeding season (Russell 2000; Griesser et al. 2017). This was beyond the scope of the current study but could potentially contribute to alarm call prevalence.

Most species included in this study are known to give a vocalisation used in alarm contexts, with only 18 of the 171 species analysed having no record of possessing an alarm call (Table S2). While the primary source of information on calling behaviour was limited to HANZAB (see Methods), further investigation of the literature on these species did not uncover evidence of alarm calling. This raises the question of why these species do not appear to alarm call. Nine of 49 families are included in the group of non-signallers, and trait correlations between species (phylogenetic signal; see Methods) was strongest for our analysis focussing on possession of a vocal alarm. Four of five cuckoos (Cuculidae) and half of the treecreepers (Climacteridae) and martins (Hirundinidae) are included in the set of non-signallers so phylogenetic constraints might be a relevant consideration. Nevertheless, after controlling for phylogeny, our analysis suggested that species not possessing a vocal alarm foraged on fewer types of food and/or were less likely to be migratory, and we have suggested that these are relevant avenues of further investigation. An additional explanation is simply that these species have not been studied sufficiently. Indeed, there is limited

knowledge on several of the species due to limited research effort and because calls might be emitted infrequently (e.g. White-Browed Treecreeper *Climacteris affinis*; Noske 2020). We must therefore interpret results cautiously until further research confirms which of these species truly does not alarm call. Finding such data is not straightforward as we have encountered with studies of Zebra Finches (*Taeniopygia guttata*). This highly-studied species possesses an alarm call directed at offspring (Zann 1996), but we found no evidence, even after controlled experiments, of an alarm call to adult conspecifics (Butler et al. 2017; 2018).

While each of the eleven variables selected could potentially influence alarm calling behaviour (see Introduction), only three variables were deemed to be important. Our analysis has focused on a specific group of birds inhabiting the Australian arid zone. As datasets that identify life history attributes increase, the possibility of using the same principles employed here on a wider group of birds offers an opportunity to expand this research into different climate zones and continents to reveal further information on the function and evolutionary history of alarm calling. We recognise the limitation of using one, albeit highly regarded, source for vocal information and acknowledge that further evidence of alarm calling behaviour will become known as research continues. In our analysis, we examined species present in Australia's largest biome, however this only included two habitat types. Future work should expand on the current study and include habitat as a factor. Our work highlights that alarm calling is ubiquitous in our focal group, which raises the question of its prevalence across other parts of the world. Clearly not all species alarm call equally, and this research has identified useful avenues for further investigation regarding the co-evolution of life history traits and the way species communicate to conspecifics about predators.

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361 **Data availability statement**

362 The data that support the findings of this study are openly available in the La Trobe
363 University FigShare repository at <https://doi.org/10.26181/5fdfe8912b098>.

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Tables

Table 1. List of alarm call categories (dependent variables) and predictor variables used in the present analysis of alarm communication in Australian arid-zone birds.

Table 2. Results of phylogenetic mixed models to predict the presence of a vocal alarm.

Table 3. Results of phylogenetic mixed models to predict the presence of a distinct alarm call.

Table 4. Results of phylogenetic mixed models to predict the presence of a distinct alarm call directed to adults.

Figure captions

Figure 1. Map of Australia showing certain climate classifications with a key indicating the four desert areas. Original map obtained from the Bureau of Meteorology (<https://www.bom.gov.au>).

Figure 2. Example phylogenetic tree of the 171 bird species used in the analysis. Species in black indicate a species that is not reported to possess a vocal alarm signal, while blue and orange coloured species names represent species that possess a distinct alarm call and a distinct alarm call directed to adults respectively.

Figure 3. Proportion of species possessing different categories of alarm calls used in this analysis. (a) Species recorded as having or not having a vocal alarm signal. (b) Species recorded as possessing only distinct alarm calls, only multi-functional alarm calls, both types, or the type is unknown. (c) Species with distinct alarm calls (either distinct only or having both types) that direct the call or calls to adults, to offspring, to both adults and offspring, or the intended receiver is unknown.

Figure 4. The presence of a (a) vocal alarm and a (b) distinct vocal alarm to adults as a function of number of food types. The solid line in each represents a logistic regression curve fit to the raw data.

575 Figure 5. The relative proportion of species (solid bars) possessing (a) a distinct vocal alarm
576 as a function of levels of mobility. The relative proportion of species (solid bars) possessing a
577 (b) distinct vocal alarm and a (c) distinct vocal alarm to adults as a function of breeding
578 system.

579 **Supplementary material**

580 Table S1. List of families (grouped by order) removed from the initial Atlas of Living
581 Australia area report.

582 Table S2. Species and data used in the current analysis of alarm calling in arid-zone birds.

583