Form and function of on-nest vocalisation and renesting behaviour in the Grey Fantail (Rhipidura albiscapa).

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Acknowledgements page

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Statement of Authentication

The work presented in this thesis is, to the best of my knowledge and belief, original except as acknowledged in the text. I hereby declare that I have not submitted this material, either in full or in part, for a degree at this or any other institution.

[redacted]

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Chapter 4: Nest placement decisions in Grey Fantails (*Rhipidura albiscapa*) relative to neighbouring conspecific nest proximity and stage.

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Nadya M. Sotnychuk	Concept, data collection, data analysis, and writing	80%	[redacted]

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Thesis Abstract

Nest predation is the most common factor impacting nest success in songbirds; therefore, we would expect behaviours present in populations to have evolved to counter this risk. However, there are behaviours present in songbirds that are risky and their benefits are unclear. One such behaviour is the presence of on-nest vocalisations; though important for intraspecific communication they increase the risk of nest predation. Therefore, we would expect birds to minimise on-nest vocalisation to decrease a predator's likelihood of finding nest locations. Yet, some songbird species continue to vocalise on the nest at high rates. Assessing behavioural trade-offs is an integral part of understanding the evolution of extant behaviours. The Grey Fantail (*Rhipidura albiscapa*) is an Australian flycatcher that has high nest predation rates. The adults vocalise on the nest and abandon a high proportion of nests during breeding season, making it an ideal model species to examine the costly behaviours of vocalising on the nest and nest abandonment. In this thesis, I study how on-nest vocalisations and nest site selection strategies, including nest abandonment, might be adaptive strategies to reduce nest predation risk. Using descriptive data, I define the occurrence of on-nest vocalisations and song types produced across nest stages and nesting attempts. The number of on-nest vocalisations decreased across nest stages but did not change with successive nesting attempts. Similarly, the proportion of song types used, and song type diversity did not vary across nesting attempts. I describe three major song types in which the proportion of Type 1 and Type 3 songs varied with nest stage. Song Type 1 increased from egg-laying to early chick and Type 3 decreased from egg-laying to early incubation. The total song type diversity per nest decreased from late incubation to early chick-rearing. My data shows vocal production appears to be strategic, potentially varying due to limited time during the breeding season and the energy costs associated with each nest stage. To examine nest site selection strategies, I used descriptive data to study nest placement of focal pairs in relation to neighbouring nests. I found focal birds placed nests closer to neighbours that were nest building and furthest from neighbours that were egg-laying. Matching neighbour activity during building could allow pairs to benefit from dilution and confusion effects, thereby reducing predation risk. Also, avoiding fertile egg-laying neighbours may save energy by reducing aggressive encounters. I conducted a predator presentation experiment during nest building and found pairs of birds neither abandoned nests nor changed on-nest vocalisation rates over time in response to the presence of a predator. This suggests that a single encounter with a predator near the nest may not be a high enough risk to abandon it, saving the birds time and energy. My thesis proposes that Grey Fantails strategically vocalise on the nest and make nesting decisions to save time and energy. This research contributes to an increased understanding of seemingly costly behaviours in relation to nest predation risk and provides further insight into the evolutionary strategies of nest abandonment and on-nest vocalisations.

Thesis Introduction

Biological Fitness

Organisms must survive and reproduce to ensure their genes persist in the future population. Survival and reproduction work together; for example organisms must provide themselves with nutrients (food/water) as well as ensure they can avoid predation (Brooker et al., 2015) and then they can invest in finding mates in order to pass on their genes to young (Darwin, 1859; Kimbrough, 1980). If individuals in a population do not reproduce successfully, then the population might be under threat of extinction, such as in the case of the decline of the Giant Panda (*Ailuropoda melanoleuca*) (Feng et al., 1991; Martin-Wintle et al., 2015; Zhang & Wei, 2006). Since both survival and reproduction are essential to organisms, it is important to understand their underlying mechanisms. Additionally, offspring must survive until reproductive age, and produce young of their own (Darwin, 1859; Kimbrough, 1980).

Through the process of natural selection, heritable traits that can increase biological fitness of individuals persist in the population (Darwin, 1859; Moodie, 1972). Usually, long-term heritable traits are biological adaptations which can be physiological, morphological, or behavioural (Moermond & Denslow, 1985; Stearns, 1992; Thorp, 1979). Adaptations influence life history traits such as individual size and shape (Moermond & Denslow, 1985; Thorp, 1979), fecundity (Llodra, 2002; Stearns, 1992), longevity (Kaplan et al., 2000; Váchová et al., 2012), and growth patterns (Greeney et al., 2012; Roff et al., 2006). In theory, most traits present in species today are beneficial to the organisms (Lytle & Poff, 2004); otherwise, they would not have persisted in the population. However, there can be cost-benefit trade-offs for many of these adaptations (Lytle & Poff, 2004). For example, humans (*Homo sapiens*) have large brains, which have the benefit of allowing for higher cognitive function and processing but come with a cost of requiring more energy, and large heads can prove problematic during childbirth (Isler & Van Schaik, 2006; Kaplan et al., 2000; Martin, 1983; Navarrete et al., 2011). Some of the functions, costs, and benefits of traits that have persisted in populations to date remain unclear (Lytle & Poff, 2004).

Avian Fitness

One of the most common factors that reduces fitness in songbirds is nest predation (Lack, 1968; Martin, 1993; Ricklefs, 1969). A predation event usually causes destruction and damage to the nest and its contents (i.e. eggs, and chicks), forcing birds to rebuild and re-lay to pass on their genes (Heske et al., 2001; Holt & Lawton, 1994; Vickery et al., 1992). Building a nest is energetically costly, as birds must start a new nest, most of the time choosing a different location, and lay eggs in a shorter amount of time since it is later in the breeding season (Collias & Collias, 1971; Gauthier & Thomas, 1993; Jose et al., 1998). Due to the energy cost and potential risks of nest predation in passerines, some birds have strategies to increase biological fitness and minimise the risk of nest predation (reviewed in Ibáñez-Álamo et al., 2015). Some such strategies include extra-pair paternity (Birkhead & Møller, 1992; Westneat & Stewart, 2003), cryptic plumage colouration of the nesting bird (De Moraes et al., 2020; Götmark, 1997; Slagsvold & Lifjeld, 1997), and discreet nest placement (Feeney et al., 2012; Martin, 1993). Not as well studied is how birds can adjust existent behaviours such as communicating in a way that is less conspicuous.

Avian Communication

Animals, including birds, communicate both within species (intraspecific) and between species (interspecific). Communication comes in the form of various signalling methods including olfactory, chemical, tactile, and audial (Brumm, 2013; Huber, 1988; Searcy & Nowicki, 2010). Each method of communication has costs and benefits, which is why animals implement many different forms of communication (Brumm, 2013; Searcy & Nowicki, 2010). Acoustic communication is prevalent in most taxa, and birds in particular, are known for their acoustics, specifically songs and calls (Baptista & Gaunt, 1994; Catchpole & Slater, 2008). Auditory information is a quick and effective way to communicate across distances (Nordell, 2014). However, auditory cues are not private and any individual hearing the sound has the opportunity to locate the individual that made the sound (Nordell, 2014). There is a trade-off between vocalising enough to communicate within species while minimising accidental interspecific communication that can alert predators or competitors. Assessing these trade-offs, in relation to behaviour and communication patterns, is an important component of investigating animal behaviours.

Acoustic communication has been well studied in birds, particularly on male song or in species where duetting occurs between the male and female (Odom et al., 2014). Recent studies, recognising this sex-based bias, provide evidence of female song across taxa (Odom & Benedict, 2018; Odom et al., 2014; Riebel et al., 2005). Recently research on bird song compared male and female vocalisations in non-duetting birds has been becoming more frequent (Rose et al., 2018; Yamaguchi, 2001). One recent study on the cooperatively breeding Australian magpie (*Cracticus tibicen*) found females sing more often than males in the breeding groups and that overall, more vocalisations were produced in the morning than the afternoon (Dutour et al., 2020). Studying how acoustics vary between sex and the functions of such vocalisations for each sex is important in understanding the evolution of avian acoustics (Mennill & Rogers, 2006). The lack of studies of female song means there is also a lack of research examining the purpose of song across sex (Odom & Benedict, 2018). Determining if males and females use the same types of vocalisations and how they might vary in structure and usage could provide a better understanding of both the functions of these vocalisations and how they have evolved (Kriesell et al., 2018).

Research shows adult and offspring vocalisations at the nest may reveal nest location and increase nest predation risk (Kleindorfer et al., 2014; Kleindorfer et al., 2017; McDonald et al., 2009). For example, nest departure calls have been shown to increase both nest predation rates (McDonald & Greenberg, 1991; Yasukawa, 1989) and nest parasitism by brown-headed cowbirds, *Molothrus ater* (Clotfelter, 1998). Therefore, birds might minimise on- or near-nest vocalisation to decrease a predator's ability to find nest locations. Birds are not limited to only minimising the number of vocalisations, rather they can use different vocalisations to communicate different needs (Hiebert et al., 1989; Marler, 1957; Sibly et al., 2012). Incubation calls or vocal passwords are an on-nest communication found in fairy-wrens that are specific to those functions. (Colombelli-Négrel et al., 2014; Colombelli-Négrel et al., 2012; Kleindorfer, Evans, et al., 2014). In Australian Magpies (*Gymnorhina tibicen*), specific alarm calls have been shown to relay information about the predator type and distance; therefore, birds can strategically alter the types of vocalisations to relay information more efficiently (Dutour et al., 2020). Since higher rates of incubation calls have led to increased rates of nest predation (Kleindorfer, Hoi, et al., 2014), it is expected that vocalisations should be limited or strategic around the nest to minimise the risk of nest predation (Kleindorfer et al., 2017).

Despite the risk, adult birds of some species have been shown to vocalise close to or while on nests (e.g. Davies et al., 2004; Kleindorfer et al., 2017; Leonard, 2008). Although some of these vocalisations have a clear function, many do not, representing a fundamental gap in scientific knowledge. To date, Leonard (2008) is the only comparative analysis of species that sing on the nest. This study is restricted to North America but found 48% of birds vocalise on or near the nest and of that 10% sing on the nest. This includes Northern Cardinal (*Cardinalis cardinalis*) (Halkin, 1997), Warbling Vireo (*Vireo gilvus*) (Howes-Jones, 1985), Least Flycatcher (*Empidonax minimus*) (Kasumovic et al., 2003), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) (Dunham, 1964).

The purpose of those on-nest or near nest vocalisations was described as related to provisioning young, communicating need for nest relief, pair-bonding, defence, or territorial maintenance (Haff et al., 2015; Halkin, 1997; Leonard, 2008). Extra pair paternity and hormones have also been suggested to influence on-nest vocalisation rates (Haff et al., 2015; Leonard, 2008). In Northern Cardinals, higher rates of on-nest singing by females increased the likelihood that the male would come to the nest, if the pair matched one another's song (Halkin, 1997). It is thought that song matching is a way for the female to let the conspicuous male know that it is safe for him to come near, or whether he needed to come in at that time. This singing is to safely coordinate biparental care, more specifically in nest switching, nest visitation, and provisioning young (Halkin, 1997). The rates and types of vocalisation birds produce on and off the nest can be influenced by many factors including past nest fate (Boulton et al., 2003), territoriality (Schmidt et al., 2007), extra pair copulations (Haff et al., 2015; Leonard, 2008), and the amount of human disturbance (Aulsebrook et al., 2020; Aulsebrook et al., 2021; Heske et al., 2001; Potvin, 2017; Potvin et al., 2020). By understanding the influences and patterns of on-nest vocalisations and breeding ecology we can better understand the cost and benefits of seemingly risky behaviours, ultimately setting the the groundwork for understanding the evolution of such life-history traits.

Study Species: Grey Fantail (Rhipidura albiscapa)

The Grey Fantail is a small (~8 g) aerial insectivore commonly found throughout Australia (Higgins et al., 2006). Grey Fantails are an extremely vocal species while on the nest (Beckmann & Martin, 2016; Berger-Tal et al., 2010); both sexes have been observed singing and calling while on the nest during nest building, incubation, and brood rearing (Beckmann unpublished data). Along with high rates of song, the Grey Fantail also has high rates of nest predation (i.e. 83% of all clutches being predated before fledging, Munro, 2007) and renesting attempts, building as many as seven nests in a breeding season (Beckmann et al., 2015). High rates of nest abandonment and on-nest vocalisations seem to be risky and energetically costly; why and how birds use these behaviours are interesting questions to be explored. Nest placement is not fully understood in Grey Fantails; it has been studied in relation to height and distance (Beckmann et al., 2015) but not in relation to the nearest neighbour, active nests nearby, or food abundance. Even with a potentially high cost, high on-nest vocalisations and nest abandonment rates still occur in Grey Fantails suggesting there must be a benefit to these behaviours. This contrary behaviour makes the Grey Fantail an ideal model species to further examine on-nest vocalisations and renesting decisions in respect to predation risk.

Aims and Objectives

I investigated the patterns and inferred potential functions of seemingly risky behaviours in Grey Fantails, to determine if there are benefits to the behaviours. My thesis investigated on-nest vocalisation, nest abandonment and renesting decisions in relation to multiple variables including nest stage, nesting attempt, and past nest fate. My thesis consists of four research chapters written in manuscript style.

Chapter 1. I used descriptive data, collected with minimal interference to the breeding season, to examine on-nest vocalisation rates throughout the breeding cycle across nesting attempts. To better understand the purpose of on-nest acoustics I assessed whether there is a relationship between Grey Fantails' on-nest vocalisations (songs, and calls) and the variables of nest stage and nesting attempt. I hypothesised that the rate of on-nest vocalisations would change across nest stage and nesting attempt. I predicted that on-nest vocalisation rates would decrease throughout the breeding season across stage and nesting attempts. I predicted this trend due to a temporal pressure on nesting birds to produce offspring and keep their from nest location hidden from predators. It is my intent to submit this chapter to *IBIS* for publication.

Chapter 2. I used the same data as Chapter 1 but examined the types of song produced on-nest. I examined song type use on the nest throughout the breeding cycle across nesting attempts. I predicted if on-nest vocalisations, specifically song, do not decrease in the results for chapter 1, that the types of songs made on the nest might vary across nesting stage and attempt. I hypothesised that the on-nest song types usage changes across nesting attempts and nest stages. I predicted that different types of songs will be used at different nest stages rather than nesting attempt because there are different messages that might need to be relayed per stage to partners, neighbours, and nestlings. I also predicted the song diversity used by a pair at the nest will increase at nest stages where more parental duties are present (i.e. in chick rearing vs incubation) in order to relay information by changing song type. The various song types could serve the purpose of relaying such information in a simple way. It is my intent to submit this chapter to *IBIS* for publication.

Chapter 3. I used a field experimental approach to examine whether birds changed on-nest vocalisation rates and nest abandonment rates in response to model type (predator vs control). I hypothesised that nesting building pairs of Grey Fantails would change their nest building behaviour and on-nest vocalisation rate in response to the predator model and not the control model. I expect nest abandonment to increase during nest building when a predator is near the nest, suggesting that nest abandonment might be influenced by predator presence. Also, after a predator is present near the nest, I predicted that birds will reduce their on-nest vocalisation rates to deflect any further attention to the nest. It is my intent to submit this chapter to *Ecology and Evolution* for publication.

Chapter 4. I used nest placement data from an entire breeding season. Nest placement distance from neighbouring nests was examined in relation to past nest fate and neighbouring nest stage. If Grey Fantails strategically build new nests in relation to existing active nests of neighbours then, I hypothesised that the new nest building bird would change its nest placement based off of neighbouring nests stage and distance. I predicted that Grey Fantails would rebuild their subsequent nesting attempts closer to active neighbouring nests and neighbouring nest stages could influence the trend in which pairs would move closer to neighbours at later nest stages (Chapter 4). Neighbouring nests, at later nesting stages have survived longer without a predation event, thereby identifying the location safer for nesting. It is my intent to submit this chapter to *Journal of field ornithology* for publication.

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Chapter 1: The occurrence of on-nest vocalisations across nest stages and subsequent nesting attempts in Grey Fantails (*Rhipidura albiscapa*).

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Abstract

Vocalisations are not a private form of communication. Predators and competitors could locate the vocalising bird, potentially increasing the risk of predation or aggressive encounters. On-nest vocalisations have been shown to increase the risk of nest predation but despite the potential risk some species of birds vocalise on or near the nest. The Grey Fantail (*Rhipidura albiscapa*) is one such species where both partners have been observed vocalising on the nest throughout the nesting cycle, even with high nest predation rates. We describe the occurrence of total on-nest vocalisations, on-nest calls, and on-nest songs in this species across multiple nesting attempts throughout the breeding season. From 203 recordings we extracted a total of 7034 on-nest vocalisations (4496 on-nest calls plus 2538 on-nest songs). The counts of total on-nest vocalisations, calls and songs decreased across nest stage from egg-laying to late chick-rearing. Therefore, pairs of birds could be maximising parental investment against seasonal pressure to reproduce and adjusting vocalisations in relation to the energy needed at each nesting stage. Additionally, counts of on-nest calls decreased slightly across renesting attempts. On-nest calls appear to be more flexible to change across nesting attempt due to higher rates of calls and the typical function of calls. Therefore, although on-nest acoustics can increase the risk of nest predation, birds appear to vary the used and type of the use of vocalisations across the breeding season.

Keywords: Animal communication, Avian breeding ecology, Avian acoustics, Nest-associated vocalisations, Renesting

Introduction

Acoustic communication is prevalent in most taxa and birds are known for their acoustics. Birds produce a wide range of vocalisations which include both songs and calls. Overall, the types of vocalisations within passerine birds appear to have high variation (Catchpole & Slater, 2008; Goretskaia, 2013; Priyadarshani et al., 2018); this variation suggests vocalisations are multifunctional (Catchpole, 1982; Goretskaia, 2013). Vocal communication is an inherently public form of communication because although vocalisations can be cryptic (i.e. quit) there is a risk of eavesdropping from neighbours (Dabelsteen, 2004) as well as predators or competitors locating the vocalising bird**.** Therefore, vocalisations are inherently risky on or near the nest as such sounds can lead to nest predation (McDonald & Greenberg, 1991; McDonald et al., 2009; Yasukawa & Searcy, 1982).

Nest predation is the most common factor that impacts nest success in songbirds (Lack, 1968; Martin, 1993; Ricklefs, 1969), accounting for ~72% of nest failures in Australian songbird species (Remeš et al., 2012). In response to the risk, birds have adapted strategies to counter the risk of nest predation. Some of these strategies include cryptic plumage (Bergerud & Gratson, 1988; Brodsky, 1988; Montgomerie et al., 2001), strategic nest placement (Collias, 1964; Liebezeit & George, 2002; Lima, 2009), and minimizing activity around the nest (Fontaine & Martin, 2006; Ghalambor & Martin, 2001; Ghalambor et al., 2013; Martin et al., 2000). However, not all strategies are used by every prey bird species. By understanding how birds use each strategy amongst and across species we can gain further insight on of the evolution of such strategies.

Trade-offs between minimising predation risk and birds' behaviours have been documented. For example, one such trade-off is evident in studies looking at shorebird nest concealment (minimising predation risk) and flight-initiation distance (Gómez-Serrano & López-López, 2014). Birds must not conceal their nest so much that they are unable to see and ultimately unable to escape from a predator; however, they also need to ensure a predator is not able to easily spot them on the nest. Similarly, a trade-off may exist regarding minimising predation risk and other seemingly risky behaviours such as on-nest vocalisations. Therefore, it would also be expected that birds would minimise their vocalisations on or around the nest to minimise the risk of predation (Kleindorfer et al., 2017) and if not, there is a purpose for those risky vocalisations to still be present in populations using them.

Despite the potential risk, adult birds of some species have been shown to vocalise close to or while on nests (e.g.Davies et al., 2004; Kleindorfer et al., 2017; Leonard, 2008). Research shows on-nest vocalisations and even sound (i.e. white noise) coming from a nest can lead to higher rates of nest predation (Kleindorfer et al., 2018; McDonald et al., 2008; McDonald et al., 2009). For example, an increase in the number of nest departure calls was correlated with an increase in both nest predation rates (McDonald & Greenberg, 1991; Yasukawa, 1989) and brood parasitism (Clotfelter, 1998). Similarly, a study on Superb Fairy-wrens (*Malurus cyaneus*) found higher rates of on-nest incubation calls correlated with an increased rate of nest predation (Kleindorfer et al., 2014). Given the high potential costs, these vocalisations must convey a benefit, or they would not have evolved to be present in the current populations.

While on-nest vocalisations may increase the likelihood of a predator finding the nest, vocalisations (songs or calls) on the nest have been shown to benefit the breeding pair, neighbours, and offspring (Haff et al., 2015; Leonard, 2008). For example, on-nest vocalisations can assist in territory defence by discouraging conspecific competition in the established territory (Small & Boersma, 1990) or as an anti-predation strategy warning both their partner and other birds of potential danger (Davies et al., 2004; Gill & Sealy, 2003; Leonard, 2008; Madden et al., 2005). However, the rates of on-nest vocalisation are potentially influenced by many factors including extra pair paternity and hormone levels in birds (reviewed in Haff et al., 2015; Leonard, 2008). Within a nesting cycle on-nest vocalisations can assist in coordinating parental care for feeding of the on-nest partner or young (Halkin, 1997; Howes-Jones, 1985; Smith & Fretwell, 1974) or relieving the on-nest bird of nest duties (Dabelsteen, 2004; Horn & Leonard, 2008; Leonard, 2008). Determining how birds maximise the benefits of vocalising on the nest while minimising the risk of nest predation can further the understanding of the evolution of bird vocalisation in response to predation risk.

The Grey Fantail (*Rhipidura albiscapa*) is an ideal model species for the study of on-nest vocalisation behaviour. Both partners sing full songs on the nest at various breeding stages (Beckmann & Martin, 2016; Berger-Tal et al., 2010) and this species also has high rates of nest failure, either from nest predation (59% Higgins et al., 2006; 82% Munro, 2007) or nest abandonment before egg-laying (56% Beckmann et al., 2015; 60% Beckmann & Martin, 2016; 47% Munro, 2007). Although the Grey Fantail has high nest failure rates, they also have a long breeding season (~5 months Higgins et al., 2006), which generally leads to multiple nesting attempts during a single breeding season (up to seven nesting attempts Beckmann et al., 2015; up to eight this study). Therefore, the relationship of on-nest vocal production across nest stage and nesting attempts within one breeding season can be examined in this species. The off and on-nest vocalisation rate of this species has yet to be quantified or described, in this thesis we examined on-nest and near-nest vocalisations.

To better understand on-nest vocalisations of Grey Fantails we gathered descriptive data of on-nest call and song counts throughout a breeding season. We predicted that the count of on-nest vocalisations would decrease both as the breeding cycle progressed and across subsequent nesting attempts. We predicted this because we expected as the breeding season progressed pairs would improve communication and coordination, thereby needing fewer vocalisations to communicate later in the season. Additionally, we predicted that the count of on-nest vocalisations would decrease as the season progressed due to the pressure on pairs to have a successful breeding attempt before the season ends, therefore, pairs would reduce on-nest vocalisations to remain cryptic.

Methods

Study Species and Nest Monitoring

We monitored a colour banded population of Grey Fantail in Brisbane Ranges National Park, Victoria, Australia (37°51'10.8"S 144°11'21.2"E), from September 10, 2018 - March 7, 2019. We colour banded birds captured using Ecotone mist nets combined with playback recordings. Birds were sexed based on secondary sex characteristics which were later confirmed based on behaviour during the breeding season. The Grey Fantail is a small (~8g) aerial insectivore with biparental care (Higgins et al., 2006). Grey Fantails build open cup nests, and their clutch size is typically three eggs (Higgins et al., 2006; Munro, 2007). We followed the breeding activities of paired birds (n = 33 pairs plus one triplet in this study) beginning prior to their first nest until two weeks after their final nesting attempt of the season.

We searched for the pairs nest every 3-4 days by following the female of the pair for 30 mins to determine if nest building behaviours were present (i.e. collecting material). Once found, nests were checked every 3-4 days. Nest checks were more frequent (1-2 days) during late building, late incubation and late chick rearing to determine the exact onset of egg laying, incubation, and fledging respectively. Nest checks allowed us to determine nest activity, if no longer active a nest search was conducted that same day.

Collection of On-nest vocalisation behaviour

Where possible, we recorded nests once during egg-laying, three times during incubation (early incubation, days 1-4; mid incubation, days 5-8, late incubation 9-12), and three times during chick-rearing (early, chick age 1-4 days; mid, chick age 5-8 days; late, chick age 9-12 days). We recorded vocalisations on the nest and nest attendance using either video cameras or in-person nest watches (see below for details). The method used was determined by logistics – primarily nest height from ground (i.e. low nests received tripod mounted cameras), and secondarily availability of cameras (i.e. some low nests were observed in person).

Video recording

To video record nests, a camera (Wimius Action Camera 4K 16MP) was mounted on a camouflaged tripod or clipped to a nearby branch (placed no closer than 50 cm from the nest). A Sennheiser MKE2-P-C MKE2 Omni Lavalier Microphone with a black foam softy was placed in line with or under the nest and connected to a Zoom (H4N, H4Npro, or H5) recorder. Both the camera and recorder were connected to a 3200mAh power bank to extend recording times. The Zoom recorder was placed in a plastic bag to protect from weather damage. Both the recorder and power bank were then placed in a camouflage pouch and taped to a tree/tripod or placed on the ground. Cameras were set out in the morning and removed before sunset. Therefore, the amount of time each camera was set up and recording duration varied. Most cameras were up for more than two hours. However due to technical difficulties (camera dying/camera falling n = 4), and adverse weather (i.e. rain; n = 2) six recordings were 74-116 minutes long. The recordings were later annotated using Behavioral Observation Research Interactive Software (BORIS; Friard & Gamba, 2016) and Raven Pro acoustic software (Bioacoustics, 2019).

In-person Nest watch

In-person nest watches typically took place on nests that were too high for a camera. An observer sat 6-15m (horizontal distance) from the nest under camouflage netting, with binoculars, and a Sennheiser ME-66 microphone (pointed at the nest) mounted on a tripod attached to a Zoom recorder. The observer dictated the bird's behaviour into the microphone, focusing on vocalisations and bird identification when the bird was on or near the nest. Most nest watches were 120 mins, however some (n = 22 of 67, 33%) were 60 -119 mins due to logistical constraints and technical or weather-related issues. Nest watches were later annotated using Raven Pro acoustic software (Bioacoustics, 2019).

Annotations

For each recording collected, we extracted two hours of continuous data between sunrise and 6hrs after sunrise. As there was variation in the start and end times of videos and nest watches, this 6-hour time block was subdivided into four bins. Data was allocated into a bin based on the number of minutes after sunrise the recording started as follows: 1) start time between 0-60 min after sunrise, 2) 61-120 min, 3) 121-180 min, and 4) 181-240 min. In order to have an even distribution of recordings across the four bins we first allocated the nest watches to bins as they were logistically constrained (i.e. maximum two hours long, and had a defined start time that was in part constrained by other work the researchers were doing that day). This resulted in an unequal number of recordings per bin. Next, we allocated the camera data to bins. First, any videos shorter than two hours were allocated into the single bin they fit into. Next, videos that did not cover the entire time period between sunrise and 6 hours after sunrise (i.e. started late or ended early) were randomly (using a random number generator) allocated to a bin from the options available given the time constraints. Finally, all remaining videos covered the entire 6-hour time block, and were randomly assigned to a bin in such a way as to ensure the number of recordings per bin was as equal as possible (See Supplementary Material 1.1 for the distribution of recordings and recording type per bin). To do so we first counted the number of recordings currently in each bin. Then, knowing the number of videos remaining, we randomly assigned these to bins until sample sizes were equal across the bins.

Annotations included identification of the bird on the nest (where possible), number and duration of on/off nest bouts, and all on-nest vocalisations (songs and calls; See Chapter 2 Figure 2.1 for example of song types in spectrogram and Supplementary Material 2.1 for examples of different note types). To be considered an on-nest vocalisation the bird must have a part of its body touching the nest at the point of sound production.

Statistical Analysis

Two nests were removed from our analysis; one due to the male having a different partner later in the season, and a second nest that had three adults attending it. These were removed as it was not possible to accurately determine new birds nesting attempt number.

We recorded four types of on-nest vocalisations: songs, calls, call series, and song starts. A song was classified as a string of notes having at least one pure tone ("B" note; See Chapter 2 Supplementary Material 2.2) and all notes were within 0.5 seconds of each other. Single notes greater than 0.5 seconds from each other were counted as calls. A call series consisted of either a single note type repeated or a string of up to four notes that are a combination of two or more note types that were less than 0.5 seconds apart. Since call series were infrequent (n = 9 consisting of 95 single notes) each note in a call series was added to the total call count. Song starts were classified as 1) a series of notes that are each within 0.5 seconds of each other and having no pure tone, 2) must contain more than one type of note, and 3) must have five or more notes. The total number of on-nest song starts was low (n = 53, <1% of the total vocalisations); therefore, we combined songs and song starts into one category. Recordings where birds never touched the nest were removed from analysis. Henceforth we use the term "on-nest acoustics" or "on-nest acoustic counts" when referring to data or results that apply to all three vocalisation types collectively; on-nest vocalisations (this includes both songs and calls), on-nest calls only, and on-nest songs only.

To test if the total number of on-nest vocalisations (i.e. 'vocalisation count') varied between nest stages and across nesting attempts we used a Quasi Poisson model (glmmPQL the package lme4 see Bates et al., 2015). We used a Quasi Poisson model due to the count nature of the data and because the data was over dispersed in a Poisson model. The model included the independent variables of sex (male, female, unknown), nest stage (see below), nesting attempt number (1-8), total nest on-bout duration per bird for each recording, and the random variable of bird identification nested within territory number. Nest on-bout duration was the total time the bird was on the nest during the recording; this was included in the model as an offset variable to control for potential influences of the amount of time spent on the nest and on-nest vocalisation rate. We repeated the above approach for two more models of on-nest calls and on-nest songs. Using these three models (on-nest vocalisation, calls and songs) allowed us to determine if changes were occurring in all on-nest vocalisations or if any trends found were specific to the type of vocalisations (i.e. calls or songs). Nest stage was originally included as a categorical factor (categories of egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing, late chick-rearing). However, the song and call models did not converge when nest stage was included. Since the ordinal variable nest stage has a linear trend, nest stage was made continuous in the final models which provided a better fit. Nest stages egg-laying through late chick-rearing were given the numbers 1-7 respectively (categories of egg-laying = 1, early incubation = 2, mid incubation = 3, late incubation = 4, early chick-rearing = 5, mid chick-rearing = 6, late chick-rearing = 7). Post hoc test were run on all three models using analysis of variance (ANOVA).

All statistical analysis was performed in R version 4.0.2 (Team, 2020 See Supplementary Material 2, 3 and 4).

Results

Breeding Ecology

We monitored 66 adult Grey Fantails and a total of 113 nests during the breeding season. Breeding pairs had between 1-8 nesting attempts during the season ($\overline{x}$ = 3.7 nests ± 1.9 SD), 43% of nests were abandoned (n = 42 during building and n = 6 during incubation), 44% (n = 50) of the nests were depredated, and 13% (n = 15) were successful. Of predated nests, 56% (n = 28) occurred during the stage of incubation, 40% (n = 20) during chick-rearing, and 4% (n = 2) during egg-laying.

The first nest of the season was found on Oct 12, 2018 and the final nest initiation date was Jan 4, 2019. The final nest monitored during the season successfully fledged on Feb 5, 2019, the last camera for that nest was placed on Feb 2, 2019. Usually, Fantail eggs hatch on day 13 of incubation but range from 12-14 days. We had five pairs over incubate eggs (<14 days) one pair was predated on day 24 of incubation and four pairs abandoned dead eggs after 19, 20, 29, and 38 days of incubation. Recordings taken outside the normal time window for incubation were not used for this analysis.

On-Nest Acoustic Counts

Of 210 recordings, we used 203 recordings in our analysis (66 in-person nest watches and 137 camera recordings; table 1.1) from 55 nests in 31 territories. Only birds that were physically on the nest during the recording were included in the analysis (i.e. if a bird did not attend the nest during the recording it was excluded). Therefore, sample sizes were n = 175 (female), n = 163 (male), and n = 83 (unknown). We recorded a total of 7034 on-nest vocalisations that were used for analysis ($\bar{x}$ = 16.4 ± 21.7 SD per recording, range of 0-167), consisting of 4496 on-nest calls and 2538 on-nest songs ($\bar{x}$ = 10.7 ± 16.7 SD per recording, range of 0-161, and $\bar{x}$ = 6.0 ± 9.3 SD per recording, range of 0-78, respectively). On-nest vocalisations by sex were n = 2961 for female ($\bar{x}$ = 16.9 ± 18.4 SD, range = 0-105), n = 2030 for males ($\bar{x}$ = 12.5 ± 18.6 SD, range = 0-140), and for unknown n = 1924 ($\bar{x}$ = 22.9 ± 30.5 SD, range = 0-167).

After controlling for any effect of incubation duration, the total number of on-nest acoustics did not differ based on bird sex (on-nest vocalisation: $\chi^2=1.5$, *df* = 2, *p* = 0.46; on-nest call: $\chi^2=0.84$, *df* = 2, *p* = 0.65; on-nest song: $\chi^2=1.7$, *df* = 2, *p* = 0.42). We found on-nest acoustic counts decreased across nest stages in all models (on-nest vocalisation: $\chi^2=47.2$, *df* = 1, *p* < 0.001; on-nest call: $\chi^2=32.7$, *df* = 1, *p* < 0.001; on-nest song: $\chi^2=34.9$, *df* = 1, *p* < 0.001; Figure 1.1). There was a significant effect of nest attempt number on the number of calls produced; as nesting attempt number increased, the number of on-nest calls decreased ($\chi^2=6.5$, df = 1, p = 0.01; Figure 1.2) but no trend was observed in relation to on-nest vocalisation and on-nest songs ($\chi^2=3.2$, *df* = 1, *p* = 0.07, and $\chi^2=0.10$, *df* = 1, *p* =0.76, respectively; Figure 1.2).

Since this data was collected using both in-person and remote recording methods context for behaviour was not able to be obtained outside the field of view. We hope these results will help in setting the groundwork in understanding the context of such behaviours.

Discussion

As predicted, the total number of on-nest acoustics decreased as nests were further along in the nesting cycle (stage of the nest). These results support the Parental investment theory which predicts as the investment into young increases parents should have behaviours that relate to the value of their offspring to maximise fitness (Trivers 1972). Therefore, in monogamous species with biparental care as the nesting cycle progresses cumulatively more time and effort are invested into the nest (see Figure 7.3 in Trivers 1972). By decreasing the number of on-nest vocalisations adult birds could be maximising their reproductive success while keeping the nest hidden from nest predation without any added direct risk to the adult.

In addition to the potential of minimising the risk of nest predation by vocalising less as the breeding season progresses the adult bird can save time and energy. This can become more important at later stages in the nesting cycle due to an increase in parental duties from egg-laying to chick-rearing as parents must feed young in addition to brooding and incubating (see Clutton-Brock, 2019). From the stage of egg-laying to late chick-rearing predicted total number of on-nest acoustics per minute decreased by 70% (on-nest vocalisation = 8.1 to 2.4, on-nest call = 5.0 to 1.5, on-nest song = 2.8 to 0.8). For on-nest vocalisations and calls there was a decrease in the predicted count of 0.5 between each nest stage. This decrease in number of on-nest acoustics across nest stage suggests that as the nesting cycle progresses pairs might be mitigating predation risk as well as saving energy by lowering the total number of on-nest acoustics.

As the breeding season progresses birds are running out of time to have a successful nesting attempt. Due to the temporal pressure and the potential increased risk of predation on-nest acoustics can cause we predicted the total number of on-nest acoustics would decrease with each nesting attempt. Contrary to our predictions, there was no change in total on-nest vocalisation and song counts across nesting attempt and nest stage; however, on-nest call counts did decrease with renesting attempts. We suspect the total number of on-nest songs is driving the non-significant result of on-nest vocalisation production. Therefore, the difference in our results between the types of on-nest vocalisations (song vs calls) could be attributed to the general function and occurrence of each type of vocalisation. Bird songs are generally louder, produced at a lower rate, and are used in many contexts while calls are produced at higher rates and are used for more short-term vocal communication (Catchpole & Slater, 2008). In most contexts, during the breeding season, bird song is used for communication such as mate attraction, and territory defence (Catchpole & Slater, 2008; Langmore, 1998).

In Grey Fantails, the context of song use is mostly unknown, however, there is evidence that males and females increase their song rate in response to playback, indicating they do use song for territory defence (Kovach unpublished data). Since the maintenance of a territory and partner is needed throughout the breeding season the use of song might need to be consistent across nesting attempt. Although there is a time pressure as the breeding season progresses, changing the rate of on-nest song might not be the most beneficial strategy. Bird calls on the other hand, typically offer short-term benefits of communication, such as contact calls (Haff et al., 2015; Halkin, 1997), individual recognition (Szipl et al., 2014), and alarm calling (Gill & Sealy, 2003; Haff et al., 2015; Welbergen & Davies, 2009). These functions are important, but pairs of birds might be able to improve on their vocal coordination over time and limit calls according to pressures during the breeding season. Additionally, since in this study there was almost double the number of calls than songs recorded (n = 4696 and n = 2538, respectively), a change in call counts might be more easily observed at later nesting attempts than in songs. The difference in the number of predicted calls count per minute from nesting attempt one to eight decreased by 52% (4.6 to 2.2 respectively). In predator model presentations when returning to nest after a model presentation female American Robins (*Turdus migratorius*) responded with two types of vocalisations that were produced at different rates depending on the predator type (Gottfried 1985). Suggesting the amount and types of calls reveal specific information about the threat further experimental manipulation will be needed to understand the context of these vocalisations in Grey Fantails.

We observed no change in the total number of on-nest acoustics due to bird sex (male, female, and unknown). Munro (2007) determined parental effort across sex in Grey Fantails is similar; females contributed to only slightly more than half of incubation and brood care. Therefore, males and females might be using on-nest acoustics for similar purposes. In recent playback experiments, male Grey Fantails increased their in-territory song rate at a higher rate than females (Kovach unpublished data). Suggesting on-nest acoustics function for more than just territory defence, if at all. Similarly, in Superb Fairy-Wrens (*Malurus cyaneus)* there was no difference in sex-specific song rates in a territory across the breeding season but once playback recordings were used to determine song function females produced higher rates of song; this was attributed to song function in the context of the playback (Cain & Langmore, 2015). Therefore, because we found no difference between sex, a playback experiment could reveal different rates of vocalisations between sex, if on-nest vocalisations are for sex-specific communication purposes. One constraint of this study is that not all birds on the nest could be identified due to poor recording quality, nest height, or rapid switches where bands are not visible. The unknown sex category makes up ~21% of the data; however, since this is a small percentage of the data, we do not expect the unknown category is driving these results. These results contribute to the knowledge of female vocalisations that has been commonly overlooked (Leonard, 2008; Odom & Benedict, 2018; Odom et al., 2014), showing similar counts of vocalisations across sex.

In conclusion, our results show that the total number of on-nest acoustics decreases across breeding stage and on-nest call counts decreases across nesting attempt, regardless of the sex of the bird in Grey Fantails. Therefore, although on-nest acoustics might increase risk of nest predation, birds could be mitigating the use of these vocalisations. Fantail pairs might be maximising the investment already made to the current nest against the temporal pressure to have successful offspring and the parental duties required at each stage. On-nest calling when compared to on-nest songs appear to have more flexibility for change across nesting attempt and we suspect this is due to the already high numbers of calls and the typical functions of calls in comparison to songs. This research sets the groundwork in understanding the frequency of occurrence of on-nest acoustics in Grey Fantails; however, future investigation into the function and diversity within these vocalisations is needed. Future studies could include; 1) examining the structure and types of songs and calls; 2) examining the spacing between song and call production; 3) analysis of the relationship between on and off nest vocalisation within a territory; and 4) experiments to determine the function of on-nest acoustics.

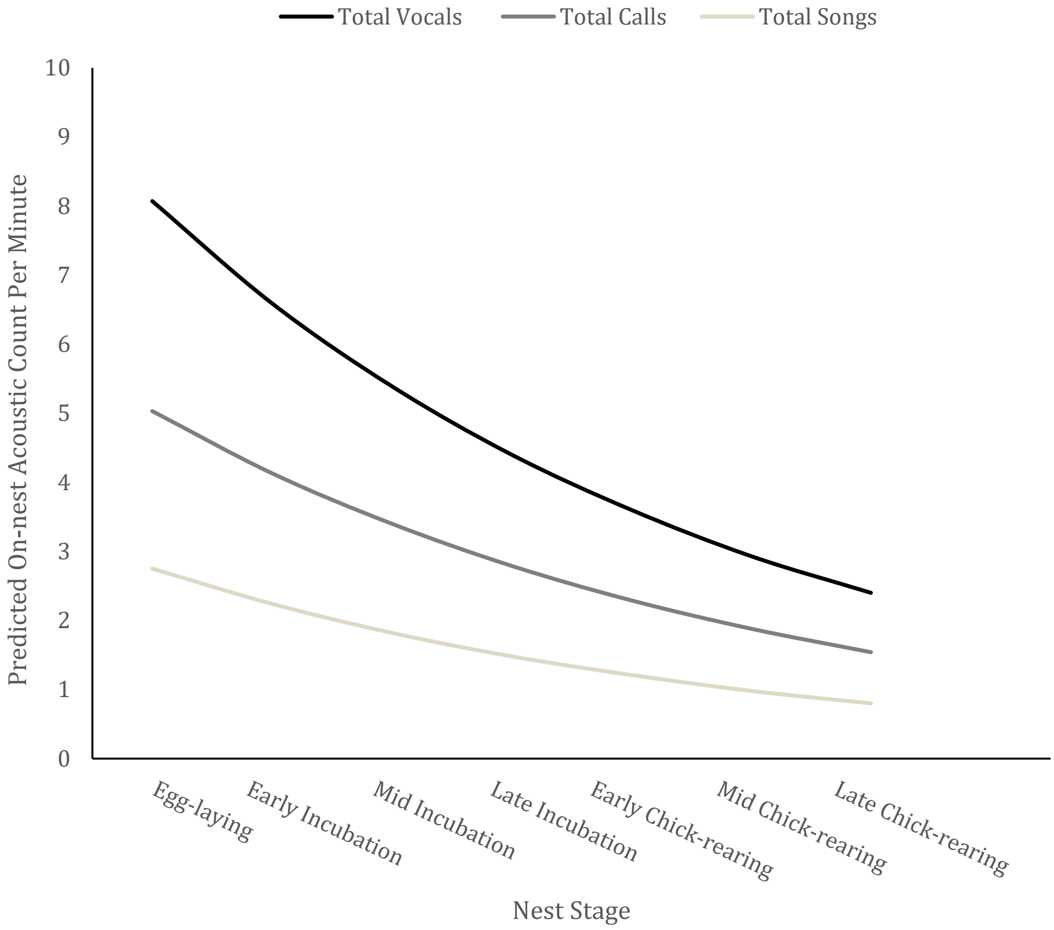

Figure 1.1: Model predicted on-nest acoustic count (total vocalisations, calls, and songs) per minute arranged by nest stage (egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing, and late chick-rearing).

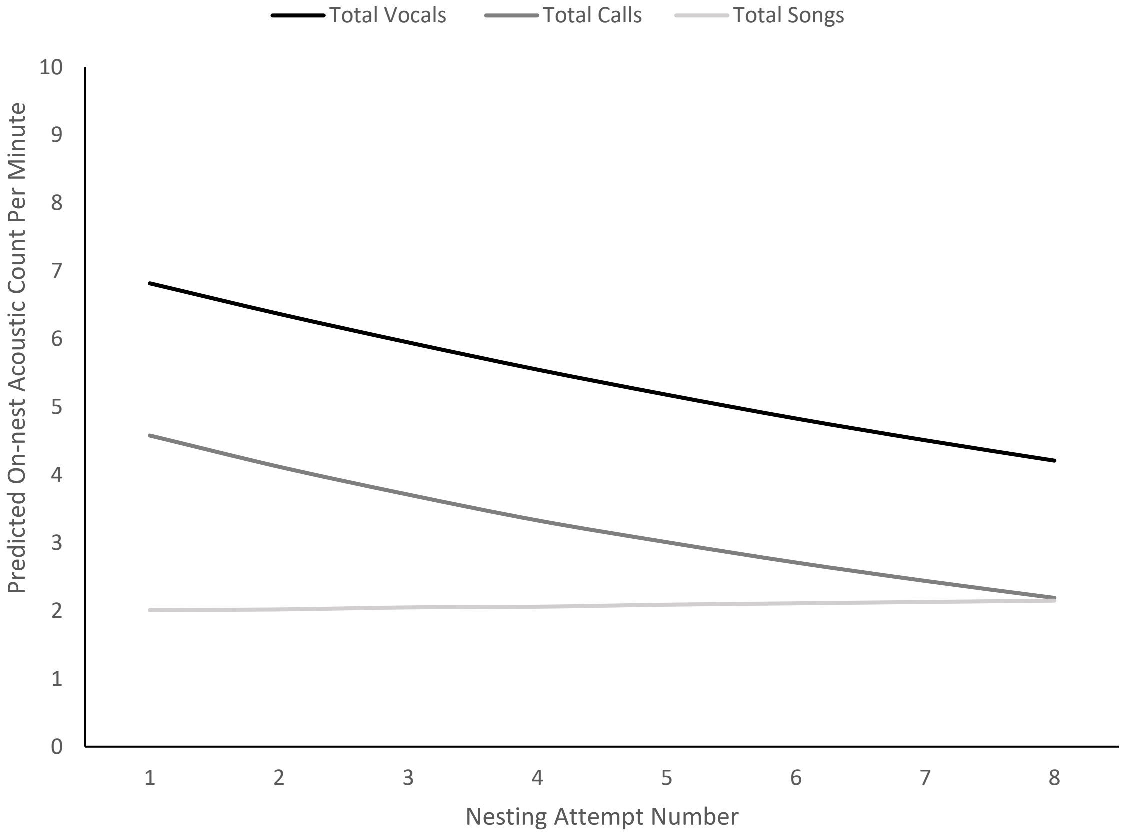

Figure 1.2: Model predicted on-nest acoustic count (total vocalisations, calls, and songs) per minute arranged by nesting attempt number from 1 nest to 8.

Table 1.1: Number of nest recordings used for analysis arranged by recording type (camera or nest watch) and nest stage (egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing, and late chick-rearing).

Nest Stage	**Number of Camera Recordings**	**Number of Nest Watches**	**Total Number of Recordings**
Egg-laying	25	5	30
Early Incubation	29	12	41
Mid Incubation	21	20	41
Late Incubation	23	12	35
Early Chick-rearing	18	6	24
Mid Chick-rearing	13	7	20
Late Chick-rearing	8	4	12

Supplementary Material 1.1: Distribution of recordings by grouped time bin (1-4), nest stage (egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing, late chick-rearing), and recording type (nest watch or camera).

Nest Stage	Bin Number	Recording Type		Total Number of Recordings
		Camera Recordings	Nest Watches	
Egg-laying	1	7	0	7
	2	5	4	9
	3	7	0	7
	4	7	1	8
Early Incubation	1	10	0	10
	2	8	3	11
	3	8	2	10
	4	4	7	11
Mid Incubation	1	10	1	11
	2	6	4	10
	3	6	4	10
	4	0	11	11
Late Incubation	1	5	4	9
	2	8	0	8
	3	7	3	10
	4	4	5	9
Early Chick-Rearing	1	7	1	8
	2	5	2	7
	3	4	0	4
	4	3	3	6
Mid Chick-Rearing	1	5	0	5
	2	4	2	6
	3	3	0	3
	4	2	5	7
Late Chick-rearing	1	4	1	5
	2	4	0	4
	3	1	2	3
	4	0	1	1
Total Number of Recordings		144	66	210

Supplementary Material 1.2: Simplified R code and output for total on nest vocalisation quasi Poisson model.

```
> qp_vocal_all <- glmmPQL(total_on_nest_vocals ~ stage_number + nest_number  +  sex +
inc_time,
+                   random = ~ 1|territory_id/bird_id,
+                   data=vocal_sex, family = quasipoisson)
iteration 1
iteration 2
iteration 3
iteration 4
iteration 5
> summary (qp_vocal_all)
Linear mixed-effects model fit by maximum likelihood
  Data: vocal_sex
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | territory_id
        (Intercept)
StdDev:   0.3576661

 Formula: ~1 | bird_id %in% territory_id
        (Intercept) Residual
StdDev:   0.4705479  3.22777

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects:  total_on_nest_vocals ~ stage_number + nest_number + sex + inc_time
                 Value  Std.Error  DF   t-value p-value
(Intercept)   2.6842174 0.21540790 330 12.461091  0.0000
stage_number -0.2026114 0.02967643 330 -6.827350  0.0000
nest_number  -0.0647753 0.03628154 330 -1.785351  0.0751
sexM         -0.0906839 0.16628501  56 -0.545352  0.5877
sexU          0.1356138 0.17057182  56  0.795054  0.4299
inc_time      0.0173329 0.00204371 330  8.481131  0.0000
 Correlation:
             (Intr) stg_nm nst_nm sexM   sexU
stage_number -0.484
nest_number  -0.379  0.002
sexM         -0.426  0.012 -0.029
sexU         -0.310 -0.010  0.073  0.401
inc_time     -0.533  0.167 -0.144  0.194 -0.089

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.4037266 -0.6492533 -0.3018735  0.2647799  5.1972734
```

```
Number of Observations: 422
Number of Groups:
          territory_id bird_id %in% territory_id
                 31                    89
> Anova(qp_vocal_all)
Analysis of Deviance Table (Type II tests)

Response: zz
           Chisq Df Pr(>Chisq)
stage_number 47.2850  1  6.138e-12 ***
nest_number   3.2335  1    0.07215 .
sex          1.5433  2    0.46225
inc_time     72.9670  1  < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Supplementary Material 1.3: Simplified R code and output for total on-nest calls (cotn) quasi Poisson model.

```
> qp_call_all <- glmmPQL(cotn ~ stage_number + nest_number + sex + inc_time,
+                   random = ~ 1|territory_id/bird_id,
+                   data=vocal_sex, family = quasipoisson)
iteration 1
iteration 2
iteration 3
iteration 4
iteration 5
> summary (qp_call_all)
Linear mixed-effects model fit by maximum likelihood
  Data: vocal_sex
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | territory_id
        (Intercept)
StdDev:   0.2965959

 Formula: ~1 | bird_id %in% territory_id
        (Intercept) Residual
StdDev:   0.5404795  3.07356

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects:  cotn ~ stage_number + nest_number + sex + inc_time
                  Value  Std.Error  DF   t-value p-value
(Intercept)   2.3066871 0.24313546 330  9.487251  0.0000
stage_number -0.1970023 0.03467932 330 -5.680685  0.0000
nest_number  -0.1017925 0.04019681 330 -2.532353  0.0118
sexM         -0.0866290 0.19261061  56 -0.449762  0.6546
sexU          0.1073066 0.19681463  56  0.545216  0.5878
inc_time      0.0181097 0.00238690 330  7.587117  0.0000
 Correlation:
             (Intr) stg_nm nst_nm sexM   sexU
stage_number -0.509
nest_number  -0.371  0.025
sexM         -0.442  0.011 -0.023
sexU         -0.315 -0.008  0.076  0.401
inc_time     -0.557  0.163 -0.143  0.197 -0.090

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.5794460 -0.6404625 -0.3287716  0.3242581  7.0373221

Number of Observations: 422
```

```
Number of Groups:
          territory_id bird_id %in% territory_id
                 31                      89
> Anova(qp_call_all)
Analysis of Deviance Table (Type II tests)

Response: zz
             Chisq Df Pr(>Chisq)
stage_number 32.7356  1  1.056e-08 ***
nest_number   6.5053  1    0.01076 *
sex           0.8417  2    0.65650
inc_time     58.3946  1  2.145e-14 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Supplementary Material 1.4: Simplified R code and output for total on-nest songs (sotn) quasi Poisson model.

```
> qp_song_all <- glmmPQL(sotn ~ stage_number + nest_number + sex + inc_time,
+                  random = ~ 1|territory_id/bird_id,
+                  data=vocal_sex, family = quasipoisson)
iteration 1
iteration 2
iteration 3
iteration 4
iteration 5
iteration 6
> summary (qp_song_all)
Linear mixed-effects model fit by maximum likelihood
  Data: vocal_sex
  AIC BIC logLik
   NA  NA     NA

Random effects:
 Formula: ~1 | territory_id
        (Intercept)
StdDev:   0.5254667

 Formula: ~1 | bird_id %in% territory_id
        (Intercept) Residual
StdDev:   0.5492947 2.310705

Variance function:
 Structure: fixed weights
 Formula: ~invwt
Fixed effects:  sotn ~ stage_number + nest_number + sex + inc_time
                 Value  Std.Error  DF   t-value p-value
(Intercept)   1.4736328 0.26468175 330  5.567565  0.0000
stage_number -0.2067866 0.03525987 330 -5.864646  0.0000
nest_number   0.0140510 0.04587485 330  0.306289  0.7596
sexM         -0.2266054 0.20200100  56 -1.121803  0.2667
sexU          0.0365766 0.20843226  56  0.175484  0.8613
inc_time      0.0161497 0.00242117 330  6.670194  0.0000
 Correlation:
             (Intr) stg_nm nst_nm sexM   sexU
stage_number -0.450
nest_number  -0.395 -0.038
sexM         -0.398  0.013 -0.031
sexU         -0.293 -0.008  0.063  0.386
inc_time     -0.507  0.167 -0.136  0.178 -0.093

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.1342802 -0.6203185 -0.3443385  0.2732340  7.1876122
```

```
Number of Observations: 422
Number of Groups:
           territory_id bird_id %in% territory_id
                   31                     89
> Anova(qp_song_all)
Analysis of Deviance Table (Type II tests)

Response: zz
             Chisq Df Pr(>Chisq)
stage_number 34.8901  1  3.488e-09 ***
nest_number   0.0952  1     0.7577
sex          1.7173  2     0.4237
inc_time     45.1332  1  1.841e-11 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

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Chapter 2: On-nest song types and song diversity across nest stages and subsequent nesting attempts in Grey Fantails (*Rhipidura albiscapa*).

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Abstract

Avian acoustic communication consists primarily of songs and calls. Due to their complexity and link to learning and language development, songs have been more widely studied than calls, and vary highly across species and the context in which they are used. Since auditory cues are not private signals, there is also a risk that predators may locate the individual singing, which can further modulate singing behaviour. On-nest vocalisations are likely to be particularly risky and have been shown to increase the rate of nest predation yet are seen in several species including the Grey Fantail (*Rhipidura albiscapa*). Grey Fantails experience high nest predation rates and engage in multiple nesting attempts, with the number of on-nest songs decreasing across nesting stages (egg-laying to late chick-rearing) but not across renesting attempts. We examined on-nest song type production and usage across different nesting stages and nesting attempts to better understand the behavioural variation of song usage. Three predominate on-nest song types (`83% of the data) were used, while all other song types were rare. We analysed how these three common song types and an 'other' category were used, and neither song diversity nor proportion of song types used varied across different nesting attempts. Song diversity and the proportion of Type 1 and Type 3 songs varied by nest stage. Song diversity decreased from late incubation to early chick-rearing, suggesting as parental effort increases parents might resort to simpler more common songs. Type 1 songs were the most common and as such were likely multifunctional, increasing in usage between egg-laying to early chick-rearing breeding stages. The proportion of Type 3 songs was highest during egg-laying, indicating that this song types might be linked to fertility or mate bonding during this critical stage. Clear patterns in the usage of Type 2 and 'other' songs were not apparent. This research provides the first description of predominant on-nest song types in Grey Fantails, with usage of the main three types varying. Despite significant costs to on-nest singing, it remained common in the population and was clearly being used at key nesting stages. Further research on the persistence and precise function of these newly identified song types is warranted.

Keywords: Animal communication, Song Repertoire, Birdsong, Song variation

Introduction

Animals use various signalling modalities to communicate, including olfactory, chemical, tactile, and acoustic pathways (Bradbury & Vehrencamp, 1998; Huber, 1988; Martinelli, 2017). In birds, one of the most studied forms of communication is acoustic communication (Baptista & Gaunt, 1994; Catchpole & Slater, 2008), with previous research focused on comparing avian signalling to human speech (Bruno, Jarvis, Liberman, & Tchernichovski, 2021; Slater, 2012) and the abundance of avian vocalisations (Baptista & Gaunt, 1994; Catchpole & Slater, 2008). Avian vocalisations consist primarily of songs and calls. In most species calls are the shorter and simpler forms of acoustic communication, while songs are longer and more complex (Catchpole & Slater, 2008; Hauser & Konishi, 2003), although both are likely the extreme ends of a continuum of vocal complexity from calls to songs. Calls are thought to be mostly innate, while songs are usually considered to be learned from a bird's social environment, with the timeframe for learning varying between species (Hauser & Konishi, 2003). Due to their repertoire complexity and link to learning and language development, songs have been more widely studied than calls (Bruno et al., 2021; Slater, 2012).

Songs have multiple defining characteristics that have been quantified across species, including the number, order, diversity, amplitude, and frequency of notes contained within the vocalisation (Catchpole & Slater, 2008; Nowicki & Searcy, 2004; Sawant, Arvind, Joshi, & Robin, 2021). A bird’s repertoire size is usually the number of distinct types of songs that a focal bird can produce (Searcy, 1984). For species with large repertoire sizes in excess of 100 different songs, it is not always possible to record the full repertoire, even with thousands of song recordings across a population, as the usage rate of song types can vary considerably, making rarer forms more difficult to encounter (Beecher & Beecher, 1979; Byers, 2017; Byers & Kroodsma, 2009; Kroodsma, 1977). Therefore, studies with birds that have large repertoires do not define a whole species repertoire but examine the diversity of song types present within a given sample. Many proposed methods have been used for defining song types (reviewed song "complexity" in Najar & Benedict, 2019). The number and function of various song types have been shown to differ across species and the song types produced within a species can have specialised functions (Catchpole & Slater, 2008; Gil & Gahr, 2002).

While the number of song types produced can vary greatly across species, in most bird species repertoire size is relatively small at less than 10 song types (Beecher, Campbell, & Stoddard, 1994; Robbins, 2018). The upper limit of repertoire size is considerable, with some species having over three thousand song types in their repertoire, such as in the Brown Thrasher (*Toxostoma rufum*) (Robbins, 2018; Tuttle-Adams, 2020). The variation across species can be attributed in part to functions of song. In some species, sexual selection drives increasing complexity as females prefer males with larger song repertoires, while in others repertoire size has no bearing on mate choice (Byers & Kroodsma, 2009).

The context in which songs are used within species also impacts repertoires, as different song types can relay different information. For example, male Yellow Warblers (*Setophaga petechia*) produce songs of two primary types; Type 1 is directed at females and Type 2 is considered territorial and directed at males (Spector, 1991; Weary, Lemon, & Perreault, 1994). Similarly, the Chestnut-sided Warbler (*Dendroica pensylvanica*) has two primary song types, the first type is used outside the breeding season while the second type is used during interactions with males (Byers, 1996; Kroodsma, Bereson, Byers, & Minear, 1989). Byers (2017) experimentally examined the rare song types (9% of 1521 songs) of the Chestnut-sided Warbler to show that the proportion of rare song types increased in an aggressive context. Although, few studies have found functional differences between vocalisation in birds another avian example is in that female American Robins (*Turdus migratorius*) returning to the nest used different vocalisation types and rates dependent on the predator type during model presentations (Gottfried 1985). This predator-specific alarm calling has also been observed in non-avian species especially in small mammals like ground squirrels (Owing & Virginia 1978; Robinson

1980). The types and rates of songs must be fully understood first to set the framework to run experimental manipulations. Using song types in specific contexts might relay information without increasing the rate of vocalisations.

While auditory cues can be helpful in relaying information, acoustic signalling in avian systems is further complicated by the fact that acoustic signals are not private, and any individual hearing the sound could locate the signaller regardless of whether or not they were the intended recipient (Nordell, 2014). This potential eavesdropping can have negative impacts on signallers, particularly if predators are able to determine the location of a signalling individual. For example, on-nest vocalisations are inherently risky and have been linked to increased nest predation rate (Kleindorfer, Hauber, & Colombelli-Négrel, 2018; McDonald, te Marvelde, Kazem, & Wright, 2008; McDonald, Wilson, & Evans, 2009). Nests are immovable structures and once found a predator can consume all nest contents. While many of on-nest vocalisations are relatively simple calls, the use of complex on-nest song has surprisingly been reported on multiple continents. In North American birds, on-nest song has been estimated to be present in about 10% of bird species (Leonard, 2008). Despite the a cost of signalling in risky situations, producing on-nest song is more common than previously thought.

Research focusing on the purpose of on-nest song and types of songs produced on the nest is a relatively new area of study. So far, the functions of near and on-nest song are primarily for mate attraction (Elie et al., 2010; Halkin, 1997; Leonard, 2008) and territory maintenance (Chiver, Morton, & Stutchbury, 2007; Howes-Jones, 1985; Kasumovic, Ratcliffe, & Boag, 2003), similar to the off-nest functions of song (Beecher, 2008; Catchpole & Slater, 2008; Kroodsma & Byers, 1991; Langmore, 1998; Nowicki & Searcy, 2004). Some on-nest songs have been shown to be used for nest defence against brood parasites (Steckler & Conway, 2012). Additionally, on-nest song can assist with parental coordination for nest relief or feedings of adult or young (Halkin, 1997; Leonard, 2008; Ritchison, 1983). Most studies of on-nest song, unless in duetting birds, have focused on the occurrence of on-nest songs in different contexts, but have not explored the types of songs being produced.

The Grey Fantail (*Rhipidura albiscapa*) is a small (~8g) flycatcher with biparental care (Higgins, Peter, & Cowling, 2006) and reportedly high vocalisation rates throughout the breeding season both on and off the nest (Beckmann & Martin, 2016; Berger-Tal, Berger-Tal, & Munro, 2010). The occurrence of on-nest vocalisations (call and songs) was quantified and the predicted occurrence of on-nest song decreased across nesting stages but not across nesting attempts (Chapter 1). Additionally, due to a combination of high nest abandonment rate (nests abandoned before egg-laying: 56% Beckmann, Biro, & Martin, 2015; 60% Beckmann & Martin, 2016; 47% Munro, 2007) and high rates of nest predation (~59% Higgins et al., 2006; ~82% Munro, 2007), the Grey Fantail has multiple nesting attempts throughout a single breeding season (up to 8 nesting attempts Chapter 1). This makes the Grey Fantail an ideal model species to study changes in on-nest song types, across nesting stages and nesting attempts within a breeding season.

To date, no publications have described the Grey Fantail's song types or repertoire on or off the nest. In this study we analysed the diversity and usage of different on-nest song types at each nesting stage and across nesting attempts in this species. We hypothesised the occurrence of each song type would vary across nest stages and nesting attempts because we speculate each song type could be used to relay different information. Additionally, we predicted that the diversity of song types used would increase linearly across nesting stages, as the overall number of songs recorded decreased. As adult birds decrease vocalisations, they still need to communicate. Increasing song diversity can be one way of minimising predation risk whilse still maintaining essential communication. Given this, we anticipated that on-nest communication would change across the nesting season as communication within pairs became more efficient, and potentially new song types were learnt within a population. Understanding the factors that influence different vocal cues (i.e. song types) and their usage context in this species will help in understanding why these risky vocalisations are maintained across a range of species.

Methods

Study Species and Nest Monitoring

The Grey Fantail is a small (~ 8g), biparental insectivore that builds open cup nests, laying a clutch of typically three eggs (Higgins et al., 2006; Munro, 2007). We monitored a colour banded population of Grey Fantails in Brisbane Ranges National Park, Victoria, Australia (37°51'10.8"S 144°11'21.2"E), from September 10, 2018 to March 7, 2019. Upon capture in Ecotone mist nets birds were colour banded and sexed, where possible, using secondary sexual characteristics (presence or absence of a brood patch or cloacal protuberance) or by behaviour during the breeding season as females complete most of the nest building. (Beckmann & Martin, 2016; Munro, 2007; Sotnychuk Chap 3 Supplementary Material 3.3). We followed the breeding activities of the birds that established a pair (and one triplet in this study), for the entire breeding season, beginning prior to their first nest until two weeks after the final nest was completed (either fledged, predated, or abandoned).

Every 3-4 days we searched for nests by following the female of the pair for 30 minutes to look for signs of nest building (i.e. collecting material). Once a nest was found, each was checked every 3-4 days while active, with more frequent checks (1-2 days) conducted during the late building, late incubation, and late chick rearing to determine the exact onset dates of egg laying, incubation, and fledging, respectively. If during a nest check the nest was no longer active (i.e. abandoned or predated), nest searches for that pair resumed that day to ensure all renesting attempts were found.

Data collection

We collected up to seven nest recordings per nesting attempt, where possible. Nests were recorded once during egg laying, three times during incubation (days after last egg laid;

early: 1-4, mid: 5-8, late: 9-12), and three times during chick-rearing (days after first chick hatched; early: 1-4, mid: 5-8, late: 9-12). Each nest recording lasted at least two hours for each nest stage, when possible, and any recordings less than one hour were not used. Recordings were conducted between civil sunrise and 6hrs after sunrise. Nest recordings were collected using either a video recording or in-person nest watches (see below for details). The method used was determined by logistics, specifically nest height from ground (i.e. low nests received tripod mounted cameras), and availability of field personnel and cameras (i.e. some low nests were observed in person if all equipment was already deployed).

Video recording

For video recorded nests, a camera (Wimius Action Camera 4K 16MP) was mounted on a camouflaged tripod or clipped to a nearby branch (no closer than 50 cm from the nest). Attached to the recorder was a Sennheiser MKE2-P-C MKE2 Omni Lavalier Microphone with a black foam softy that was placed in line or under the nest. Both the camera and a Zoom (H4N, H4Npro, or H5) recording device were connected to a 3200mAh power bank to extend recording times. To protect from weather damage the recorder was placed in a plastic bag, and both the recorder and power bank were placed in a camouflage pouch and taped to a tree/tripod or placed on the ground nearby. Cameras were set out in the morning and removed before sunset, therefore the amount of time each camera was set up/recording varied. Six camera recordings were under two hours in length (between 74-116 minutes long) due to technical difficulties (power failing, camera falling from tree, n = 4), and adverse weather (i.e. rain; n = 2). The recordings were later annotated using Behavioral Observation Research Interactive Software (BORIS; Friard & Gamba, 2016). The video annotation was later matched with the audio file times for song typing in Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2019).

In-person Nest watch

During in-person nest watches, an observer sat with binoculars under camouflage netting 6-15m from the nest. A Sennheiser ME-66 microphone attached to a Zoom H4N recorder was mounted on a tripod and pointed at the nest. The observer sat for up to two hours dictating into the microphone the bird's identification and behaviour (particularly singing behaviour) on or near the nest. From a total of 67 nest watches n = 22 were under the 2-hour recording time (60 -119 minutes) due to logistical constraints. Nest watches were later annotated, and song types were visualised using Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2019).

Annotations

For each recording collected, we extracted two hours of continuous data between sunrise and 6hrs after sunrise. As there was variation in the start and end times of videos and nest watches, this 6-hour time block was subdivided into four bins. Data was allocated into a bin based on number of minutes after sunrise the recording started as follows: 1) start time between 0-60 min after sunrise, 2) 61-120 min, 3) 121-180 min, and 4) 181-240 min. Nest watches were binned first as they were logistically constrained by the start time of the recording and only two hours in duration. This resulted in an un-equal number of recordings in each bin. Next, we allocated camera recordings into bins. Any camera recordings that were not long enough to extract two hours of data fit into all the 4 bins was first allocated into a bin, where possible, using a random number generator. Finally, all remaining camera recordings were randomly assigned to a bin such that the number of recordings per bin was as equal as possible (See Supplementary Material 2.1 for the distribution of recordings and recording type per bin). To do so we counted the number of samples currently in each bin, then knowing the number of remaining samples we calculated how many samples should go in each bin. We then randomly assigned recordings to bins until each bin reached the max.

Annotations included identification of the bird on the nest (where possible), and on-nest songs. Bird identification was used to give a classification by sex of male, female, and unknown.

Novel situations during a recording were documented, such as potential predators nearby, interactions with a heterospecific/conspecific, building two nests at once and predation events (n = 1 occurrence on camera). We removed two nests from our analysis as there would be no way of accurately knowing the birds nesting attempt number. At one nest the male paired with a different female in later nesting attempts, and the other nest had a parental triplet on the second nesting attempt.

Song Type Classification

All songs used were produced while the bird was physically touching the nest. Songs were visualised using Raven Pro 1.6 (Cornell laboratory of Ornithology 2004, Ithaca, NY, U.S.A.) and the notes that made up the full song were recorded and used for classification. Consecutive individual notes were only included as part of the same song if there was no more than 0.5 seconds between them. A song was distinguished from other vocalisations (i.e. calls, call series, and song starts) by the presence of at least one pure tone (“B” or “Z” note; See Supplementary Material 2.2). Any component of songs given prior to the pure tone we refer to as the ‘preface’, with the pure tone and subsequent sounds referred to as the ‘base’ (See Figure 2.1). Song typing for our analysis was carried out using the song base, as there was high variability in song prefaces and six songs had no preface. Of those song types with preface in our data there were 644 different song preface types that were 1 – 27 ($\bar{x}$ = 9.4 ± 5.2 SD) notes in length, with the number of times each was recorded varying greatly, from 1-356 occurrences ($\bar{x}$ = 3.7 ± 20.1 SD) in our dataset. This variability underpinned our decision to use the ‘base’ component of songs for type analysis.

Six different note types were identified in song bases (A, B, C, D, E, and Z; Supplementary Material 2.2). We collected high quality on-nest song recordings and classified each song base that had any single note difference in the base as a different song type. This classification gave us a total of 124 different song types ranging from 1-22 base notes ($\bar{x}$ = 9.9 ± 2.5 SD), however three song types made up approximately 80% of all data. Therefore, we condensed song types using the following rules. First, we grouped all songs with 5 or less notes together (this included 15 variants). The remaining song type groupings followed these rules: 1) B and Z are interchangeable, 2) C and D are interchangeable, 3) a single note can be changed in the middle of the song, except for an A note, and 4) the removal of a single note at the end of the song. Grouping applied to the predominant song type (highest frequency of occurrence; See Supplementary Material 2.3 for predominant types and variants). To be considered the most predominant song type the song must have occurred at least three times. After this categorisation of of song types based there were 85 different types, each song type had 0-5 song variants (other than the <5 base notes group as previously mentioned). From these 85 types 3 main types persisted making up 83% of the data (1954 songs out of 2354). Additionally, 40 of those 85 song types occurred only a single time. For these reasons, statistical analysis included four types: the three main types (Type 1, 2, 3) and a category called “rare” which included all other song types. The other category will henceforth be referred to as Type 4 for our analysis.

Statistical Analysis

All statistical analyses were performed in R version 4.0.2 (Team, 2020; See Supplementary Material 2.4-8).

Song Types

To study how song type usage varies throughout the breeding season, we ran four separate statistical models to compare each song type to all others. We examined the proportion of occurrence of each song type (1-4) using a binomial generalized linear mixed model using the package lme4 (Bates et al., 2015). The proportion of each song type (1-4) was analysed against each other song types (1-4) with the variables of nest stage (egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing, late chick-rearing), nesting attempt number (1-8), and sex (male, female, unknown). Individual bird identification was nested within territory number as a random variable to account for repeated measures and individual variation.

The model including all the fixed variables (nest stage, nesting attempt, and sex) had a convergence warning for song types 2, 3, and 4; therefore, we removed the random term of bird identification and the variable sex from all models to improve model fit. Sex was not a significant variable in the number of songs produced regardless of song type, as shown in Chapter 1 ($p = 0.42$). No convergence warnings were present following this reduction, therefore the final model for each type included the fixed variables of nest stage and nesting attempt with the random factor of territory number.

Song Diversity

To test if pairs used a larger number of on-nest song types throughout the breeding season, we calculated a given pairs' song diversity score (1-4, four types of songs used in this analysis). Diversity scores were a summation of the number of different song types used by the pair in each recording. A linear mixed model song diversity score was used with the fixed variables of nest stage, and nesting attempt number. The number of total songs in the recording was included as an offset to account for low song diversity due to smaller song counts, and the random variable of territory number was used to account for differences across pairs. Post hoc analysis was run using a least square means pairwise comparison (Tukey's method).

Results

From a total of 210 recordings, we examined 203 recordings of which only 160 recordings (79%) had one or more on-nest songs produced on the nest. There were no songs on the nest recorded during late chick-rearing (stage 8; n = 13 recordings); therefore, the nest stage variable only included recordings from nest stages 2-7 (egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing; with the following number of recordings n = 22, 36, 39, 32, 19, 12, respectively). The number of songs produced on the nest per recording ranged from 1-71 ($\bar{x}$ = 14.7 ± 14.2 SD). For analysis we classified 2354 songs produced by 30 pairs, consisting of n = 998 on-nest songs from n = 28 different females, n = 730 on-nest songs from n = 24 different males, and n = 626 on-nest songs from n = 25 different unknowns. There was a range of 1-135 ($\bar{x}$ = 30.6 ± 31.5 SD) songs per individual bird and 1-258 ($\bar{x}$ = 78.5 ± 64.8 SD) songs per territory.

Song Types

Song Type 1 (predominate type: BBABBABAAB; see Figure 2.1) occurred most frequently n = 1459 (62%) in the data set, while the other song types were more evenly dispersed intheir number of occurrences. Song Type 2 (predominate type: BBABBAB; n = 306, 13%; see Figure 2.1), 3 (predominate type: BACAABBABBAB; n = 189, 8%; see Figure 2.1), and 4 (all other types; n = 400, 17%). Across all song types, nesting attempt number had no influence on the proportion of occurrence of the song type (Type 1: $\chi^2 = 2.4$, $df = 1$, $p = 0.12$; Type 2: $\chi^2 = 0.60$, $df = 1$, $p = 0.44$; Type 3: $\chi^2 = 2.6$, $df = 1$, $p = 0.11$; Type 4: $\chi^2 = 3.2$, $df = 1$, $p = 0.07$; Figure 2.2). However, nest stage influenced the proportion of occurrence in song Types 1 and 3 (Type 1: $\chi^2 = 15.0$, $df = 5$, $p = 0.01$; Type 3: $\chi^2 = 18.6$, $df = 5$, $p < 0.01$; Figure 2.3), but not in song Type 2 and 4 (Type 2: $\chi^2 = 8.0$, $df = 5$, $p = 0.16$; Type 4: $\chi^2 = 7.4$, $df = 5$, $p = 0.19$; Figure 2.3).The proportion of Type 1 songs significantly increased from 57% to 72% between egg-laying and early chick-rearing (0.76 ± 0.24 SE, $p = 0.02$; Figure 2.3). The estimated proportion of Type 3 song decreased from 3% to 1% between egg-laying to early incubation (0.86 ± 0.28 SE, $p = 0.02$; Figure 2.3).

Song Diversity

Pairs of birds produced 1-4 ($\bar{x}$ = 2.3 ± 0.9 SD) song types per recording. Of all 160 recordings, song Type 1 occurred in 97% (n = 155), Type 2 occurred in 56% (n = 90), Type 3 in 42% (n = 26%), and Type 4 occurred in 53% (n = 86) of recordings. After controlling for effect of total songs produced on the nest for each recording, we found that while nesting attempt number did not influence song diversity score ($F_{1,92}$ = 0.98, p = 0.98), nest stage did have a significant influence on diversity score ($F_{5,146}$ = 3.1, p = 0.01; Figure 2.4). Song diversity decreased between the nest stages of late incubation and early chick-rearing (estimate mean difference 0.71 ± 0.21 SE, df =155, p = 0.01; Figure 2.4).

Discussion

This is the first manuscript to categorize the song types used by Grey Fantails on the nest, however, is also the first quantitative analysis of song types in any context for this species. We found a large diversity in song types (n=124). However, these could be condensed down to three primary types that made up 83% of songs and grouped all other types as rare (Type 4). Our song type classification was modelled on structural aspects of the end of the song alone, as preface vocalisation components were highly varied. Including other aspects such as frequency (Hz) of the vocalisations or spacing between notes might increase the numbers of song types within this species repertoire. Expanding the parameters to include other song aspects could increase the amount of song types produced or increase the proportion of songs especially those classified as ‘rare.’ Given the level of variation observed and large repertoire documented, it is highly likely that Grey Fantail populations in other areas have additional song types, and that this would likely be further expanded if off-nest songs were also examined.

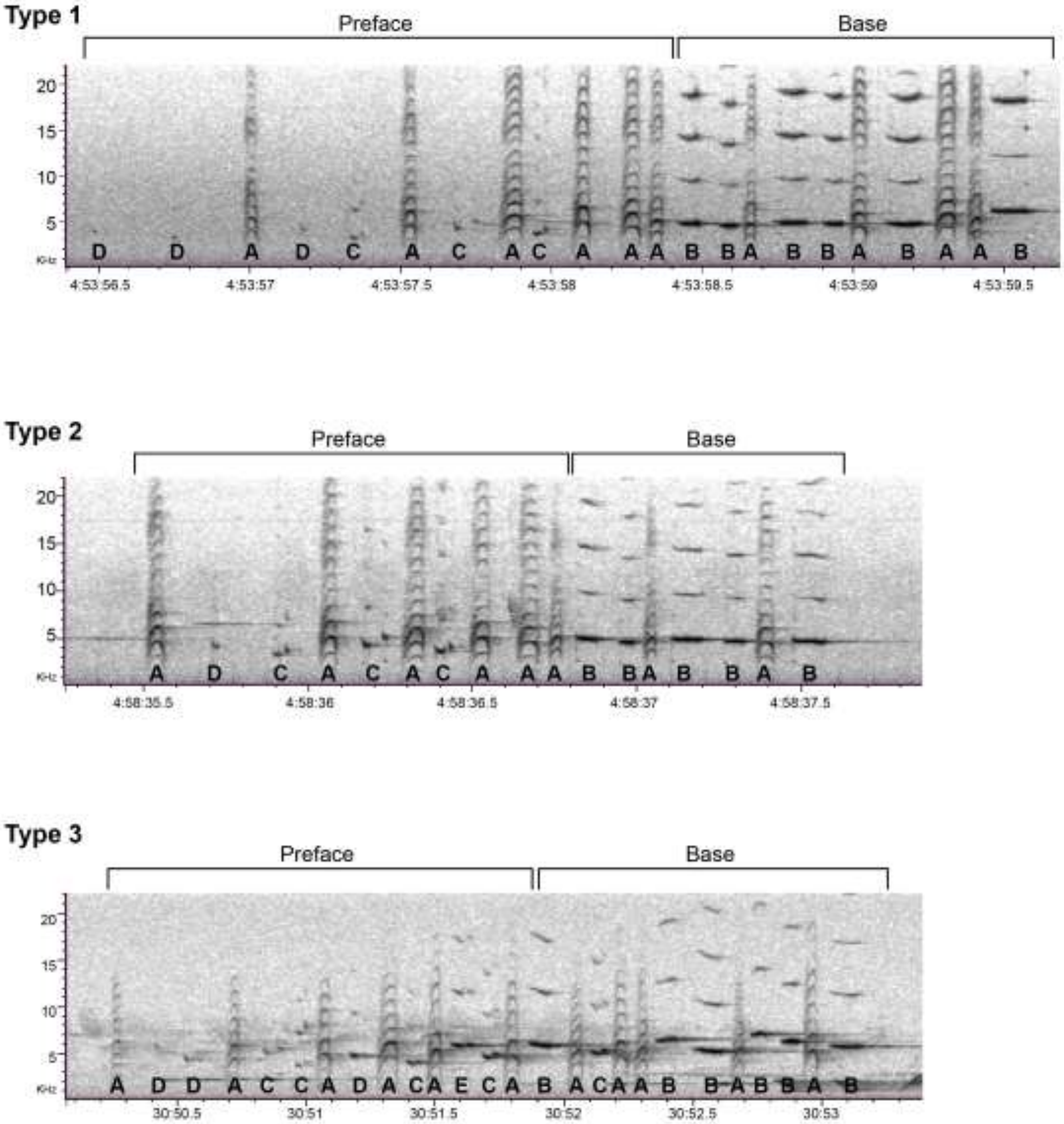
Few studies have found functional differences between vocalisation, however, one study on American Robins (*Turdus migratorius*) found females returning to the nest used different vocalisation and vocalised at different rates dependent on the predator type during model presentations (Gottfried 1985). Predator-specific alarm calling has also been observed in non-bird species such as monkeys and small mammals (Owing & Virginia 1978; Robinson 1980). The aim of this study was to define on-nest song types and understand the proportion of each throughout the season to set the groundwork to look at context of these vocalisation in future experimental studies.

We suggest the quantity and variety of songs that were placed in the ‘rare’ category (Type 4) may be attributed to a combination of learning and migration among the population. Using atlas data, the range maps for Grey Fantails show movement up and down the east coast of Australia (Griffioen & Clarke, 2002). Grey Fantails have six subspecies, four of which are migratory or semi-nomadic (Blakers et al., 1984; Griffioen & Clarke, 2002; Higgins et al., 2006), but migration has not been closely monitored in any of these subspecies. We studied the subspecies *alisteri* which is reported to migrate north in the non-breeding season from Victoria, Australia to as far as New Guinea (Higgins et al., 2006). As birds migrate, they can learn different song types or songs with different dialects, and during migration some subspecies range maps overlap. In some species, larger song repertoires have been linked to migration (Catchpole & Slater, 2008; Read & Weary, 1992; reviewed in Najar & Benedict, 2019). In the New Zealand fantails song, characteristics differed between subspecies (Heaphy & Cain, 2021). Further exploration of song types in different populations or in different subspecies is necessary to determine if there are more than three predominant song types. The ‘rare’ songs could be the result of dialects picked up during migration in the non-breeding season, however, whether Grey Fantails learn songs over time or have a sensitive period for song learning is unknown. Contrary to our predication, the proportion of each song type did not change across nesting attempts during the breeding season. The mechanisms and timing of song learning have not been explored in Grey Fantails, so how many song types birds can learn, and whether birds require a tutor to do so (Beecher, 2008; Kroodsma, 1977) remains unknown. However, the absence of a change in the proportion of song types across nesting attempts suggests that Grey Fantails do not appear to be incorporating new song types throughout the 6-month breeding season. We can speculate this might be due to song matching and learning from neighbours or tutors occurring early in life (within the first year) or at the start of the breeding season as observed in Great Tits (*Parus major*) (McGregor & Avery, 1986) and Song Sparrows (*Melospiza melodia*) (Beecher, 2008; Beecher et al., 1994), however further study of any open learning period in this species is warranted. The proportion of song types did not vary across nesting attempt but did differ across nest stage, suggesting that Type 1 and Type 3 songs might have uses relating to these nest stages regardless of the nesting attempt. The proportion of the most prevalent song type (Type 1) increased between the stages of egg-laying and early-chick rearing in contrast to all other song types. This difference was a steady increase suggesting the function of Type 1 songs is constant throughout the nesting stages and increases as the nesting cycle progresses. Such usage might be multifunctional including assisting in territorial defence and/or within pair communication to coordinate parental care. Alternatively, pairs could improvise less sticking to the main song type at this stage so chicks the population-typical song type. The proportion of Type 3 song exhibited a drop from egg-laying to early incubation, suggesting a function for this song type may be specific to egg-laying, and perhaps mate bonding. Type 3 songs have a longer base (12 notes in comparison to Type 1 and 2, 10 and 7 notes respectively) and the base has up to one additional note type. This makes Type 3 songs more complex. In *Acrocephalus* warblers more complex song types were used for courtship (Catchpole, 2000). Since Type 3 song is produced at the greatest proportion during egg-laying, its function may be related to courtship or fertility. Additionally, similar to the Chestnut-sided Warbler (Byers, 1996; Kroodsma et al., 1989), Grey Fantails might use Type 3 songs outside of the breeding season. Further assessment of how all song types are used in an off the nest context would help elucidate any functional component to these song types.

Contrary to our prediction, song diversity (the number different song types) did not increase across nesting attempts or linearly across nest stages. Song diversity decreased between the stages of late incubation to early chick-rearing only. Type 1 songs occurred in 97% of all the recordings (155 out of 160), therefore most birds diversity score would have included Type 1. The decrease could be a result of the sudden change in parental duties increasing from incubation to chick-rearing, as parents must feed young in addition to brooding (Clutton-Brock, 2019). Additionally, higher song diversity during late incubation could indicate that parents are teaching unhatched chicks the repertoire. Colombelli-Negrel and colleagues (2012) found superb fairy-wrens (*Malurus cyaneus*) teach embryonic chicks begging calls before hatching so that parents can differentiate their offspring from brood parasites; however, their study did not look at the types of vocalisations and was on calls. The decrease from late incubation to early chick-rearing is a difference of 0.71. Although statistically significant, less than one song type and might not be biologically significant.

In conclusion, we have defined three main on-nest song types in our population of Grey Fantails. All other song types grouped in the rare category of Type 4, did not occur more than 35 times each. These rarer songs likely reflect song types that this migratory species may have learned elsewhere, or perhaps include songs that are more regularly voiced away from the nest area. Song diversity scores differed between late incubation and early chick-rearing, which suggests that breeding birds with high brood demands may resort to simple, more commonly used songs during this phase. Additionally, we found that the proportion of Type 1 and Type 3 songs varied between nest stages. Type 1 songs are present throughout nest stages but increased from egg-laying to early chick-rearing. This song type could be multifunctional and used for territory defences and inter-pair communication. The proportion of Type 3 was highest during egg-laying compared to early incubation, suggesting a function linked to fertility and mate bonding during this critical period. This research provides a preliminary study of the use and potential function of on-nest song types in Grey Fantails. Further studies in this area would benefit by focusing on 1) determining the function of song types using playback-response experiments, 2) quantifying geographical and subspecific impacts on song type usage, 3) determining differences in on versus off the nest song types, 4) studying song learning and any potential effects of senescence on song type diversity.

Figure 2.1: Spectrogram examples of three predominant Grey Fantail Song Types 1, 2, and 3. Song types are defined by their base which is the start of the phrase that includes a ‘B’ or ‘Z’ note. Both the song preface and base are labelled in each example song along with the letter associated with each note type (note types A, B, C, D, and E shown).



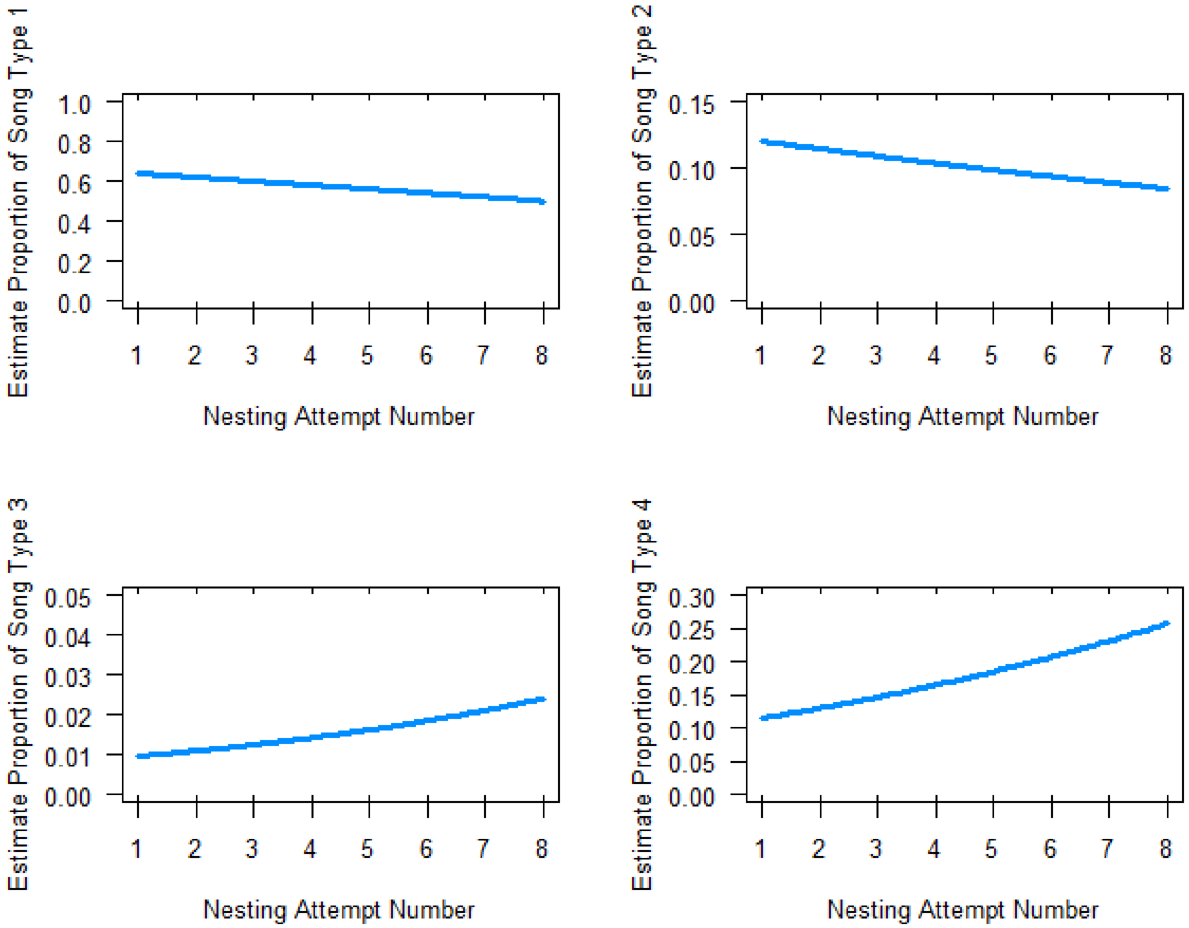


Figure 2.2: Model predicted estimates of the propotion of each song type (1-4) across nesting attempt (1-8).

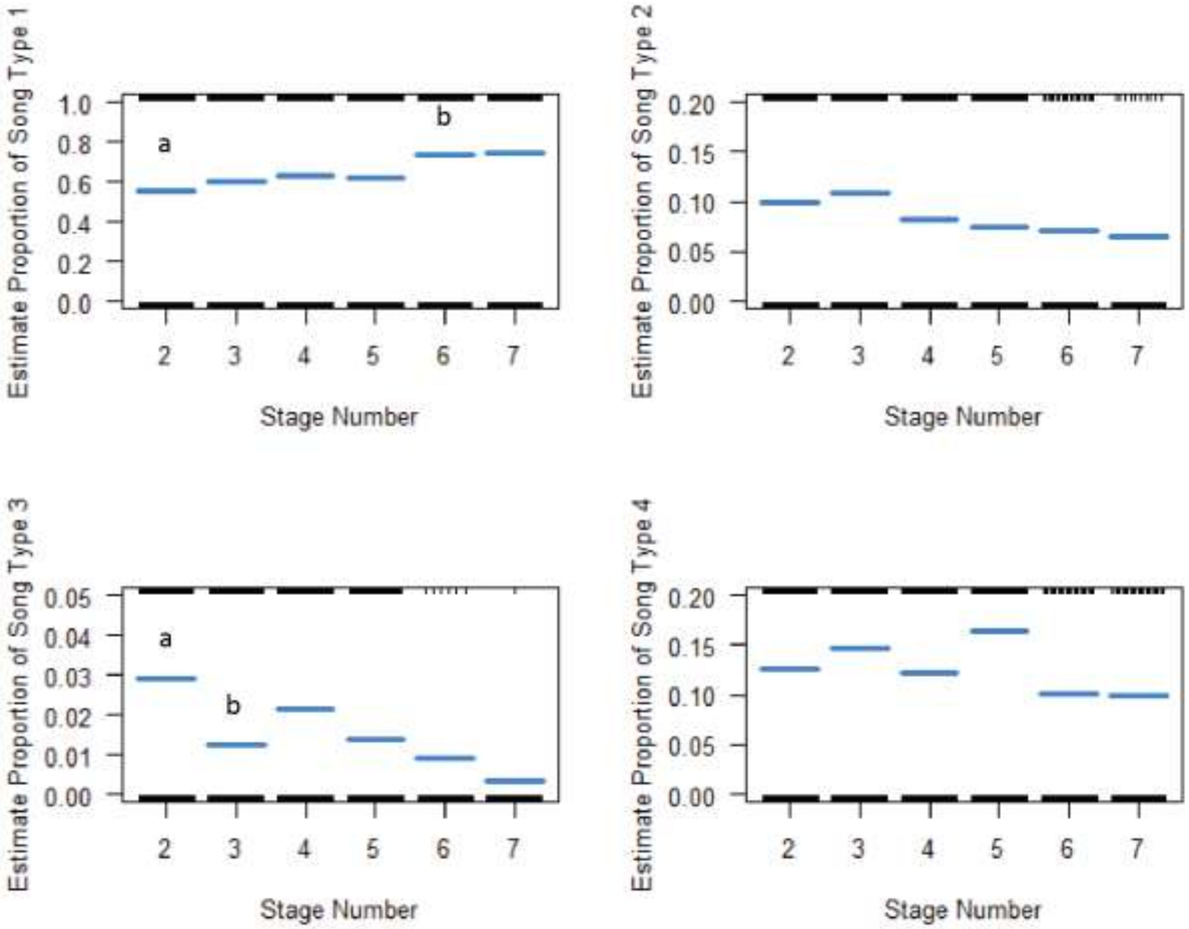


Figure 2.3: Model predicted estimates of the proportion of each song type (1-4) across nest stage (2-7; egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing, respectively). Letters (‘a’ and ‘b’) refer to the significant difference between estimated proportion of song type at nest stages.

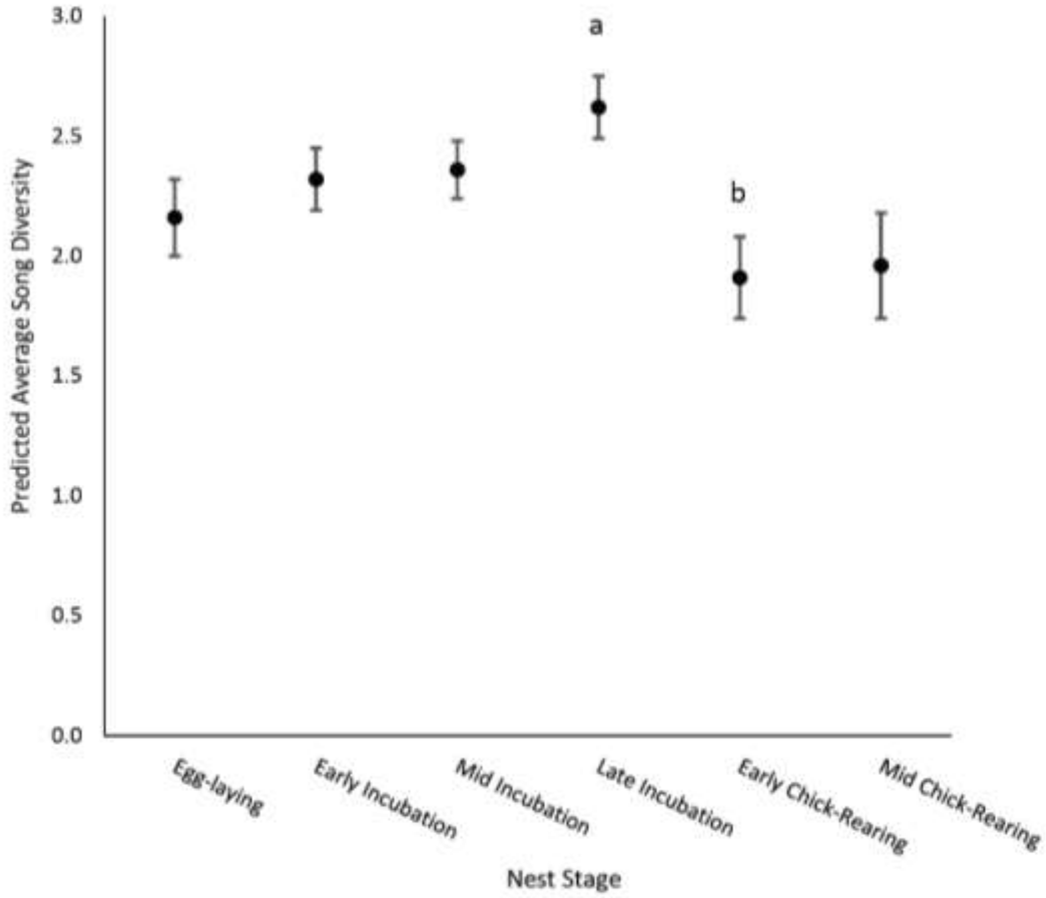
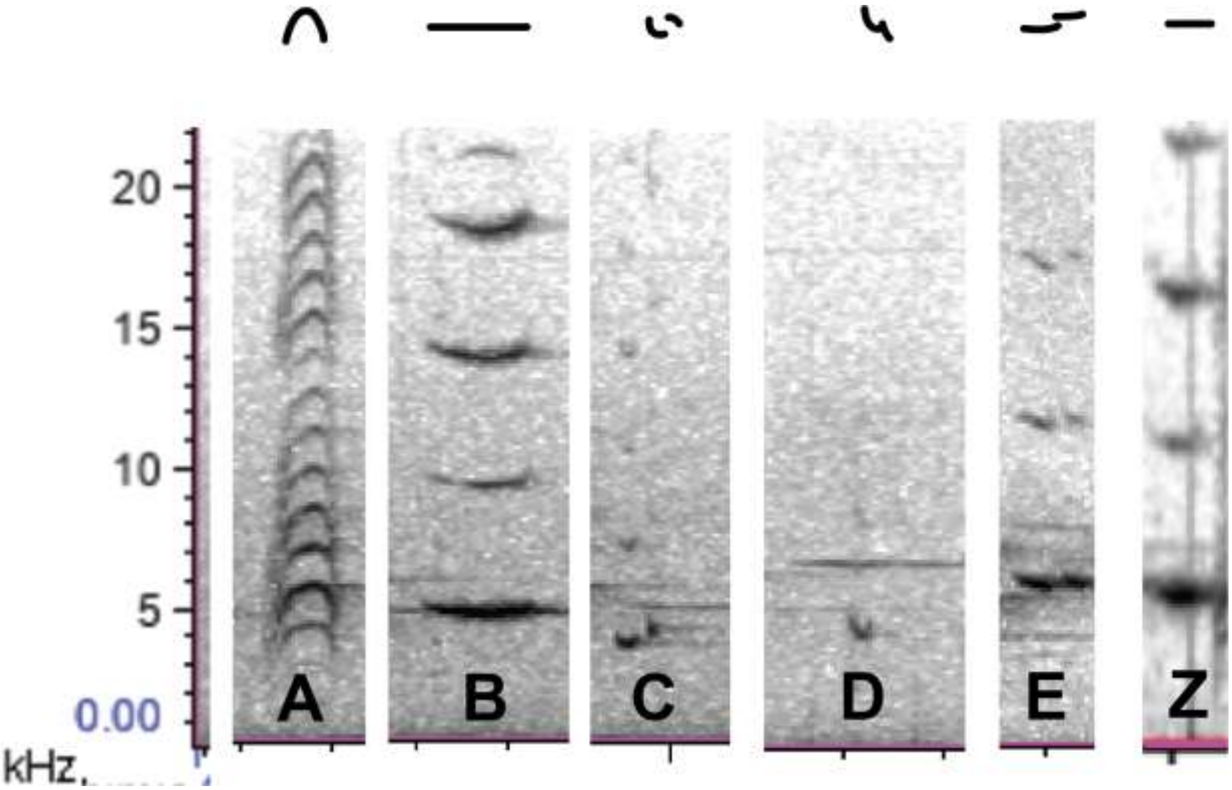


Figure 2.4: Model predicted on-nest song diversity (mean ± SE) arranged by nest stage (egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, and late chick-rearing). Letters (‘a’ and ‘b’) refer to the significant difference between average song diversity at nest stages.

Supplementary Material 2.2: Distribution of recordings by grouped time bin (1-4), nest stage (egg-laying, early incubation, mid incubation, late incubation, early chick-rearing, mid chick-rearing, late chick-rearing), and recording type (nest watch or camera).

Nest Stage	**Bin Number**	**Recording Type**		**Total Number of Recordings**
		Camera Recordings	**Nest Watches**	
Egg-laying	1	7	0	7
	2	5	4	9
	3	7	0	7
	4	7	1	8
Early Incubation	1	10	0	10
	2	8	3	11
	3	8	2	10
	4	4	7	11
Mid Incubation	1	10	1	11
	2	6	4	10
	3	6	4	10
	4	0	11	11
Late Incubation	1	5	4	9
	2	8	0	8
	3	7	3	10
	4	4	5	9
Early Chick-Rearing	1	7	1	8
	2	5	2	7
	3	4	0	4
	4	3	3	6
Mid Chick-Rearing	1	5	0	5
	2	4	2	6
	3	3	0	3
	4	2	5	7
Late Chick-rearing	1	4	1	5
	2	4	0	4
	3	1	2	3
	4	0	1	1
Total Number of Recordings		144	66	210

Supplementary Material 2.3: Song note types present in Grey Fantail song bases (A,B,C,D,E, and Z). Top Panel is hand drawn representations of note types and bottom panel are clips of note types from spectrograms.



Supplementary Material 2.4: Distribution song type occurrence displaying song base note structure after types were grouped (* = denotes the song type is the predominate type if variations are present).

Song Type and Base Notes	Count of Occurrence	Percentage of Occurrence
1	**1459**	**61.98%**
BBABBABAAB*	1456	61.85%
BBABBABAA	3	0.13%
2	**306**	**13.00%**
BBABBAB*	298	12.66%
BBABBA	8	0.34%
3	**189**	**8.03%**
BACAABBABBAB*	151	6.41%
BAZAABBABBAB	19	0.81%
BADAABBABBAB	9	0.38%
ZAZAABBABBAB	9	0.38%
ZABAABBABBAB	1	0.04%
4	**53**	**2.25%**
BBAB	15	0.64%
B	11	0.47%
BAABB	5	0.21%
BBABB	4	0.17%
BBBBA	3	0.13%
BBA	3	0.13%
BB	3	0.13%
ZAZ	2	0.08%
BCAB	1	0.04%
ZAABB	1	0.04%
BZ	1	0.04%
BABA	1	0.04%
BA	1	0.04%
BAB	1	0.04%
BBB	1	0.04%
5	**38**	**1.61%**
BBABBABAB*	34	1.44%
BBABBABA	4	0.17%
6	**36**	**1.53%**
BACAABB*	21	0.89%

BACAAB	5	0.21%
BAEAABB	5	0.21%
BADAABB	3	0.13%
BAZAABB	1	0.04%
BABAABB	1	0.04%
7	**27**	**1.15%**
ZABADADABAABBABBA	27	1.15%
8	**20**	**0.85%**
BAABBABBAB	20	0.85%
9	**19**	**0.81%**
BBABBABZDB	19	0.81%
10	**14**	**0.59%**
BBBBAB	14	0.59%
11	**12**	**0.51%**
BACABBBBAB	12	0.51%
12	**10**	**0.42%**
ZABAABBABBAB*	6	0.25%
BAZAABBABBA	3	0.13%
ZAZAABBABBA	1	0.04%
13	**9**	**0.38%**
ZAABBABBAB	9	0.38%
14	**8**	**0.34%**
ZZABACCCABACAABBABBAB	8	0.34%
15	**7**	**0.30%**
BADABAABBABBAB	7	0.30%
16	**7**	**0.30%**
ZZABZZZBACAABB	7	0.30%
17	**6**	**0.25%**
ZZADAZACCABADABBABBA	6	0.25%
18	**6**	**0.25%**
ZACAECCACACAABBABBAB*	5	0.21%
ZACAECCACACAABBABBABB	1	0.04%
19	**6**	**0.25%**
ZADZAZAZABZABABBABBAB	6	0.25%
20	**5**	**0.21%**
ZZAZAZABAZAZABABBABBAB	5	0.21%
21	**5**	**0.21%**
ZCAZAZ	3	0.13%
ZCABAB	1	0.04%
ZCABAZ	1	0.04%
22	**5**	**0.21%**
BDADABBABBAB	5	0.21%

23	**5**	**0.21%**
BACAABBAB	5	0.21%
24	**4**	**0.17%**
BBBBABAAB	4	0.17%
25	**4**	**0.17%**
ZZABAZABAZAZABABBABBAB	4	0.17%
26	**4**	**0.17%**
BCCAABBABBAB	4	0.17%
27	**4**	**0.17%**
ZAZZAB	2	0.08%
BABBAB	1	0.04%
ZAZBAZ	1	0.04%
28	**4**	**0.17%**
BACAABBABB*	3	0.13%
BACAABBABBA	1	0.04%
29	**3**	**0.13%**
ZZABACCCABACAABBABBAB	3	0.13%
30	**3**	**0.13%**
BBABBABBAB	2	0.08%
ZZABBABBAB	1	0.04%
31	**3**	**0.13%**
ZZABAECCABACAABB	3	0.13%
32	**3**	**0.13%**
ZAZABAZAZAB	3	0.13%
33	**3**	**0.13%**
ZAZCABBAB	3	0.13%
34	**3**	**0.13%**
ZAZABAZABABBABBAB	3	0.13%
35	**3**	**0.13%**
ZABADABABBABBAB	3	0.13%
36	**3**	**0.13%**
ZZAZAZABAZAZABABBA	2	0.08%
ZZAZAZABAZAZABABBAB	1	0.04%
37	**2**	**0.08%**
ZZAZAZAZAAB	2	0.08%
38	**2**	**0.08%**
BAZABAABBABBAB	2	0.08%
39	**2**	**0.08%**
ZCAZACAZ	2	0.08%
40	**2**	**0.08%**
BDABABB	2	0.08%
41	**2**	**0.08%**

ZZABAZZZBACAABB	2	0.08%
42	**2**	**0.08%**
ZZABAZZZABACAA	2	0.08%
43	**2**	**0.08%**
ZABZAZABABBABBAB	2	0.08%
44	**2**	**0.08%**
ZABAABBB	2	0.08%
45	**2**	**0.08%**
ZABAABBBBAB	2	0.08%
46	**1**	**0.04%**
ZACAECCACAC	1	0.04%
47	**1**	**0.04%**
ZZAZAECCABADAAZZ	1	0.04%
48	**1**	**0.04%**
BAABBABBABAAB	1	0.04%
49	**1**	**0.04%**
ZZACAABB	1	0.04%
50	**1**	**0.04%**
ZZADAZA	1	0.04%
51	**1**	**0.04%**
BBABABACCBABABB	1	0.04%
52	**1**	**0.04%**
ZZAZAZAZAABBBBAB	1	0.04%
53	**1**	**0.04%**
ZCABBABBAB	1	0.04%
54	**1**	**0.04%**
ZCABAZABB	1	0.04%
55	**1**	**0.04%**
BDABADAABB	1	0.04%
56	**1**	**0.04%**
ZACAZACABBBBAB	1	0.04%
57	**1**	**0.04%**
ZADABZABAZZAB	1	0.04%
58	**1**	**0.04%**
BAZZAABBABBA	1	0.04%
59	**1**	**0.04%**
BACCABABABBABBAB	1	0.04%
60	**1**	**0.04%**
BZAZABBABBAB	1	0.04%
61	**1**	**0.04%**
BBABAZZCA	1	0.04%
62	**1**	**0.04%**

ZAZACCCAZAZAAZ	1	0.04%
63	**1**	**0.04%**
ZAZAZAZABBABBAB	1	0.04%
64	**1**	**0.04%**
ZAZABAZAZABAB	1	0.04%
65	**1**	**0.04%**
BBABZZZABACAAB	1	0.04%
66	**1**	**0.04%**
BCCACACAABBABBAB	1	0.04%
67	**1**	**0.04%**
BDDABADAABB	1	0.04%
68	**1**	**0.04%**
BDDABADAAABB	1	0.04%
69	**1**	**0.04%**
BCCAABB	1	0.04%
70	**1**	**0.04%**
BACABB	1	0.04%
71	**1**	**0.04%**
ZAZABAABBBBAB	1	0.04%
72	**1**	**0.04%**
BABABB	1	0.04%
73	**1**	**0.04%**
ZCAZACABB	1	0.04%
74	**1**	**0.04%**
ZACAECCACA	1	0.04%
75	**1**	**0.04%**
BAZAZAZAABBABBABAAB	1	0.04%
76	**1**	**0.04%**
BBABABACCBABABBABBAB	1	0.04%
77	**1**	**0.04%**
BBABZZZABACAABBBBAB	1	0.04%
78	**1**	**0.04%**
ZABAZAZABAABBABBABABBA	1	0.04%
79	**1**	**0.04%**
ZAZABADADAABBABBAB	1	0.04%
80	**1**	**0.04%**
ZAZABAZAZABABBABBA	1	0.04%
81	**1**	**0.04%**
ZAZAZAZABZABABBABBAB	1	0.04%
82	**1**	**0.04%**
ZZADAZACCBABABBABBAB	1	0.04%
83	**1**	**0.04%**

ZZAZAZABAZABAABBABBAB	1	0.04%
84	**1**	**0.04%**
ZACAECCACACAABBBBAB	1	0.04%
85	**1**	**0.04%**
ZAZABAZ	1	0.04%

Supplementary Material 2.5: Simplified R code and output for song type 1 using a general linear mixed model.

```
fit_a1sr = glmer(type_1 ~ stage_no + nest_number +(1|territory), data=rep_size, family =
"binomial")
> summary(fit_a1sr)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: type_1 ~ stage_no + nest_number + (1 | territory)
   Data: rep_size

     AIC      BIC   logLik deviance df.resid
  2829.5   2875.6  -1406.8   2813.5     2346

Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.2426 -0.8497  0.4668  0.6872  2.0308

Random effects:
 Groups    Name        Variance Std.Dev.
 territory (Intercept) 1.148    1.072
Number of obs: 2354, groups:  territory, 30

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  0.46843    0.27139   1.726  0.08435 .
stage_no3    0.17885    0.17417   1.027  0.30450
stage_no4    0.29386    0.17790   1.652  0.09856 .
stage_no5    0.27045    0.18236   1.483  0.13807
stage_no6    0.76757    0.24368   3.150  0.00163 **
stage_no7    0.85647    0.32602   2.627  0.00861 **
nest_number -0.08078    0.05168  -1.563  0.11807
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) stg_n3 stg_n4 stg_n5 stg_n6 stg_n7
stage_no3   -0.338
stage_no4   -0.337  0.738
stage_no5   -0.343  0.712  0.710
stage_no6   -0.282  0.535  0.535  0.512
stage_no7   -0.227  0.388  0.390  0.365  0.292
nest_number -0.391 -0.250 -0.251 -0.219 -0.103 -0.071
> Anova(fit_a1sr, component = "cond", type = 3) #type 3 anova
Analysis of Deviance Table (Type III Wald chisquare tests)

Response: type_1
              Chisq Df Pr(>Chisq)
(Intercept)  2.9791  1    0.08435 .
stage_no    15.0025  5    0.01035 *
```

```
nest_number  2.4428  1    0.11807
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> emmeans_fit1 <- emmeans(fit_a1sr, list(pairwise ~ stage_no))
> emmeans_fit1
$`emmeans of stage_no`
 stage_no emmean    SE  df asymp.LCL asymp.UCL
 2         0.247 0.252 Inf   -0.2477     0.741
 3         0.426 0.223 Inf   -0.0112     0.863
 4         0.541 0.224 Inf    0.1018     0.980
 5         0.517 0.227 Inf    0.0720     0.963
 6         1.014 0.280 Inf    0.4651     1.564
 7         1.103 0.351 Inf    0.4151     1.792

Results are given on the logit (not the response) scale.
Confidence level used: 0.95

$`pairwise differences of stage_no`
 1     estimate    SE  df z.ratio p.value
 2 - 3  -0.1788 0.174 Inf -1.027  0.9091
 2 - 4  -0.2939 0.178 Inf -1.652  0.5639
 2 - 5  -0.2704 0.182 Inf -1.483  0.6752
 2 - 6  -0.7676 0.244 Inf -3.150  0.0203
 2 - 7  -0.8565 0.326 Inf -2.627  0.0908
 3 - 4  -0.1150 0.128 Inf -0.902  0.9461
 3 - 5  -0.0916 0.136 Inf -0.676  0.9846
 3 - 6  -0.5887 0.211 Inf -2.797  0.0580
 3 - 7  -0.6776 0.304 Inf -2.227  0.2253
 4 - 5   0.0234 0.137 Inf  0.171  1.0000
 4 - 6  -0.4737 0.211 Inf -2.242  0.2184
 4 - 7  -0.5626 0.304 Inf -1.848  0.4346
 5 - 6  -0.4971 0.217 Inf -2.290  0.1978
 5 - 7  -0.5860 0.310 Inf -1.890  0.4083
 6 - 7  -0.0889 0.345 Inf -0.257  0.9998

Results are given on the log odds ratio (not the response) scale.
P value adjustment: tukey method for comparing a family of 6 estimates
```

Supplementary Material 2.6: Simplified R code and output for song type 2 using a general linear mixed model.

```
fit_a2sr = glmer(type_2 ~ stage_no + nest_number +  (1|territory), data=rep_size, family =
"binomial")
> summary(fit_a2sr)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: type_2 ~ stage_no + nest_number + (1 | territory)
   Data: rep_size

     AIC      BIC   logLik deviance df.resid
  1650.2   1696.3   -817.1   1634.2     2346

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.9948 -0.4362 -0.2732 -0.1755  9.0194

Random effects:
 Groups    Name        Variance Std.Dev.
 territory (Intercept) 1.609    1.268
Number of obs: 2354, groups:  territory, 30

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -2.04316    0.36051  -5.667 1.45e-08 ***
stage_no3    0.10841    0.24616   0.440    0.660
stage_no4   -0.20499    0.25389  -0.807    0.419
stage_no5   -0.31525    0.26812  -1.176    0.240
stage_no6   -0.38038    0.33173  -1.147    0.252
stage_no7   -0.44681    0.41629  -1.073    0.283
nest_number -0.05615    0.07256  -0.774    0.439
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) stg_n3 stg_n4 stg_n5 stg_n6 stg_n7
stage_no3   -0.404
stage_no4   -0.380  0.762
stage_no5   -0.402  0.716  0.708
stage_no6   -0.335  0.577  0.565  0.540
stage_no7   -0.282  0.446  0.435  0.408  0.337
nest_number -0.421 -0.208 -0.230 -0.153 -0.075 -0.036
> Anova(fit_a2sr, component = "cond", type = 3)
Analysis of Deviance Table (Type III Wald chisquare tests)

Response: type_2
              Chisq Df Pr(>Chisq)
(Intercept) 32.1194  1   1.45e-08 ***
stage_no     7.9866  5      0.157
```

```
nest_number  0.5989  1      0.439
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Supplementary Material 2.7: Simplified R code and output for song type 3 using a general linear mixed model.

```
> fit_a3sr = glmer(type_3 ~ stage_no + nest_number + (1|territory), data=rep_size, family =
"binomial")
> summary(fit_a3sr)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: type_3 ~ stage_no + nest_number + (1 | territory)
   Data: rep_size

     AIC      BIC   logLik deviance df.resid
  1086.4   1132.6   -535.2   1070.4     2346

Scaled residuals:
    Min      1Q  Median      3Q     Max
-0.8292 -0.3662 -0.1158 -0.0503  9.6727

Random effects:
 Groups    Name        Variance Std.Dev.
 territory (Intercept) 4.807    2.192
Number of obs: 2354, groups:  territory, 30

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -3.91346    0.64358  -6.081  1.2e-09 ***
stage_no3   -0.86672    0.27564  -3.144  0.00166 **
stage_no4   -0.31902    0.26258  -1.215  0.22438
stage_no5   -0.77179    0.30437  -2.536  0.01122 *
stage_no6   -1.19542    0.50032  -2.389  0.01688 *
stage_no7   -2.23778    1.05844  -2.114  0.03450 *
nest_number  0.13426    0.08304   1.617  0.10592
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) stg_n3 stg_n4 stg_n5 stg_n6 stg_n7
stage_no3   -0.145
stage_no4   -0.141  0.651
stage_no5   -0.138  0.552  0.599
stage_no6   -0.103  0.333  0.348  0.289
stage_no7   -0.076  0.152  0.164  0.127  0.085
nest_number -0.252 -0.304 -0.361 -0.316 -0.103 -0.034
> Anova(fit_a3sr, component = "cond", type = 3)
Analysis of Deviance Table (Type III Wald chisquare tests)

Response: type_3
              Chisq Df Pr(>Chisq)
(Intercept) 36.9755  1  1.196e-09 ***
stage_no    18.5725  5   0.002308 **
```

```
nest_number  2.6141  1   0.105917
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> emmeans_fit3 <- emmeans(fit_a3sr, list(pairwise ~ stage_no))
> emmeans_fit3
$`emmeans of stage_no`
 stage_no emmean    SE  df asymp.LCL asymp.UCL
 2         -3.55 0.626 Inf     -4.77     -2.32
 3         -4.41 0.615 Inf     -5.62     -3.21
 4         -3.86 0.609 Inf     -5.06     -2.67
 5         -4.32 0.622 Inf     -5.54     -3.10
 6         -4.74 0.743 Inf     -6.20     -3.28
 7         -5.78 1.180 Inf     -8.10     -3.47

Results are given on the logit (not the response) scale.
Confidence level used: 0.95

$`pairwise differences of stage_no`
 1     estimate    SE  df z.ratio p.value
 2 - 3   0.8667 0.276 Inf  3.144  0.0207
 2 - 4   0.3190 0.263 Inf  1.215  0.8298
 2 - 5   0.7718 0.304 Inf  2.536  0.1138
 2 - 6   1.1954 0.500 Inf  2.389  0.1599
 2 - 7   2.2378 1.058 Inf  2.114  0.2797
 3 - 4  -0.5477 0.225 Inf -2.431  0.1454
 3 - 5  -0.0949 0.276 Inf -0.344  0.9994
 3 - 6   0.3287 0.484 Inf  0.679  0.9843
 3 - 7   1.3711 1.053 Inf  1.303  0.7837
 4 - 5   0.4528 0.257 Inf  1.765  0.4888
 4 - 6   0.8764 0.477 Inf  1.837  0.4421
 4 - 7   1.9188 1.048 Inf  1.831  0.4457
 5 - 6   0.4236 0.505 Inf  0.839  0.9603
 5 - 7   1.4660 1.064 Inf  1.378  0.7402
 6 - 7   1.0424 1.132 Inf  0.921  0.9412

Results are given on the log odds ratio (not the response) scale.
P value adjustment: tukey method for comparing a family of 6 estimates
```

Supplementary Material 2.8: Simplified R code and output for song type 4 using a general linear mixed model.

```
fit_a4sr = glmer(type_4 ~ stage_no + nest_number + (1|territory), data=rep_size, family =
"binomial")
> summary(fit_a4sr)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: type_4 ~ stage_no + nest_number + (1 | territory)
   Data: rep_size

     AIC      BIC   logLik deviance df.resid
  1922.4   1968.5   -953.2   1906.4     2346

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.1657 -0.4769 -0.3139 -0.1898  6.5462

Random effects:
 Groups    Name        Variance Std.Dev.
 territory (Intercept) 2.033    1.426
Number of obs: 2354, groups:  territory, 30

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -2.35579    0.39352  -5.986 2.14e-09 ***
stage_no3    0.17031    0.23614   0.721   0.4708
stage_no4   -0.04091    0.24304  -0.168   0.8663
stage_no5    0.30602    0.24508   1.249   0.2118
stage_no6   -0.24245    0.32232  -0.752   0.4519
stage_no7   -0.27834    0.45883  -0.607   0.5441
nest_number  0.13994    0.07815   1.791   0.0734 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) stg_n3 stg_n4 stg_n5 stg_n6 stg_n7
stage_no3   -0.353
stage_no4   -0.357  0.768
stage_no5   -0.377  0.760  0.746
stage_no6   -0.310  0.573  0.566  0.556
stage_no7   -0.213  0.403  0.398  0.387  0.307
nest_number -0.488 -0.192 -0.173 -0.142 -0.047 -0.063
> Anova(fit_a4sr, component = "cond", type = 3)
Analysis of Deviance Table (Type III Wald chisquare tests)

Response: type_4
              Chisq Df Pr(>Chisq)
(Intercept) 35.8376  1  2.145e-09 ***
stage_no     7.3801  5    0.19387
```

```
nest_number  3.2063  1    0.07336 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Supplementary Material 2.9: Simplified R code and output for on-nest song diversity score using a linear mixed model.

```
diversity <- lmer(song_diversity_simp ~ stage_no + nest_number + total_song_count   +
(1|territory_id), data=song_div, REML= FALSE)
> summary (diversity)
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method
['lmerModLmerTest']
Formula: song_diversity_simp ~ stage_no + nest_number + total_song_count + (1 | territory_id)
   Data: song_div

     AIC      BIC   logLik deviance df.resid
   367.3    398.1   -173.7    347.3      150

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.45246 -0.64558 -0.04284  0.65898  2.34150

Random effects:
 Groups       Name        Variance Std.Dev.
 territory_id (Intercept) 0.09303  0.3050
 Residual                 0.44944  0.6704
Number of obs: 160, groups:  territory_id, 30

Fixed effects:
                   Estimate   Std. Error      df      t value   Pr(>|t|)
(Intercept)       1.691e+00  1.950e-01  1.415e+02   8.672   9.01e-15 ***
stage_no3         1.614e-01  1.892e-01  1.461e+02   0.853   0.3951
stage_no4         1.976e-01  1.859e-01  1.463e+02   1.063   0.2897
stage_no5         4.589e-01  1.920e-01  1.473e+02   2.390   0.0181 *
stage_no6        -2.482e-01  2.184e-01  1.513e+02  -1.137   0.2575
stage_no7        -1.979e-01  2.557e-01  1.562e+02  -0.774   0.4401
nest_number      -9.596e-04  3.738e-02  9.621e+01  -0.026   0.9796
total_song_count  3.226e-02  4.577e-03  1.439e+02   7.047   7.02e-11 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
             (Intr) stg_n3 stg_n4 stg_n5 stg_n6 stg_n7 nst_nm
stage_no3    -0.484
stage_no4    -0.500  0.653
stage_no5    -0.524  0.621  0.635
stage_no6    -0.546  0.509  0.526  0.516
stage_no7    -0.517  0.424  0.443  0.438  0.436
nest_number  -0.502 -0.109 -0.127 -0.066 -0.012  0.041
ttl_sng_cnt  -0.329 -0.178 -0.144 -0.113  0.110  0.162  0.093
```

```
> aovv <- anova(diversity, type=3)
Type III Analysis of Variance Table with Satterthwaite's method
                   Sum Sq  Mean Sq NumDF   DenDF   F value   Pr(>F)
stage_no            6.8954   1.3791     5    146.865  3.0685   0.01153 *
nest_number         0.0003   0.0003     1     96.206   0.0007   0.97957
total_song_count  22.3166  22.3166     1    143.898  49.6545  7.02e-11 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> emmeans_div <- emmeans(diversity, list(pairwise ~ stage_no))
$`emmeans of stage_no`
 stage_no emmean    SE  df lower.CL upper.CL
 2          2.16 0.166  150     1.83     2.49
 3          2.32 0.134  120     2.06     2.59
 4          2.36 0.128  118     2.11     2.61
 5          2.62 0.137  133     2.35     2.89
 6          1.91 0.178  158     1.56     2.27
 7          1.96 0.225  164     1.52     2.41

Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95

$`pairwise differences of stage_no`
 1        estimate    SE   df  t.ratio p.value
 2 - 3  -0.1614    0.195 152 -0.830  0.9616
 2 - 4  -0.1976    0.191 152 -1.034  0.9059
 2 - 5  -0.4589    0.198 153 -2.323  0.1913
 2 - 6   0.2482    0.225 158  1.103  0.8794
 2 - 7   0.1979    0.264 164  0.749  0.9753
 3 - 4  -0.0362    0.160 143 -0.226  0.9999
 3 - 5  -0.2975    0.170 146 -1.747  0.5033
 3 - 6   0.4097    0.210 158  1.952  0.3746
 3 - 7   0.3593    0.254 165  1.417  0.7166
 4 - 5  -0.2613    0.165 141 -1.579  0.6135
 4 - 6   0.4458    0.205 156  2.177  0.2543
 4 - 7   0.3955    0.248 163  1.594  0.6038
 5 - 6   0.7072    0.209 155  3.383  0.0115
 5 - 7   0.6568    0.251 164  2.614  0.0998
 6 - 7  -0.0504    0.261 152 -0.193  1.0000
```

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Chapter 3: The effects of predator presence on nest abandonment and on-nest vocalisation rates during nest building.

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Abstract

One of the greatest influences on songbird breeding success is nest predation. Vocalising near the nest can have benefits, such as coordinating parental care, but may also reveal the nest location to predators. Therefore birds are expected to be sensitive to risk and reduce vocalisation rates accordingly. Interestingly, the Grey Fantail (*Rhipidura albiscapa*), frequently vocalise on their nests during nest building. Using a model presentation experiment, we tested if fantails would reduce vocalisation rates at the nest during building in response to predator presence. We recorded vocalisation rates on the nest during each build trip, then presented models (predator/control) determing how long it took pairs to return afterwards, and the next day observed the pair to determine if they altered on-nest vocalisation rates based on recent experience. After the nest was no longer in use we collected measurements of vegetation density from a 5 m radius of the nest. We found that changes in vocalisation rates and the occurrence of nest abandonment were not related to predator presence. We also found vegetation density immediately around the nest had a minor positive effect on on-nest vocalisation counts. Additionaly, birds took longer to return to the nest after exposure to the predator model and longer to return to the nest if they received the control model first. These results demonstrate that while birds altered behaviour in response to immediate risk, on-nest vocalisations rates and nest abandonment behaviour in Grey Fantails might be driven by a factors other thananti-predator response.

Keywords: Nest Desertion, Avian Acoustics, Predation risk, Risk assessment, Reproductive success

Introduction

Predation risk is a main driving force affecting the evolution of life histories (Ellrich et al., 2016; Mukherjee et al., 2014; Ricklefs, 1969; Vermeij, 1982). Organisms have many strategies to increase survival rates when facing predation risk, often in the form of morphological, physiological, and behavioural adaptations (Caro, 2005; Lima & Dill, 1990). In most songbirds, nest predation is the principal cause of nest failure, followed by starvation and nest desertion (Ricklefs, 1969). In response to nest predation risk, many songbirds have developed strategies to keep their nests hidden. These can include cryptic colouration of plumage, eggs, or nest, often in combination with secretive behaviours around the nest.

Many species of birds build nests, which are immovable structures that house eggs and young until they are ready to leave the nest (Collias, 1964; Healy et al., 2008; Purcell et al., 2008), leaving the nest contents vulnerable to predators during this time. Additionally, nest building is both time consuming and energeticially costly (Collias & Collias, 1971; Hansell, 2000; Komdeur et al., 2005; Withers, 1977). Some birds, such as many cuckoo species, lay their eggs in nests of other bird species, thus avoiding nest building completely thereby saving time and energy (Payne, 1977). Given a limited number of re-nesting attempts in a breeding season, we would expect most birds to optimise each attempt for success. For example, birds might reduce activity at the nest (Eggers et al., 2005; Reviewed in Ibáñez-Álamo et al., 2015), and minimise vocalisations on and near the nest (Duncan & Bednekoff, 2006) to reduce nest predation risk. Placing nests in concealed locations (Martin, 1995) and using camouflaged nesting material (Collias & Collias, 2014; Goodfellow, 2011; Hansell, 2000) can also reduce risk.

While on-nest and near-nest vocalisations may have useful functions (i.e. territory defense, communication with partner, alerting other birds of a potential risk), there is a potential cost of attracting predators that use acoustic cues to locate prey (Kleindorfer et al., 2018; McDonald et al., 2008; McDonald et al., 2009). For example, nest departure calls can increase both nest predation rates (McDonald & Greenberg, 1991; Yasukawa & Searcy, 1982) and nest parasitism by Brown-headed Cowbirds, *Molothrus ater* (Clotfelter, 1998). Similarly, playing higher rates of sound (white noise or nestling begging calls) near nests is related to higher rates of nest predation (McDonald et al., 2009). As near-nest sounds may attract predators to nests, adults often vocalise away from the nest to minimise the risk of nest predation (Kleindorfer et al., 2018; Magrath et al., 2015; McDonald et al., 2009). Despite the risk, in some species, adult birds vocalise close to or while on their nests (e.g. Davies et al., 2004; Hall et al., 2015; Ritchison, 1983). Vocalising despite the potential cost of attracting nest predators suggests there is a benefit of vocalising on and near the nest.

The Grey Fantail (*Rhipidura albiscapa*) is an ideal model species to study, such seemingly risky on-nest vocalisations, as it produces both songs and calls on the nest during all nest stages, including nest building (Beckmann & Martin, 2016; Berger-Tal et al., 2010). One potential hypothesis for the birds’ frequent vocalising is that the birds are attempting to determine if predators are nearby during nest building, ultimately helping them decide if the nest site location is safe or whether they should abandon. If a predator discovers the nest during building, the pair may be more likely to abandon that nesting attempt and re-nest in a new and safer location (Beckmann et al., 2015; Berger-Tal et al., 2010). Indeed, rates of nest predation (59% Higgins et al., 2006; 82% Munro, 2007; 44% Sotnychuk unpublished data) and nest abandonment before egg-laying (56% Beckmann et al., 2015; 60% Beckmann & Martin, 2016; 47% Munro, 2007; 37% Sotnychuk unpublished data) are high in this species, resulting in multiple nesting attempts across the breeding season (7 nests Beckmann et al., 2015; 8 nests Sotnychuk unpublished data). As Grey Fantails have a long breeding season (~5 months; Higgins et al., 2006), they have time to re-nest if they suspect a predator has located their current nest, before investing in thenest even further. While nest abandonment behaviour is primarily thought to be linked to predation risk (Beckmann et al., 2015; Munro, 2007), other factors such as adverse weather (Beckmann et al., 2015) and intraspecific competition

(Flegeltaub et al., 2017) may play a lesser role.To gain a better understanding of the rates of on-nest vocalisations and nest abandonment during nest building in relation to predator presence, we conducted an experiment in which we manipulated predation risk by presenting two taxidermy models (predator/control) to nest-building pairs and measured near-nest vocalisation rates and nest abandonment rates. Acoustic behaviour change in response to a predator has primarily examined mobbing calls (i.e. Dutour et al., 2017; Kalb et al., 2019; Kaplan et al., 2000) and intraspecific communication (i.e. Courter & Ritchison, 2010; Gottfried et al., 1985; Morton & Shalter, 1977). Those studies examine the short-term responses to predators but often assume that the cost is long-term. The assumption that the acoustic changes observed in vocal behaviour would persist is not often confirmed by future research. Therefore, in this study, we hope to fill a gap by examining a longer-term behavioural change by comparing on-nest acoustic rate the day before and after a model presentation rather than all in one day.

We hypothesised that nesting behaviour is influenced by predation risk and predicted that there will be a carry-over effect of vocalisation rates decreasing across days, and an immediate response of nest abandonment will increase in response to the predator model. We predict this because we expect pairs to respond to predation risk becoming more cryptic (less vocalisations) or attempting to avoid the predator completely by nesting again. We aimed to analyse the longer-term carryover effects of a single encounter with a model predator rather than the immediate impact of predator presence, by analysing on-nest vocalisations across days rather than minutes/hours.

Methods

Study Site and Species

We studied a colour banded population of Grey Fantails in Brisbane Ranges National Park, Victoria, Australia (37°51'10.8"S 144°11'21.2"E) from October to December 2019. Grey Fantails are small (~8 g) socially monogamous passerines with bi-parental care (Higgins et al., 2006). They build open cup nests often covered on the outside with spider silk, and a typical clutch size is 3 eggs (Higgins et al., 2006).

During the breeding season, pairs showing nest building behaviours were followed. Pairs without a nest were systematically searched 2–3 times per week by following the female for 30 minutes. Nests were monitored once every 3–5 days until the nesting attempt was complete (abandoned, fledged, or predated). Nests that were low enough to place a model level with the nest using a tripod were selected for trials. Pairs provisioning fledged young were not used in trials, as pairs will often provision older fledglings in between nest building trips, which may bias both nest building and near-nest vocalisation behaviour. Each pair of birds were assigned a territory number.

Nests under construction were categorised into one of six ‘stages’ of construction: 1) wrapping – strands of web and sometimes bark being placed and wrapped around the tree branch, 2) nest tail/base – building the platform attaching the nest to branch and the part hanging under nest (tail), 3) low cup walls, 4) mid walls, 5) high walls, and 6) lining the cup (see Figure 3.1). Nests at stage one were not used as this stage may form part of the bird’s nest site selection process. Likewise, we did not start a trial on nests at Stage 6 to minimise the female’s time and energy costs in case of nest abandonment due to model presentation. Thus, trials were only initiated when nests were between stages 2-5. Additionally, as the trial spanned three days (see below), if the nest was nearing completion the bird could lay eggs before the end of the trial. Pairs that laid an egg during the trial were removed from the data set (*n*=1).

Once a nest was selected, it was visited for three consecutive days during the trial (see Table 3.1), except in extreme weather (i.e. high wind, or storms; *n*=1) or if the nest was abandoned. In such cases the trial would resume the following day when possible. All trials took place between 45 minutes and 5.5 hours after sunrise, which allowed for sufficient lighting to observe behaviours and accurately read color bands, and avoided extreme summer heat, when birds may reduce nest building activity to save energy (Bibby et al., 2000). All trial obervations on Day 2 and 3 were run within one hour of the first day's sampling time. Post-trial all nests were monitored to determine their fate.

We measured vegetation density immediately around the nest, because some studies have shown it impairs the vision of predators, minimising the risk of predation as well as influencing fleeing behaviours of nesting birds (Gómez-Serrano & López-López, 2014; Ydenberg & Dill, 1986). Research has shown that nests placed in areas with higher vegetation density have increased likelihood of survival (Deeming & Reynolds, 2015; Fulton, 2018). We assessed vegetation density at the nest site using a visual obstruction board: 30.48 x 30.48cm red and white checked board demarcated into 5.08cm^2 squares (Modified Jones, 1968). The board was placed level with and directly facing the nest, at a 5m distance from the nest. The researcher, standing with their head level with the nest, counted the total number of individual squares that were at least 50% visible. Vegetation density was measured at the four cardinal directions, then averaged for each nest and used as percent out of 100 for analysis.

Experimental manipulation of predation risk

We presented two taxidermy models to each pair on two subsequent days: Pied Currawong (*Strepera graculina)* and Crimson Rosella (*Platycercus elegans)*. The Pied Currawong is a known nest predator of Grey Fantails (Beckmann & Martin, 2016; Guppy et al., 2017). The Crimson Rosella was selected as a control as it is similar in size to the Currawong, frequently forages lower in the habitat at similar heights to lower fantail nests, and is a non-competitor and non-predator. Both species are common at our field site. Fantail pairs received one control model and one predator model over the course of the first two days of the trial; we had two different models of both the control and predator. To control for an order effect due to the specific model, the presentation order and model selected were randomized.

The trial took place over three days and contained seven parts (see Table 3.1). On the first day of the trial, nests were observed; vocalisations and bird activity were recorded or dictated for one hour using a Sennheiser ME-66 microphone and Zoom H4N recorder (Part 1, see Table 3.1). The observer was positioned 5-12m ($\bar{x}$ = 7m) from the nest under camouflage netting. The distance was dictated by vegetation density and how well the observer could see behaviours at the nest, with the aim to sit as far from the nest as possible, yet still be able to make accurate observations. For each build trip to the nest the following data were collected: bird identification, duration of build trip (from when the bird first physically touched the nest to when it got off the nest), the number of on-nest songs/calls (vocalisations made while the bird was physically touching the nest), and the number of near-nest songs/calls (vocalisations made while 0-2.5m from the nest immediately before and after a build trip).

After the one-hour watch, while neither member of the pair was present, the taxidermy model was mounted on a tripod at nest height at a distance between 2-2.5m from the nest ($\bar{x}$= 2.1m; Part 2, see Table 3.1). The model was left up for three minutes after one member of the pair noticed it. This was determined by the bird’s behaviour, including swooping at model, inspecting model, vocalising at the model, dropping nest material in presence of the model, a quick change in activity from building to ‘foraging’, and actively avoiding the nest/model area. To account for cryptic behaviour (avoiding the nest completely from a distance), the model was never left out for longer than ten minutes. After the model was removed, the birds were observed for either 32 minutes or three build trips (whichever came first) to determine if the pair abandoned the nest due to the model (Part 3, see Table 3.1).

For those pairs that did not abandon, we recorded the amount of time it took a bird (female *n* = 36, male *n* = 0, unknown *n* = 2) to make its first trip to the nest after the model was presented (latency to return). Due to many birds returning to build while the model was up, we set the latency start time from when the model was first seen by the birds until the bird returned (for a maximum possible time of 35 minutes; three minutes model presentation plus 32 minute post-watch). Pairs that did not abandon the nest and did not return to build during the 32-minute post-watch were allocated a ceiling latency value of 35 minutes. Experiment Day Two followed the same methodology, but with the second model presented (Parts 4,5,6, see Table 3.1), followed by the one-hour watch on Day Three (Part 7 see Table 3.1).

We recorded if nest abandonment occurred following model presentation. A nest was confirmed to be abandoned if the pair left and did not return to the nest for seven days, or they began building a new nest and made no further progress on the previous nest following model presentation. If nests were inactive, the female of the pair was followed for a minimum of 30 minutes to determine if nest building was occurring at a new location. If the nest was abandoned during the trial, to locate the next nesting attempt, the pairs were monitored for nest building behaviour daily for three consecutive days, and then every other day for a week.

Nest abandonment was attributed to the model if abandonment happened during the post watch (i.e. after the model was removed; Parts 3 and 6, see Table 3.1) and was confirmed on the following day. If abandonment occurred at other times, it was considered due to some other unknown factor. If the subsequent nest was located within five days of the abandonment, was at an appropriate stage of building and located low enough to the ground, the trial continued as if it had not been interrupted *(n=1)*.

Statistical analysis

All statistical analysis were performed in R version 4.0.2 (RStudio Team 2020; See Supplementary Material 3.1 and 3.2 for R code and output).

(a) Vocalisations

The total number of near-nest and on-nest songs (physically touching the nest) was low (near nest vocalisations before build trip n = 13, near nest vocalisations after build trip n = 88, on-nest n = 31; Supplementary Material 3.3). Therefore, we counted each song as one vocalisation, and thus songs and calls combined made up the total number of vocalisations made by the female per build trip. There was a high percentage of trips (over 70%) with no near-nest vocalisations (songs and calls); therefore we removed near-nest vocalisations from statistical analysis (before 78% and after 79%, compared to on-nest at 48%; see Supplementary Material 3.4).

The number of on-nest vocalisations across day were analysed using a zero-inflated Poisson model using the package GlmmTMB (Brooks *et al.* 2017). This was due to the count nature of the data, and the high proportion of zeros in the data that exceeded that predicted from a Poisson model alone (48% of trips had no vocalisations). The zero-inflated Poisson model consists of two parts; 1) a binomial model that fits the probability of occurrence of a 0-vocalisation count, and 2) a Poisson model that fits the counts greater than zero.

The model for on-nest vocalisations included the fixed variables of model order, model type, their interaction, and the averaged visual obstruction count at 5m. Territory number was included as a random intercept effect to account for repeated measures and individual variation. We sequentially evaluated terms to be included in the zero-inflated part of the model to find the minimal adequate model, beginning with our null Poisson model containing the terms described above. Adding a zero-inflation term to the model (an intercept) greatly improved fit versus a model without it (reduction in AICc: *dAICc* = -140). Adding the random effect to the zero-inflation model improved model fit further (*dAICc* = -62.5). However, adding additional fixed effects of model order and model presented, either alone or in combination, as well as the interaction, did not improve model fit further (all *dAICc* values = 0.2 and greater).

(b) Latency to return after model presentation

We used a linear mixed model to analyse latency to return to the nest (in square root transformed minutes) after model placement. The statistical model included the fixed effects of model presented (Predator/Control), model order (0,1), the interaction, and the percent visual obstruction count at 5m. To control for variation among pairs in their overall building activity, we included the average time (in minutes) between build trips during the pre-model interval as a predictor variable. Territory number was included as a random effect to account for individual differences in behaviour and non-independence of repeated observations within individuals.

Four pairs did not return after the model was placed, one of which ultimately abandoned the nest while the other three continued building the following day. The pair that abandoned the nest was removed from the analysis. The birds that returned the next day (n=3) received a ceiling value of 35 minutes.

(c) Nest abandonment

Only one pair was considered to have abandoned the nest due to the model presentation. For the nest to be considered abandoned due to the model presentation, the pair must have done both of the following 1) not have returned to the nest during the post watch (n = 4), and 2) not have returned to the nest on subsequent days (n = 2). Using these criteria, only one pair abandoned the nest after presentation of the predator model. With so little data, no analysis meaningful analysis could be conducted. The pair that abandoned due to the predator model presentation was removed from the latency analysis. The remaining pairs that did not return during the post watch were given a ceiling value for the latency analysis. The other pair that abandoned the subsequent day returned during the post watch; therefore, that nest was not considered abandoned due to the model presentation and the second model presentation was conducted at its next nest.

Results

We monitored 79 pairs through the field season and ran trials on 20 pairs (predator model presented first n = 10, and control model presented first n = 10); mean nest height of nests used for trials was 2.12 ± 0.87 SD meters (range 0.8-4.85 meters).

Of the 20 pairs, only 12 had a male visit the nest at least once during the three-day trial. Out of 1029 recorded build trips, males went to the nest only 33 times (3.2%), females 984 times (95.6%), and unknown fantail identification 12 times (1.2%). Male trips were an average of

0.6 trips/hour (range of 0-7); female trips averaged at 16 trips/hour (range of 4-47). In this study, an average on-nest build trip lasted 26 seconds for females and 14 seconds for males. Additionally, in 34% of the trips males brought no material and seemed to be mostly shaping the nest (See Supplementary Material 3.5 for details on male trips). Due to limited trips by males and trips from birds we were unable to identify at the time of the trip, we removed trips from male (n = 35; 0.03%) and unknown birds (12 of the 1029 trips; 0.01%) from the vocal analysis, thereby only including data collected on positively identified females.

(a) Vocalisation Rates

Daily vocalisation rate did not differ in response to the model presentation order (χ^2= 3.6, df = 1, p = 0.06), model type presented (χ^2 = 2.5, df = 2, p = 0.28) or their interaction (χ^2 = 1.7, df = 2, p = 0.43; Figure 3.2). However, vegetation density immediately around the nest had an effect on vocalisations (p < 0.01). This effect predicted an increase of 4 vocalisations for an increase in density from 0 to 100% (predicted value back transformed).

(b) Latency to return after model presentation

Our analysis included 39 presentations (control, n = 20; predator, n = 19). Three pairs did not return to the nest during the post-watch period but returned the following day (therefore not considered abandoned due to the model presentation); these pairs received the ceiling value. All three instances occurred after the predator model presentation. Some birds returned to the nest while the models were still up (control, n = 15; predator, n = 5). After controlling for effects of vegetation density and time between build trips, there were significant effects of model type and order on the latency to return. Pairs took 4.8 minutes longer to return to the nest after the predator model in comparison to the control ($F_{1,20}$ = 30.2, p < 0.01; Figure 3). Additionally, pairs took 3.2 minutes longer to return to the nest if the control model was presented first ($F_{1,19}$ = 20.6, p < 0.01; Figure 3). There was no interaction between model order and model type ($F_{1,19}$ = 2.3, p = 0.15; Figure 3). Vegetation density influenced the length of time to return to the nest after model placement ($F_{1,19}$ = 7.3, p = 0.02). The effect of density was substantial and predicted an increase of 5.3 min latency to return coincident with an increase of density from 0-100% (predicted value back-transformed). Therefore, pairs took longer to return to the nest if the nesting habitat around the nest was denser. Lastly, pairs took longer to return after the model presentation if they were taking longer to return between build trips prior to the model presentation ($F_{1,33} = 5.6$, $p = 0.02$).

(c) Nest Abandonment

Only one pair was considered to have abandoned the nest due to the model presentation following the predator model. Therefore, 1 of 19 (5%) abandoned after the predator model and 0 of 20 (0%) after the control model.

Discussion

Contrary to our predictions, Grey Fantails nest abandonment during nest building did not increase in relation to increased predation risk. In contrast, Berger-Tal et al. (2010) found Grey Fantail pairs abandoned nests under construction due to the presence of a taxidermied predator model (4 of 6 nests abandoned) in comparison to the control model (0 of 7 nests abandoned). Their study assessed nest abandonment the following day; by doing this, there is a potential in the interim time other disturbances (i.e. inclement weather, territory loss, interspecific competition) that could cause nest abandonment. If we had assessed abandonment using the same methodology, our rates of nest abandonment are still lower (4 out of 39 presentations). Berger-Tal et al. (2010) placed models 1m from the nest whereas we placed models 2.0-2.5m, suggesting distance of model placement may have impacted our results. Birds may perceive a substantial increase in risk the closer a model is placed to the nest. For example, Willow Tits (*Poecile montanus*) produced fewer alarm calls when a predator was 10m from the nest in contrast to 40m (Alatalo & Helle, 1990). Similar to our results, Northern Flickers (*Colaptes auratus*) pairs did not abandon the nest more frequently when presented a predator model in comparison to control, suggesting that the predator might have to reoccur to cause nest predation (Fisher & Wiebe, 2006). We suspect that in order to be a large enough risk to cause nest abandonment or changes in behaviour the predator model might need to recur or be closer to the nest than it was in our study.

Nest abandonment in Grey Fantails is more likely to occur during earlier stages of nest building process than during other nest stages (Beckmann et al., 2015; Beckmann & Martin, 2016; Berger-Tal et al., 2010), suggesting that a single visit of a predator near the nest may be sufficient to result in abandonment. Since trials did not include the earliest stage of nest building (Stage 1), our experimental design could have led to lower abandonment rates in general. Some predators, such as Corvids, have the capacity for long-term memory and have been shown to return to nests they have previously visited (Sonerud, 1985; Sonerud & Fjeld, 1987), making the costly decision to abandon the nest (in terms of time and energy) outweighed by the reduced risk of nest predation in some species. However, at early stages of building, nests lack any real shape. We do not know at what point predators such as currawongs visually recognize the nest as such. Given the low rates of nest abandonment we found, and that nests are more often abandoned at early building stages (catergorized as start of building up until base of nest cup; Beckmann & Martin, 2016), this suggests there may be alternative primary reasons for nest abandonment during building.

Alternative hypotheses for nest abandonment during nest building include adverse weather (~5% this study; predicted to be ~10% Beckmann et al., 2015), and intraspecific competition (Flegeltaub et al., 2017). We suspect only one of our pairs abandoned due to adverse weather (5% of all nests trialed; 25% of the abandoned nests). Guppy and colleagues (2017) studied Australian woodland birds and concluded 8% of abandonment nests (post laying) were due to a combination of weather damage and partner death. All birds that abandoned a nest during our trial were re-sighted after the abandonment event, except for one female that was not colour banded; therefore we cannot confirm this individual’s survival. Komdeur et al. (2005) found Penduline Tits (*Remiz pendulinus)* in better condition abandoned nests more often than birds in poor condition and attributed this to nest building being more energetically costly than incubation. Although we did not measure body condition through the breeding season, it is possible birds in our study were in poor condition and therefore were less likely to abandon nests. If health and stamina influnces abandonment decsions this could account for the large variation between Grey Fantail pairs in number of nesting attempts and nest abandonment rates (7 nests Beckmann et al., 2015; 8 nests Sotnychuk unpublished data), if body condition influences abandonment decisions.

Another alternate reason for nest abandonment is brood parasitism (Goguen & Mathews, 1996; Graham, 1988; Guigueno & Sealy, 2011; Hill & Sealy, 1994). Grey Fantails may be abandoning nests as an anti-parasitism strategy, prior to a parasitism event. The presence of a brood parasite that observes the nest building bird to locate potential nests to parasitize, could be a trigger for nest abandonment (Norman & Robertson, 1975). Brood parasitism by cuckoos has been recorded in Grey Fantails (Higgins et al., 2006), although it was not recorded at our field site, though Fan-tailed Cuckoos (*Cacomantis flabelliformis*) and Shiny Bronze-Cuckoos (*Chrysococcyx lucidus*) were observed in Grey Fantail territories. The lack of brood parasitism at our field site may be due to strategic nest abandonment during nest building if a cuckoo has located the nest site.

Overall, our results suggest that a predator near the nest might not pose as great a threat as previously thought and nest abandonment during nest building might not be the direct result of predators locating nests under construction. Our results suggest that nest abandonment might be a strategy used to avoid nest parasites or perhaps have other functions. Given the time and energy costs of nest building (Collias & Collias, 1971; Hansell, 2000; Komdeur et al., 2005), abandoning when a nesting attempt has not been directly impacted by predation (i.e. eggs/chicks predated) may be too costly. Rather than abandoning nests, pairs might changebehaviour in other ways such as reducing on-nest vocalisation.

Contrary to our predictions, we found Grey Fantails did not change on-nest vocalisation rates in response to either model type, or whether they received a threatening or non-threatening model first. However, the rate of on-nest vocalisations increased as the vegetation density around the nest increased. Since, birds nesting in denser vegetation might be harder for predators to locate, increasing vocalisation rates over time may be less risky than pairs nesting in more open habitat. On-nest vocalisations could be an adaptive strategy for alternative purposes such as intra-pair communication (Beletsky & Orians, 1985; Kavelaars et al., 2019; Ritchison, 1983), alarm calling (Gill et al., 1997; Gill & Sealy, 2003), or assisting in mate guarding (Sonnenschein & Reyer, 1983). If one or more of these functions are employed by Fantails, this may preclude us observing a carry-over effect of predator presence on vocalisation rates. We observed that near nest songs before a build trip occurred more frequently than on-nest songs. A study focusing on song only near the nest, specifically song type, might find the birds are altering song near the nest rather than on the nest.

Additionally, our experimental time frame may have affected our results. Little is known about the acoustic behaviours of Grey Fantails across the day, especially regarding on-nest song rates and nest abandonment times. We know they sing throughout the day, however, we assume it is similar to the Northern Hemisphere system where the peak song rate is in the morning (Burt & Vehrencamp, 2005; Staicer et al., 1996; Wright, 1912, 1913). Some studies have observed the various functions of the dawn chorus in Australian species (Barnett & Briskie, 2007; Dalziell & Cockburn, 2008; Dutour et al., 2020). In general, singing in the morning is more common, and might serve multiple functions in Grey Fantails (i.e. territorial defence, mate guarding, advertise fitness) while vocalising later in the day is less common and might be reserved for other functions such as predator avoidance. If there are multiple reasons for the vocalisations and a higher rate of vocalisations in the morning it might be more difficult to observe a change in vocalisations at that time. Differences could be easier to observe later in the day when there are fewer vocalisations that are for a more specific purpose. Due to no carry-over effects in on-nest vocalisation rates after predator presentation, our results suggest that nest abandonment and on-nest vocalisations do not appear to be a defence strategy to avoid nest predators, at least in our population.

To examine immediate changes in behaviour, we observed the latency to return to the nest directly following model presentation. As predicted, fantails took longer to return (4.8 minutes) after the predator model in comparison to the control. Currawongs are a threat to the adult as well as nest contents, so this result is not surprising. Interestingly, many pairs returned to build while the model was up, with 5 (26%) and 15 (75%) returning to build when the predator and control models were up, respectively. Additionally, pairs also took longer to return if they had received the control model as their first model presentation (3.2 minutes). It is important to note that time remaining in the breeding season, and/or nesting attempt number may play a role in the birds' decision making, thereby influencing the latency value, with birds possibly returning sooner the later in the season it is. Unfortunately, we do not have the statistical power to test for effects of these variables. Both these trends could also be a reflection of individual variation in responsiveness to risk, and is captured by the significant random effect in the model. We did, however, control for previous build trip frequency, and found birds took longer to return if build trip activity before model placement was slower that day. Additionally, birds with nests that are placed in higher density vegetation took longer to return after a disturbance, regardless of the level of threat. This may be due to the assessment of immediate risk after a disturbance near the nest, delaying their return to the nest helps contribute to cryptic behavior at the nest.

While birds showed a response to the models, the degree of the response may not have long term consequences for that nesting attempt. As nest building spans multiple days, a difference to return to the nest of only a few minutes may not negatively influence the nesting attempt and could help minimize the adult's immediate danger. Birds may simply survey the area and return quickly once they have ascertained the predator/threat has left the immediate nest area. While we did not find any predator presentation studies conducted during nest building on song birds, a study on wood warblers (*Phylloscopus sibilatrix*) examined time to return to the nest after four presentations of various threat levels (an empty mount, a mug, Least Weasel (*Mustela nivalis*), and Eurasian Jay (*Garrulus glandarius*)) during both incubation and chick-rearing (Maziarz et al., 2018). Similar to our results, the authors found a pattern associated with predator threat level and a large range in latency to return after each model presentation from seconds to minutes. Additionally, they also observed pairs returning to the nest while models were still up (Maziarz et al., 2018). Further analysis of whether 35 minutes longer to return to the nest is biologically significant to the nesting attempt would need to be conducted in Grey Fantails to fully understand this result. Ultimately, the changes in latency to return to the nest after model presentations suggests the birds might see the disturbance as an immediate threat. It also indicates that we may not have observed vocal rate changes because the threat might be assessed as an immediate danger, and not a threat that carries over to subsequent days.

In conclusion, our results suggest that rates of nest abandonment during nest building may not be primarily due to predator presence near the nest, and Fantails do not adjust their on-nest vocalisation rates across days in response to predator presence. Collectively, these results suggest that both nest abandonment and on-nest vocalisations have alternative functions rather than anti-predator response, such as inter-pair communication or territorial defence. Grey Fantail pairs do seem to be risk aware as evidenced by their delay in returning to the nest after model presentation, with longer latencies after the predator model. This suggests while birds respond to immediate predation risk, there is no carryover effect across days. Further research on the function of nest abandonment and on-nest vocalisations during nest building could lead to a to better understanding of these behaviours. Future studies could include; 1) examining nest abandonment rates in response to cuckoos, 2) assessing rates of nest abandonment at various building stages due to predators, 3) analysis of time-of-day predation events occurring naturally in Grey Fantail populations, and 4) exploring the function of on-nest vocalisations in relation to territory size, partner presence and territorial defence.

Figure 3.1: Grey Fantail nest building stage reference guide (stages 0-6). Stage 0) no building – no evidence of a nest or building in the territory, 1) wrapping – the bird has material wrapped around branches or hanging from the tree but it is not distinctly conical, 2) tail and/or base – there is a cone-shaped tails or a flat stand on base; nest has a tail and is starting to be build upwards, 3) low walls (1/4) - Nest has the beginnings of walls, but they are less than ½ built, 4) medium walls (1/2) – nest wall are about half of a typical cup height but not yet ¾, 5) high walls (3/4) - Nest walls are ¾ completed but the tops are still ragged and unfinished, 6) cup/lining – Nest appears finished with rounded top but bird still brings webs or material for cup lining and no eggs have been laid inside the nest. Note tail length, cup depth, and the amount of spider web can vary look for rough edges on tops of wall, which indicates the bird has not yet finished the nest. Rounded and smooth walls indicate completion or near completion.

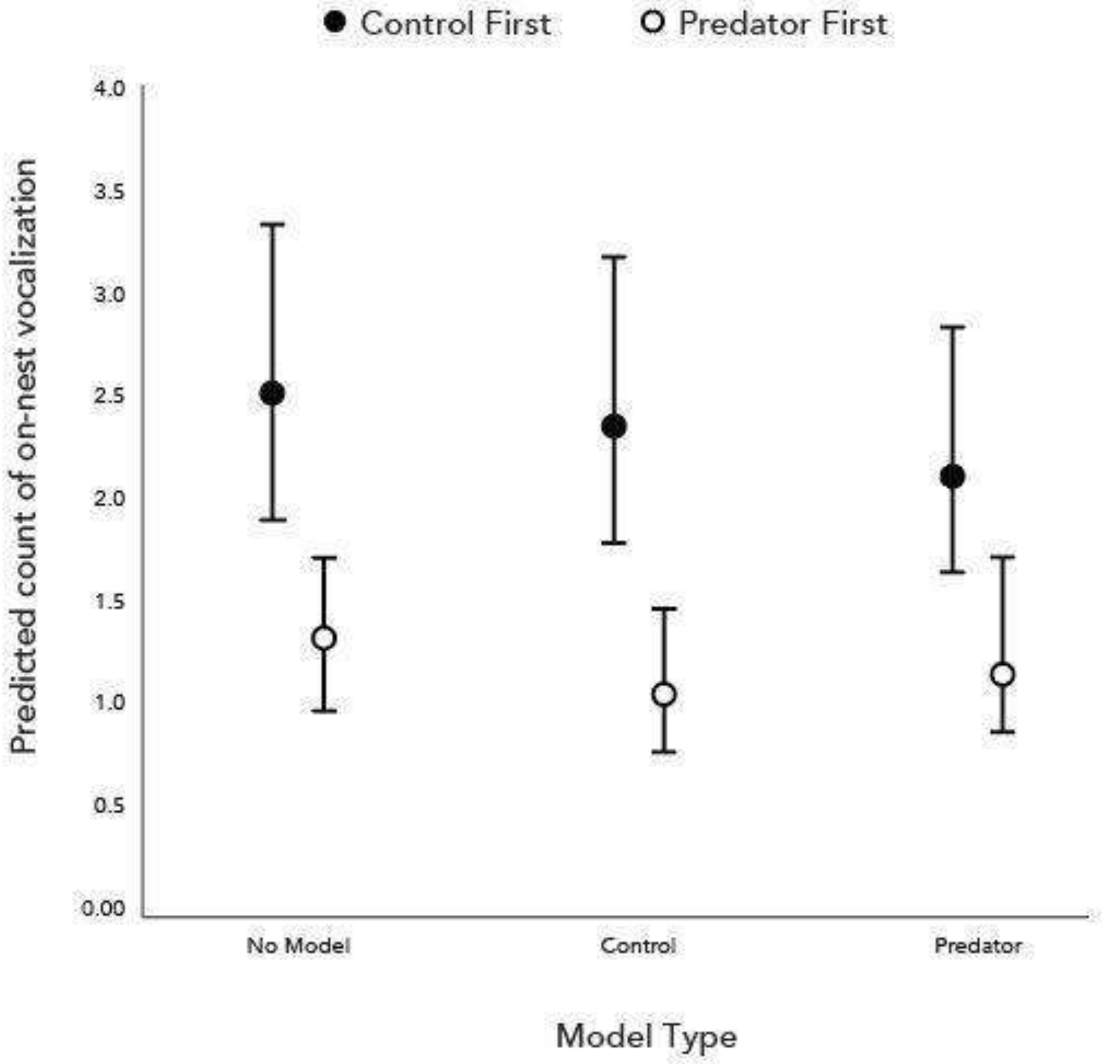

Figure 3.2: Model predicted count of on-nest vocalisations for each build trip arranged by model type presented (mean ± SE), no model, control, or predator. Pairs receiving the control model first are represented as closed circles, and pairs that received predator model first open circles.

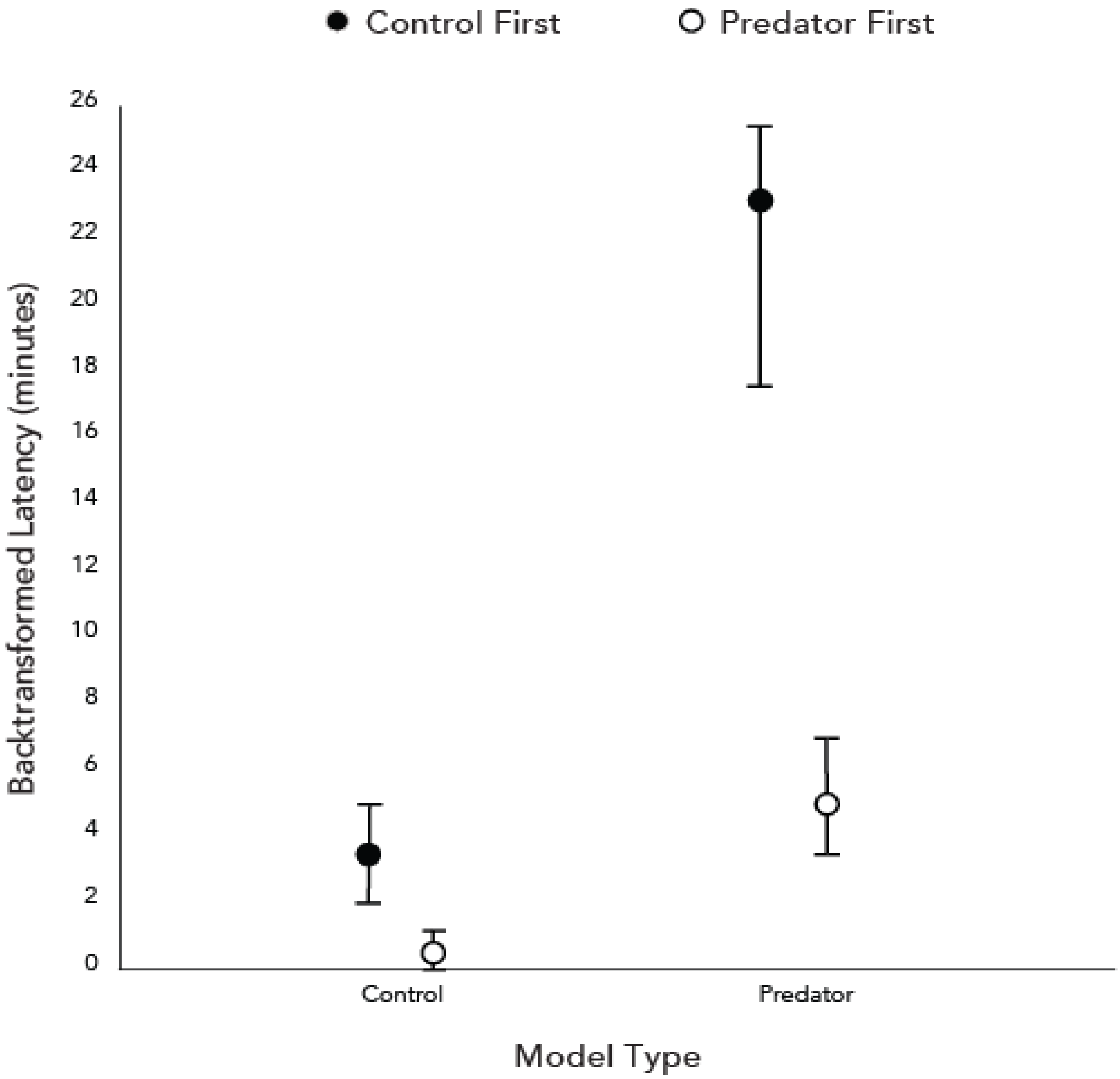

Figure 3.3: Average time (minutes) to return to the nest after model presentation by model type (mean ± SE) control, or predator. Pairs receiving the control model first are represented as closed circles, and pairs that received predator model first open circles.

Table 3.1: Observational sampling methodology by day and part; details of observer activity, duration of activity, and data collected across the 3-day 7-part trial.

Trial Day	**Day 1**			**Day 2**			**Day 3**
Part	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Observer Activity	Nest Watch	First Model up	Post watch	Nest Watch	Second Model up	Post watch	Nest Watch
Duration	1 hour	3 minutes	3 nest visits or 32 minutes	1 hour	3 minutes	3 nest visits or 32 minutes	1 hour
Data Collected	Vocalisation Count (No Model)	Latency/Abandonment		Vocalisation Count (First Model)	Latency/Abandonment		Vocalisation Count (Second Model)

Supplementary Material 3.1: Simplified R code and output for on-nest vocalisation data.

```
> pos_veg <- glmmTMB(boa_data_raw_count~model_order + model_presented +
jones_cover_percent + (model_presented:model_order) +(1|territory),
data = BOA_data, ziformula=~1+(1|territory), family=poisson)
> summary(pos_veg)
 Family: poisson  ( log )
Formula: boa_data_raw_count ~ model_order + model_presented + jones_cover_percent +
(model_presented:model_order) + (1 | territory)
Zero inflation: ~1 + (1 | territory)
Data: BOA_data

     AIC      BIC   logLik deviance df.resid
  3134.6   3183.5  -1557.3   3114.6      974

Random effects:

Conditional model:
 Groups    Name        Variance Std.Dev.
 territory (Intercept) 0.7568   0.8699
Number of obs: 984, groups:  territory, 20

Zero-inflation model:
 Groups    Name        Variance Std.Dev.
 territory (Intercept) 1.802    1.342
Number of obs: 984, groups:  territory, 20

Conditional model:
                                    Estimate Std. Error z value Pr(>|z|)
(Intercept)                         0.196466   0.339263   0.579 0.562524
model_orderPred1                   -0.807676   0.426702  -1.893 0.058380 .
model_presentedNone                 0.063064   0.083008   0.760 0.447415
model_presentedPred                -0.078066   0.091506  -0.853 0.393589
jones_cover_percent                 0.020496   0.005751   3.564 0.000365 ***
model_orderPred1:model_presentedNone  0.138714   0.166353   0.834 0.404363
model_orderPred1:model_presentedPred  0.225056   0.172784   1.303 0.192736
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Zero-inflation model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   -1.033      0.360   -2.87   0.0041 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> emmeans(pos_veg, poly~model_presented| model_order,
back.transform = TRUE, component = "cond")
$emmeans
model_order = Control1:
 model_presented emmean    SE  df lower.CL upper.CL
 Control         0.8629 0.288 974    0.297    1.429
```

```
 None           0.9260 0.288 974    0.361    1.491
 Pred           0.7849 0.290 974    0.216    1.354

model_order = Pred1:
 model_presented emmean    SE  df lower.CL upper.CL
 Control         0.0553 0.316 974   -0.565    0.676
 None            0.2570 0.296 974   -0.325    0.839
 Pred            0.2023 0.305 974   -0.396    0.800

Results are given on the log (not the response) scale.
Confidence level used: 0.95

$contrasts
model_order = Control1:
 contrast  estimate     SE  df t.ratio p.value
 linear     -0.0781 0.0915 974 -0.853  0.3938
 quadratic  -0.2042 0.1461 974 -1.397  0.1626

model_order = Pred1:
 contrast  estimate     SE  df t.ratio p.value
 linear      0.1470 0.1466 974  1.003  0.3162
 quadratic  -0.2566 0.2194 974 -1.169  0.2426

Results are given on the log (not the response) scale.

> #type 3 anovas are the same for both- happened before as well not sure why
> Anova(pos_veg, component = "cond", type = 3) #type 3 anova
Analysis of Deviance Table (Type III Wald chisquare tests)

Response: boa_data_raw_count
                          Chisq Df Pr(>Chisq)
(Intercept)              0.3354  1  0.5625237
model_order              3.5828  1  0.0583802 .
model_presented          2.5038  2  0.2859621
jones_cover_percent     12.7016  1  0.0003653 ***
model_order:model_presented  1.6981  2  0.4278152
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Supplementary Material 3.2: Simplified R code and output for latency to return to the nest data.

```
> latency_sqrt <- lmer(latency_sqrt ~ model_order + model_type + jones_cover_percent +
avg_time_between_build_min + (model_order:model_type) + (1|latency$territory),
data=latency, REML= FALSE)
> summary (latency_sqrt)
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method
['lmerModLmerTest']
Formula: latency_sqrt ~ model_order + model_type + jones_cover_percent +
    avg_time_between_build_min + (model_order:model_type) + (1 | latency$territory)
   Data: latency

     AIC      BIC   logLik deviance df.resid
   141.4    154.7    -62.7    125.4       31

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.51183 -0.47800 -0.05566  0.57869  2.56718

Random effects:
 Groups            Name        Variance Std.Dev.
 latency$territory (Intercept) 0.01325  0.1151
 Residual                      1.44641  1.2027
Number of obs: 39, groups:  latency$territory, 20

Fixed effects:
                            Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                 3.182877   0.539396 35.389493   5.901 1.00e-06 ***
model_order1               -2.390730   0.569282 38.981975  -4.200  0.00015 ***
model_typeR                -2.781517   0.557590 19.076621  -4.988 8.06e-05 ***
jones_cover_percent         0.022742   0.008408 19.871727   2.705  0.01368 *
avg_time_between_build_min  0.156759   0.065916 33.055349   2.378  0.02333 *
model_order1:model_typeR    1.177752   0.779591 18.693684   1.511  0.14758
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) mdl_r1 mdl_tR jns_c_ av____
model_ordr1 -0.522
model_typeR -0.449  0.514
jns_cvr_prc -0.448 -0.170 -0.108
avg_tm_bt__ -0.542  0.121 -0.088  0.120
mdl_rdr1:_R  0.425 -0.717 -0.698  0.055 -0.128

> aovj <- anova(latency_sqrt, type=3)
> aovj
Type III Analysis of Variance Table with Satterthwaite's method
                           Sum Sq Mean Sq NumDF  DenDF F value    Pr(>F)
model_order                29.751  29.751     1 18.667 20.5691 0.0002356 ***
model_type                 43.672  43.672     1 20.069 30.1933 2.201e-05 ***
jones_cover_percent        10.582  10.582     1 19.872  7.3158 0.0136845 *
```

```
avg_time_between_build_min  8.180   8.180     1 33.055  5.6557 0.0233338 *
model_order:model_type      3.301   3.301     1 18.694  2.2823 0.1475768
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> ranova(latency_sqrt)
ANOVA-like table for random-effects: Single term deletions

Model:
latency_sqrt ~ model_order + model_type + jones_cover_percent +
    avg_time_between_build_min + (1 | latency$territory) + model_order:model_type
                        npar  logLik    AIC       LRT Df Pr(>Chisq)
<none>                     8 -62.713 141.43
(1 | latency$territory)    7 -62.713 139.43 0.0013336  1     0.9709

> lsmj <- ls_means(latency_sqrt)
> lsmj
Least Squares Means table:

                         Estimate Std. Error   df t value    lower    upper  Pr(>|t|)
model_order0              3.19759    0.28186 19.2 11.3444  2.60797  3.78720 6.032e-10 ***
model_order1              1.39574    0.27414 17.7  5.0913  0.81918  1.97229 7.966e-05 ***
model_typeC               3.39298    0.28241 39.0 12.0142  2.82174  3.96423 1.115e-14 ***
model_typeR               1.20034    0.27484 39.0  4.3675  0.64442  1.75626 9.000e-05 ***
model_order0:model_typeC  4.58835    0.40875 39.0 11.2253  3.76157  5.41512 8.781e-14 ***
model_order1:model_typeC  2.19762    0.39304 38.9  5.5914  1.40259  2.99265 1.921e-06 ***
model_order0:model_typeR  1.80683    0.38376 39.0  4.7082  1.03060  2.58306 3.132e-05 ***
model_order1:model_typeR  0.59385    0.38928 39.0  1.5255 -0.19357  1.38128    0.1352
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

  Confidence level: 95%
  Degrees of freedom method: Satterthwaite
```

Supplementary Material 3.3: Number of female vocalisations (songs/calls) on and near (before and after) the nest out of all trips to the nest. Near-nest vocalisation counts are either before or after a build trip within 2.5m of the nest.

	Total Number of Calls	Total Number of Songs	Total Number of Vocalisations
Before	270	13	283
On	502	31	533
After	176	87	263

Supplementary Material 3.4: Number of trips where a bird vocalised and did not vocalise (n=984 for each of the following before, on, and after). Includes the maximum number of vocalisations made per trip and the percentage of trips birds vocalised on. Near-nest vocalisation counts are either before or after a build trip within 2.5m of the nest.

	Number of Trips with Vocalisation	**Number of Trips without Vocalisation**	**Maximum Number of Vocalisations per Trip**	**Percentage of Trips with Vocalisation**
Before	204	780	7	21
On	513	471	27	52
After	210	774	4	21

Supplementary Material 3.5: Build trip material breakdown and percentages for males and females.

Material Type	Female Trip Count	Female Trip Percentage	Male Trip Count	Male Trip Percentage
None	15	2	12	34
Bark	251	26	1	3
Web	248	25	0	0
Unknown	470	48	22	63
Total	984		35	

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Chapter 4: Nest placement decisions in Grey Fantails (*Rhipidura albiscapa*) relative to neighbouring conspecific nest proximity and stage.

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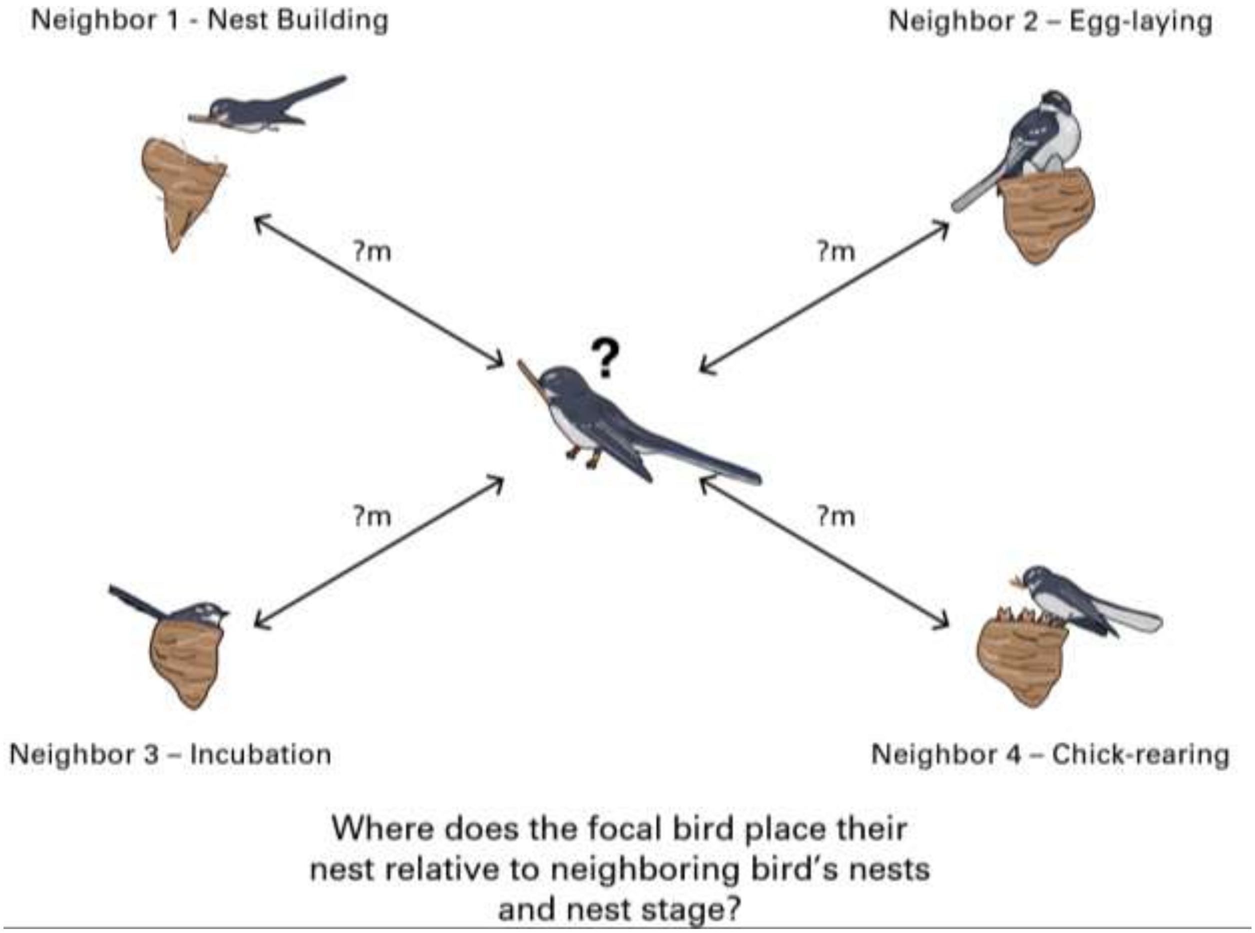

Abstract

Numerous factors can affect breeding success, with nest predation considered the greatest contributor to nest failure in passerines. Due to this strong selection pressure, birds use tactics to reduce nest predation risk, such as strategic nest placement. However, studies in nest placement and nest abandonment strategies in relation to predation risk and nest placement relative to neighbours' nests in non-colonial passerines is understudied. The Grey Fantail (*Rhipidura albiscapa*) experiences high nest predation and abandonment rates, which results in multiple renesting attempts per pair breeding season. We studied nest site selection relative to the proximity to conspecific nests, and nest stage of the conspecific neighbour. Distance to neighbour nests were not different from random points. However, the neighbour's nest stage was related to nest placement distances. Nests were placed an average of 147m, 208m, 154m, and 182m from neighbours that were at the stages of building, egg-laying, incubation, and chick-rearing, respectively. Our results suggest that activity levels at neighbours’ nests at different stages may influence placement choices. For example, when placing nests closer to neighbours that are nest building, pairs may be matching similar activity to take advantage of dilution and confusion effects if a predator is nearby. Additionally, building a nest closer to egg-laying neighbours may be more energetically costly if intraspecific competition is present. Overall, these patterns suggest that renesting Grey Fantails are strategically placing nests relative to neighbours to increase fitness.

Keywords: Nest-site selection, nest abandonment, renesting decision, nearest neighbour, perceived predation risk

Introduction

Nest predation is considered the greatest contributor to nest failure in most songbirds (Martin, 1992; Ricklefs, 1969). In response, birds have developed a variety of strategies to reduce the risk of nest predation (Caro, 2005; Reviewed in Ibáñez-Álamo et al., 2015), such as adaptations to nest structure and nest placement. Nest-site selection has been well studied in relation to vegetation cover and changes to the nest-site. Initially, researchers thought the primary function of nest concealment was to limit visual cues to predators and brood parasites (Conover, 2007; Deeming & Reynolds, 2015; Haff & Magrath, 2011). However, there is a trade-off between the degree of nest concealment and the level of visibility for the nesting bird. Ideally, nests should be hidden from predators, but the adult also needs be able to detect and escape from a predator (Götmark et al., 1995; Magana et al., 2010; Seltmann et al., 2014).

Trade-offs in other changes to the nest-site have also been observed. When renesting, nest height from the ground can be influenced by several factors including habitat type, predator type, and weather (Deeming & Reynolds, 2015). The variation in nest height is thought to involve a trade-off in which higher nests are more susceptible to the weather, specifically wind (Caro, 2005; Marzluff, 1988); but nests placed higher up in trees are harder for terrestrial predators (such as small mammals and snakes) to access. Finally, there has been a relationship observed between nest fate and renesting distance in which pairs with predated nests placed new nests at further distances from their previous nest in comparison to pairs that had successful broods (Beckmann et al., 2015; Boulton et al., 2003; Deeming & Reynolds, 2015; Fisher & Wiebe, 2006).

Nest site selection may be associated with the placement of already established nests of neighbouring pairs. As predation risk increases, theassumption is that prey species will increase nest dispersal to reduce such risk (Krebs & Davies, 2009; Tinbergen, 1963). A study of New Zealand Fantails (*Rhipidura Fuligwosa)*, suggested nests located further away (>70m) from neighbouring pairs were more likely to fledge offspring (McLean, 1980). However, some studies have found no difference in nest dispersal and predation and suggest the hunting strategies of the predator need to be accounted for when examining these relationships (Andrén, 1991). Similarly, a study of predation rates on the nests of two Kingbird species (*Tyrannus verticalis* and *T. vociferans)* found no relation to distance from neighbouring conspecific nests (Blancher & Robertson, 1985). However, Ringelman et al. (2012) studied nest density in non-colonial waterfowl (mostly mallard *Anas platyrhynchos* and gadwall *Anas strepera*) and found birds with a shorter nearest neighbour distance to other waterfowl were more likely to be successful and share the same nest fate as the neighbour. There may be different trade-offs influencing nest placement to near neighbours across species. Determining the factors that influence nest placement can provide insight as to the potential risks and benefits affecting nest placement by birds, especially with the influence of nest predation risk.

Many studies have found nest predation rates increase as on-nest vocalisations increase (i.e. Kleindorfer, Evans, et al., 2014; Kleindorfer et al., 2017; McDonald et al., 2009). Additionally, increased sound (i.e. white noise) on the nest was found to increase nest predation risk (McDonald et al., 2009). Therefore, focal bird nest placement closer to more vocal neighbours could increase nest predation risk, by attracting predators to the area. Nest placement near neighbours at nest stages that have less frequent on-nest vocalisations might be a useful strategy in maintaining cryptic behaviour. However, a trade-off in nest placement increasing attention from predators due to nearby vocalisations might outweigh the potential benefits of nesting in close proximity to neighbours.

Nesting closer to neighbours may be beneficial because increased group sizes can lower predation risk (Beauchamp, 2019). Placing nests closer to neighbouring nests might aid in selfish herd and dilution effect, where predators may find the neighbour’s nest rather than the focal bird’s nest and move on (Hamilton, 1971; Mooring & Hart, 1992), this might be espiecally likely if the neighbours are vocalising near or on the nest. A potential benefit of placing a nest closer to a neighbouring nest at a later nesting stage is that the area could be “safer” from predators since the nest has lasted more days without being predated. In New Zealand Fantails, McLean (1980) observed new nest placement was further away (>70m) from neighbour nest sites; however, their study did not consider neighbour nest stage. If a bird in the nesting pair is seeking extra-pair mates, initiating a nest near a neighbour while the neighbours are most fertile could be beneficial in securing those copulations. Therefore, certain neighbour nest stages might influence the nest placement decision of the nesting bird. Like many species, Grey Fantails (*Rhipidura albiscapa*) are thought to be socially monogamous (Higgins et al., 2006), but sexually promiscuous (Munro, 2007). In addition to sexual promiscuity the Grey Fantail has high nest failure rates due to a combination of high nest predation rate and high rates of nest abandonment (Munro, 2007).

Nest abandonment in birds is thought to partially be a response to predation (Caro, 2005). Grey Fantails have multiple nesting attempts each breeding season (up to 7 nest Beckmann et al., 2015; up to 8 Sotnychuk this study) many of which are abandoned, primarily during nest building (Beckmann et al., 2015; Munro, 2007). Previous studies on Grey Fantails suggest nest site selection (Beckmann et al., 2015; Beckmann & Martin, 2016) and abandonment (Flegeltaub et al., 2017) are a response to predation risk. Beckmann and Martin (2016) found that nests abandoned by Grey Fantails had lower concealment than successful nests, suggesting that nest abandonment is because insufficient concealment increased the risk of predation. Additionally, Grey Fantails renested further away after a predation event, at higher tree heights, and with increased nest concealment, in comparison to pairs that had successfully fledged their previous nest (Beckmann et al., 2015). To date no studies have investigated the influence of nearest neighbour on individual bird nest placement.

We evaluated the association of neighbouring conspecific nest placement and nest stage on nest site selection in Grey Fantails. We focused on the distance of the focal bird’s nest from conspecific neighbours with active nests and how the stage of the neighbouring nest might predict nest site selection. We predicted that focal Grey Fantail pairs would place nests closer to neighbouring birds if the neighbours were at a later stage in the nesting cycle. Nest placement closer to neighbours might be viewed as less risky nesting locations due to a neighbours' success, as well as produce a dilution effect, in which the neighbours nest acts as another focus for predators. Lastly, since previous nest fate has been shown to influence nest placement decisions (Beckmann et al., 2015; Boulton et al., 2003; Deeming & Reynolds, 2015; Fisher & Wiebe, 2006), we tested if previous nest fate of the focal nesting bird had an influence on the distance from neighbouring nests. We predicted that the fate of the focal pair's previous nest would impact renesting distance to neighbours nest, and pairs would move further away from neighbours after a nest failure event (i.e. predation). By evaluating factors that may influence Grey Fantails' nest site selection we can enhance our understanding of renesting behaviours.

Methods

Study Species and Nest Monitoring

As part of a longer-term study, we monitored a colour banded population of Grey Fantail (*Rhipidura albiscapa*) in Brisbane Ranges National Park, Victoria, Australia (37°51'10.8"S 144°11'21.2"E) from September 10, 2018 to March 7, 2019. Birds were captured using Ecotone mist nets and individuals banded with a unique colour band combination. Birds were sexed in the hand using secondary sexual characteristics and after capture, using behavioural cues. We identified and monitored breeding pairs throughout the entire breeding season, starting from before their first nest until two weeks after their final nest.

Grey Fantails are small (~8 g) aerial insectivores found throughout Australia. They build open cup nests placed on a variety of trees species, and tree heights (Beckmann & Martin, 2016; Higgins et al., 2006; Munro, 2007). Grey Fantails have biparental care (Higgins et al., 2006; Munro, 2007), but nest-site selection and nest building is primarily done by the female (Beckmann & Martin, 2016; Munro, 2007; Sotnychuk Chap 3). We systematically searched for nests every 3-4 days by following the female for 30 minutes and watching for nest building behaviours (i.e. collecting or carrying nest material). If a nest was not located during that time, we made notes of the bird’s behaviours and activities observed during the nest searching period (i.e. foraging, interacting with neighbours, singing in territory, etc). Once located, nests were checked every 3-4 days. If a nest was no longer active when we checked, a search for another nest was conducted that same day.

Nest outcomes were categorised as successful, predated, or abandoned. Nests were were successful if one or more offspring fledged, while failed nest were either abandoned or predated. A nest was categorized as predated if after at least one egg was laid, the nest was empty, had eggshells cracked/crushed in or near the nest, and/or the nest had been damaged. An exception was where the nest was on day 12, or later of chick-rearing, in which case we would search the territory for minimum of 30 minutes for fledglings being fed by the parents. The nest outcome was categorized as predated if there were no signs of fledglings within two weeks (searches every two days). Nests were considered abandoned if the pair did not progress nest structure, or we did not observe any build trips during nest checks for up to five days. Additionally, nests were considered abandoned if the pair was found actively building a new nest and there were no signs of predation at the previous nest. Nest abandonment usually occurred during the nest building stage but can occur during other stages. For example, we observed one occurrence of nest abandonment during the incubation stage.

Nest initiation dates were estimated by back-calculating from the date the nest was found, building stage of the nest when found, and the birds’ observed behaviour while searching for nests (See Chapter 3 Figure 3.1 for a description of each building stage), which provided a level of accuracy of approximately three days. For example, if the new nest was found at a late stage of building 3 days after the previous nest failed, the initiation date was determined to be the day after the last nest search where no nest building behaviours were observed. Additionally, if birds displayed nest building behaviour while being followed on previous search days, but no nest was found, the nest initiation date was dated back to the day they were seen displaying nest build behaviour, depending on building stage. In contrast, nests located at an early build stage, with no observations of nest building behaviour when followed on previous days, were assigned an initiation date the day the nest was found. For this analysis, we only used pairs where all the surrounding Grey Fantail neighbour home ranges and all nests were confidently identified.

Home Range Estimates

We needed an estimate of home range sizes to determine if nest placement was different from a random point within the focal pair's territory. We could then generate random nest points within those estimated home ranges. We characterized the boundaries of the Grey Fantails' home ranges by following and recording locations of adults during the breeding season. These locations consisted of both singing points and capture locations collected with GPS between October-November 2018. As part of a larger study, pairs on territories were followed and acoustically recorded for 30 mins per bird once every 3-4 days before midday. Singing points were opportunistically recorded during those focal periods and can be defined as the location where the individual spent most of its time singing during the observation period. We were using these locations to locate individuals quickly in the future between field crew members. We also included bird capture locations as they reflect defended territory space.

We used the point locations to estimate home range boundaries and assessed the fit of two estimation methods: kernel analysis and 95% minimum convex polygon (MCP; Millspaugh & Marzluff, 2001). Kernel home range analyses overestimated the home range area due to the small number of GPS points for each home range (ESRI, 2020). Therefore, we estimated home range boundaries using MCP (ESRI, 2020) as they provided the most conservative estimates. We used a home range area asymptote analysis (i.e. home range area curves) (Calenge, 2006; Team, 2020) to determine the sample size of point locations required to accurately estimate the area of a home range. Asymptote analyses assesses whether a home range was sampled with a sufficient number of point locations to estimate a home range area, where the estimated area is expected to asymptote as the number of point locations are cumulatively added to the analysis (i.e. home range area reached asymptote given the number of points).

Using the home ranges that reached asymptote, we calculated an average home range size, which was to applied to the remaining home ranges. The number of locations needed to accurately describe home ranges varied widely (SD = 17 points, range of 9-54 points)so using a minimum number of points as a threshold to estimate home range area was not appropriate. Instead, we used an average of the area home ranges that reached asymptote (i.e. area at asymptote). We estimated the centre of each home range by generating a centroid in each MCP and simulated a home range of average area around the centroid. Four random points were generated within each home range using GIS. Linear distance between nests and random points were calculated to the nearest meter.

Statistical analysis

We examined distance (m) from neighbour's' nests GPS point to the newly building focal pairs' nest with two linear mixed models. Pair ID was included as a random effect in both models to account for repeated measures and variation between pairs.

First, we tested if the distance to all neighbour's with an adjacent territory and an active nest was predicted by point type (random or focal nest) and the neighbour's nest stage. All neighbouring nests in the analysis were defined as one of the four following stages at the time the focal bird began nest building: nest building, egg-laying, incubation, and chick-rearing (n = 43, 8, 24, 9, respectively). Due to the varied sample size for each stage, we also ran the analysis with a simplified 2-level nest stage variable; nest building (n = 43), and nests with contents (egg-laying, incubation, and chick-rearing combined; n = 41). Simplifying the nest stage variable did not improve model fit as the AIC increased (dAICc = +25.1); therefore, we retained the original model.

Next, we tested if the distance to a neighbour's nest was predicted by point type and previous nest fate of the building bird. Previous nest fate of focal pairs consisted of four categories: none (first nesting attempt of the season), abandoned, predated, or successful. Only the fate of the nest immediately prior to the current building attempt was used for analysis.

Statistical analysis were performed in R version 4.0.2 (Team, 2020; See Supplementary Material 4.1 and 4.2).

Results

We had 14 focal breeding pairs (n= 46 nests) for the nest placement analysis, of which 9 pairs (16 nests) were also used as neighbouring territories for some of the focal pairs, and an additional 11 other neighbouring territories (29 nests) to compare distances. Therefore, a total of 25 Grey Fantail pairs and 75 nests were used in the analysis. The number of neighbouring territories per focal pair ranged from 2-4. Home range area for the territories that reached asymptote (n = 13 territories out of 23), average of 13.3 km^2 (SD = 9.6 km^2, range of 1.2 – 28.5 km^2). We determined that a circle radius of 65 m produced a home range of similar size.

We found no difference in nest placement distance in relation to point type (focal nest or random point) in either model (nest stage or previous nest fate) ($\chi^2 = 0.03$, df = 1, p = 0.86 and $\chi^2 = 0.22$, df = 1, p = 0.64, respectively; Figure 4.1). Focal pairs did not vary the distance they placed nests from neighbours based on their previous nest fate ($\chi^2 = 4.8$, df = 3, p = 0.19; Figure 4.2). However, the distance of focal pair nest placement did vary in relation to the neighbours' nest stage ($\chi^2 = 24$, df = 3, $p < 0.01$; Figure 4.3). Focal nests were placed an average of 147 m, 208 m, 154 m, and 182 m from neighbours that were at the stages of building, egg-laying, incubation, and chick-rearing respectively. There were significant differences between the distance focal nests were placed from a neighbours' nest for the following nest stages: 1) egg-laying and nest building (61m), 2) egg-laying and incubation (55m), and 3) chick rearing and nest building (36m).

Discussion

As predicted, observed focal nest distance to neighbouring birds' nest could be predicted by the stage of a neighbours' nests. However, contrary to our prediction, the relationship was not associated with solely how long the neighbour's nest had been established, but rather by specific nest stages which suggests activity at those stages is important. Focal pairs placed nests 61m and 36m closer to nest building (mean distance 147m) Grey Fantail neighbours than egg-laying and chick-rearing birds, respectively. Additionally, neighbours' nest placement was 55m closer to incubating Grey Fantail neighbours than egg-laying neighbours (208 m). These results suggest Grey Fantail pairs may be matching the level of activity of neighbouring birds to remain cryptic, trying to save energy from fighting for or finding resources, and/or preventing extra-pair copulation of their mates.

Generally, during nest building Grey Fantail pairs showed high activity on and near the nest, as they made frequent trips to and from the nest with material (See Thesis Chapter 3 Supplementary Material 3.3 for a breakdown of trips to the nest during building). Therefore, placing a nest closer to neighbouring pairs that are also active might be a useful strategy in reducing nest predation. If a predator spots an individual building, there is time for the targeted bird to temporarily stop nest building while the predator focuses on an actively building neighbour. This behaviour could align with the selfish herd hypothesis in which an individual puts a member of the group in between them and a predator (Hamilton, 1971; Mooring & Hart, 1992). Matching the activity levels of neighbours might allow the focal bird to remain hidden from predators; therefore, benefiting from close proximity to other birds with a combination of dilution and confusion effect. For example, the predator will only find one nest at a given time (dilution effect) and could target other birds if they are doing the same activity (confusion effect) (Hamilton, 1971; Lehtonen & Jaatinen, 2016; Mooring & Hart, 1992). Additionally, the focal bird may gain other benefits, such as identifying locations for quality nest building material from neighbours, limiting the search time and energy for the focal bird.

We found renesting pairs placed their nests closer to neighbours that were building, but also placed their nests further away from pairs feeding chicks. Since vocalisations on or near the nest can attract predators and increase nest predation risk (Kleindorfer et al., 2017; Kleindorfer, Hoi, et al., 2014; McDonald et al., 2009), avoiding noisy neighbours might be a useful strategy in maintaining cryptic behaviours. During chick-rearing, not only are the adult birds producing on-nest vocalisations, but the nestlings produce vocalisations as well. Therefore, it may be beneficial to avoid neighbours with nests at a stage in which more individuals are producing sound on the nest. The mean distance moved was an additional 36m from 147m. At such a far distance already (147 vs 183m) though statistically significant the increase might not be biologically significant. Sounds from the neighbours’ nests with chicks might not actually increase the risk of nest predation to the focal pairs nest.

Finally, we found pairs placed their nests further from egg-laying birds (208m) in comparison to nest building and incubating birds (147 and 153m, receptively). In addition to the benefits of nest placement near neighbours' building nests (mentioned previously), there is also an inherent risk in placing nests closer to pairs during egg-laying. Females are most fertile a few days preceding or during ovulation, the time coinciding with late nest building or egg-laying (Birkhead & Biggins, 1987; Gill, 2006). By placing nests further away from ovulating birds, Grey Fantails could be preventing easy access to extra-pair copulations of their partners. Although Grey Fantails are considered socially monogamous (Higgins et al., 2006), they have been reported to be sexually promiscuous (Hoffman et al., 2010; Munro, 2007). Hoffman et al. (2010) reported 55% of Grey Fantail offspring were sired by an extra-pair male and 64% of all clutches contain extra-pair young, females also appeared to mate with extra-pair males in nearby territories. Additionally, during the egg-laying stage both the male and female are not required to be as active on the nest, allowing more time for territorial defence and mate guarding (Beecher

& Beecher, 1979; Birkhead, 1979; Komdeur, 2001). Building a nest closer to egg-laying neighbours may be more energetically costly if intraspecific competition is present; therefore, avoiding egg-laying neighbours may be an energy saving strategy.

Contrary to our predictions, we did not observe a difference in distances to neighbouring nests between focal nest points and random points within the territory. We estimated a generalized territory size and shape for all pairs, which may not have accurately characterized actual home ranges. Realistically, territories are not uniform in shape and size and have been shown to change throughout the breeding season in many species (Butchart et al., 1999; Hixon et al., 1983; Møller, 1990; Odum & Kuenzler, 1955; Wiktander et al., 2001). In New Zealand Fantails, the location of morning singing posts changed in relation to nest placement and when pairs renested song posts usually changed to be near the new nest location (McLean, 1980). Therefore, the territory size used could be either under or overestimated for some pairs. Without detailed tracking (i.e. vis transmitters), each pair must have their territory mapped multiple times throughout the breeding season. Our suggestion is a minimum of 60 GPS points based on our calculated home ranges, for each mapping attempt (i.e. monthly). Additionally, the random points did not account for specific land and vegetation characteristics at the given point this does not guarantee that the specific point is one that birds could nest at (i.e. on a road, in a creek bed, open grassy area, etc).

Birds’ past experiences and learning regarding nest predation risk can influence behaviours and renesting decisions (Chalfoun & Martin, 2010; Guillette & Healy, 2015; Halupka et al., 2014; Styrsky, 2005), including nest-site selection (Marzluff, 1988). In Grey Fantails, renesting decisions have been reported to be influenced by the past nest fate as pairs moved greater distances to re-nest after unsuccessful nesting attempts in contrast to after a successful attempt (Beckmann et al., 2015). However, a relationship between previous nest fate and nest placement in relation to distance to neighbouring conspecific nests in Grey Fantails has not been examined. Ringelman et al. (2014) suggested that the varying results between nest distribution in relation to predation exist in the literature because studies to date have used large territory ranges across many years. Using Grey Fantails, which have multiple nesting attempts within one season (up to 8 nests this study), allows us to use a small spatial and temporal scale. We found no difference in nest placement distance from neighbours based on the previous nest fate of the focal bird. This suggests that Grey Fantail pairs are not influenced by their most recent nesting experience outcome when making decisions on the subsequent nest's placement in relation to the location of their neighbours' nests. Additionally, there may be no benefit in nesting closer to or further from a neighbour after a given nest fate as our results showed the stage of the neighbouring bird/nest might be more influential on nesting distance.

In conclusion, our results suggest that the choice of nest placement by renesting Grey Fantail pairs is potentially influenced by neighbouring nest placement in relation to the neighbour's behaviours at the specific nesting stage. Activity at the nest varies with nest stage. Our results suggest the activity of the neighbours has a greater influence on renesting distance than the stage in the nesting cycle (early vs late stages), as we originally predicted. Grey Fantails pairs may be trying to minimise detection by predators by avoiding neighbours with noisy nests (chick-rearing) and matching their activity level to the neighbours (building birds). Their choice to place the nest further away from neighbours during egg-laying also potentially increases fitness by reducing the likelihood of extra-pair copulations and avoiding additional interspecific interactions. Additionally, previous nest fate does not influence nest placement distances from neighbours. A better understanding of nest placement and renesting behaviours in Grey Fantails could help to explain the high rates of nest abandonment in this species. Since many of the suggested causes of observed patterns in our data are speculative in nature future research must be conducted to better understand the relationships. Future studies could include 1) an analysis of nest placement that accounts for heterospecific neighbour nests, and determining 2) the distance at which sound around the nest increases nest predation in Grey

Fantails, 3) exact nest predator species of Grey Fantails, and 4) the distance travelled by Grey Fantails for extra-pair copulations.

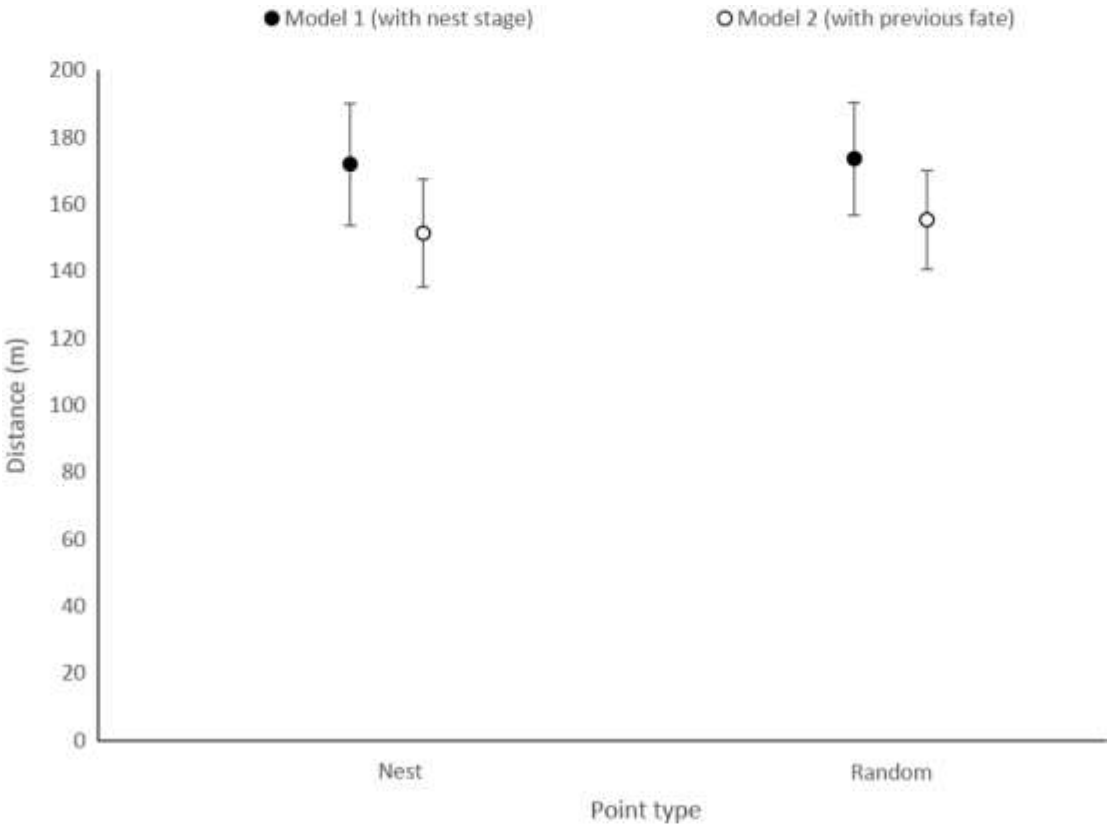

Figure 4.1: Average distance (mean ± SE), in meters, from neighbour arranged by point type of either nest site or randomly generated point within the territory. For both the statistical models, open circles representing values for first model that included neighbour nest stage and closed circles for second model including nesting bird's previous nest fate.

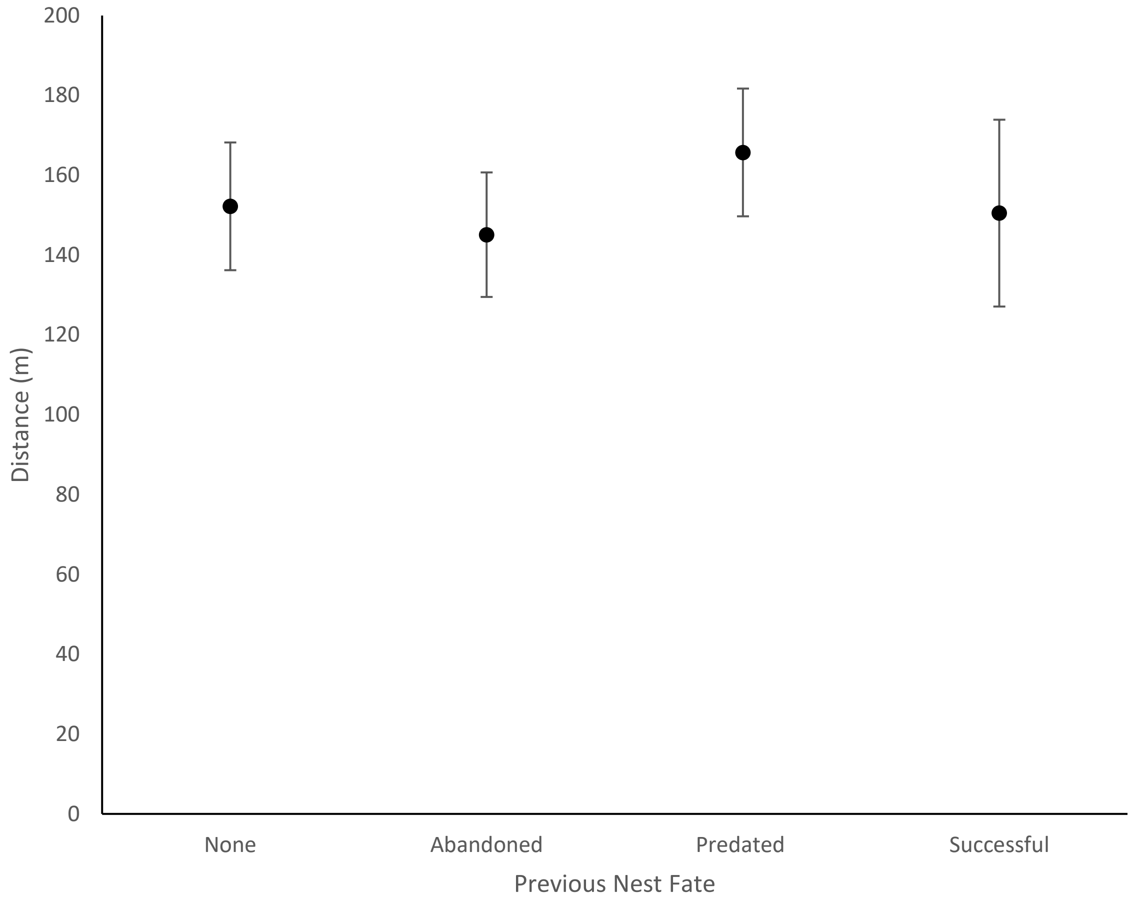

Figure 4.2: Average distance (mean ± SE), in meters, moved from neighbouring nest arranged by previous nest fate of nesting bird; none (first nest of the breeding season), abandoned, predated, and successful nest.

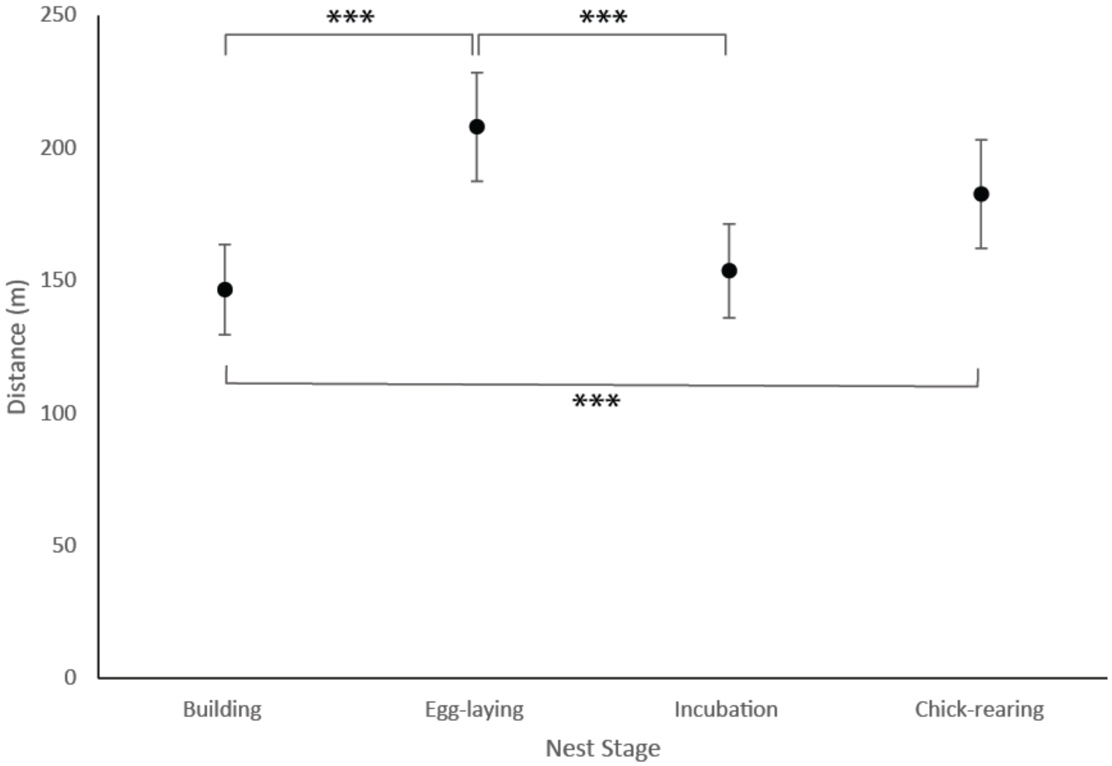

Figure 4.3: Average distance (mean ± SE), in meters, moved from neighbours arranged by nest stage of neighbouring birds (building, egg-laying, incubation, and chick-rearing).

Supplementary Material 4.1: Simplified R statistical code and output for nest placement distance looking at point type and nest stage.

```
> nearneighbour1 <- lmer(distance ~  point_type + stage + (1|territory_number) ,data=np)
> summary(nearneighbour1)
Linear mixed model fit by REML. t-tests use Satterthwaite's method [
lmerModLmerTest]
Formula: distance ~ point_type + stage + (1 | territory_number)
   Data: np
REML criterion at convergence: 4827.4

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-2.6933 -0.6336  0.0041  0.5576  3.9285 

Random effects:
 Groups           Name        Variance Std.Dev.
 territory_number (Intercept) 3465     58.86   
 Residual                     5749     75.82   
Number of obs: 420, groups:  territory_number, 14

Fixed effects:
                Estimate Std. Error      df  t value   Pr(>|t|)    
(Intercept)      145.831     18.437  20.149   7.910 1.32e-07 ***
point_typeRandom   1.591      9.249 401.847   0.172  0.86350    
stagee            61.476     13.827 407.908   4.446 1.13e-05 ***
stagei             7.062      9.432 412.998   0.749   0.45444    
stagec            35.980     13.851 412.846   2.598  0.00972 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) pnt_tR stagee stagei
pnt_typRndm -0.401                     
stagee      -0.120  0.000              
stagei      -0.193  0.000  0.251       
stagec      -0.137  0.000  0.169  0.268
> Anova(nearneighbour1)
Analysis of Deviance Table (Type II Wald chisquare tests)
Response: distance
             Chisq Df Pr(>Chisq)    
point_type  0.0296  1     0.8634    
stage      23.9979  3  2.501e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> lsmnearneighbour1 <- ls_means(nearneighbour1)
> lsmnearneighbour1
Least Squares Means table:
                Estimate Std. Error   df t value   lower   upper  Pr(>|t|)    
point_typeNest   171.960     18.229 19.3  9.4334 133.853 210.067 1.133e-08 ***
```

```
point_typeRandom   173.551     16.762 13.9 10.3538 137.564 209.538 6.695e-08 ***
stageb              146.626     17.113 15.0  8.5680 110.147 183.106 3.694e-07 ***
stagee              208.102     20.564 30.7 10.1198 166.146 250.057 2.664e-11 ***
stagei              153.688     17.736 17.4  8.6654 116.334 191.043 1.010e-07 ***
stagec              182.606     20.364 29.5  8.9670 140.986 224.227 6.357e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Confidence level: 95%
Degrees of freedom method: Satterthwaite
```

Supplementary Material 4.2: Simplified R statistical code and output for nest placement distance looking at point type and previous nest fate.

```
> nearneighbour6 <- lmer(distance ~  point_type + previous_nest_fate + (1|territory_number)
,data=np)
> summary(nearneighbour6)
Linear mixed model fit by REML. t-tests use Satterthwaite's method [
lmerModLmerTest]
Formula:
distance ~ point_type + previous_nest_fate + (1 | territory_number)
   Data: np
REML criterion at convergence: 4395.2

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.6082 -0.6573 -0.0086  0.4838  3.8354

Random effects:
 Groups           Name        Variance Std.Dev.
 territory_number (Intercept) 2606     51.05
 Residual                     4612     67.91
Number of obs: 390, groups:  territory_number, 14

Fixed effects:
                    Estimate Std. Error   df      t value     Pr(>|t|)
(Intercept)          150.209   17.189  23.965   8.739   6.46e-09 ***
point_typeRandom       4.036    8.597 370.997   0.469   0.639
previous_nest_fatea   -7.095    9.980 384.738  -0.711   0.478
previous_nest_fatep   13.519   11.119 384.769   1.216   0.225
previous_nest_fates   -1.675   21.411 320.247  -0.078   0.938
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
             (Intr) pnt_tR prevs_nst_ft prvs_nst_ftp
pnt_typRndm  -0.400
prevs_nst_ft -0.327  0.000
prvs_nst_ftp -0.325  0.000  0.601
prvs_nst_fts -0.223  0.000  0.222        0.246
> Anova(nearneighbour6)
Analysis of Deviance Table (Type II Wald chisquare tests)
Response: distance
                    Chisq Df Pr(>Chisq)
point_type         0.2204  1     0.6387
previous_nest_fate 4.7805  3     0.1886
> lsmnearneighbour6 <- ls_means(nearneighbour6)
> lsmnearneighbour6
Least Squares Means table:
                     Estimate Std. Error   df     t value   lower   upper        Pr(>|t|)
point_typeNest        151.397     16.109   18.9  9.3985 117.672 185.121    1.466e-08 ***
```

```
point_typeRandom      155.433     14.668   13.0 10.5970 123.751 187.115   8.995e-08 ***
previous_nest_fatena  152.228     15.962   17.9  9.5367 118.675 185.780   1.962e-08 ***
previous_nest_fatea    145.133    15.565   16.0  9.3242 112.130 178.136   7.345e-08 ***
previous_nest_fatep    165.747    15.942   17.5 10.3971 132.189 199.304   6.427e-09 ***
previous_nest_fates   150.553     23.433   60.5  6.4249 103.688 197.417   2.299e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Confidence level: 95%
Degrees of freedom method: Satterthwaite
```

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Thesis Discussion/Conclusion

Using Grey Fantails as the model species, my thesis explored the trends of on-nest vocalisations and the strategies birds use while nesting, including the function of nest abandonment. The Grey Fantail has high nest failure rates due to high nest predation (59% Higgins et al., 2006; 82% Munro, 2007) and nest abandonment rates before egg-laying (56% Beckmann et al., 2015; 60% Beckmann & Martin, 2016; 47% Munro, 2007). Therefore, there are multiple nesting attempts during the ~5-month field season (up to seven nesting attempts Beckmann et al., 2015; up to eight this thesis), which allowed me to study renesting attempts within a single breeding season. The Grey Fantail also appeared to have high rates of on-nest vocalisations (Beckmann & Martin, 2016; Berger-Tal et al., 2010); however, vocalisation rates and structure had not previously been quantified. In songbird species, near-nest and on-nest vocalisations have only recently been studied and research is lacking that describes how these vocalisations vary across nest stages and nesting attempts (reviewed in Haff et al., 2015; Leonard, 2008). My thesis is the first to present the count of on-nest calls and songs across the breeding season in Grey Fantails. It is also the first to define and present on-nest song types within the species across nesting attempts and nest stages. This research expands our knowledge of the form of on-nest vocalisations and will promote further exploration of the function behind such vocalisation.

My research sets the groundwork for understanding the frequency of occurrence of on-nest vocalisations and the proportion of song diversity in Grey Fantails. I found on-nest vocalisation rates and the proportion of some song types varied at certain nest stages. This suggested that, although on-nest acoustics can be costly by increasing the risk of nest predation, such vocalisations still have benefits for communication and birds might mitigate the use of vocalisations depending on nest stage. I can hypothesise about the potential reasons and infer functions behind the trends, but playback experiments need to be conducted to determine the functions. Additionally, I determined that the number of on-nest vocalisations and the types of songs did not vary based on sex. These sex-based results add to the exploration and comparison of on-nest vocalisation in males and females, as female vocalisations have often been overlooked in the literature (Leonard, 2008; Odom & Benedict, 2018; Odom et al., 2014).

I determined that exposure to a predator model during nest building did not influence the total count of on-nest vocalisation across days, nor did predator presence cause nest abandonment, as previously suggested. This suggests that nest abandonment in Grey Fantails may not be an immediate response to predator presence during nest building. Therefore, pairs might need to encounter a predator multiple times to elicit a response or predator presence may not have as great of an influence on bird decisions while nesting or vocalising. On-nest vocalisations and nest abandonment may be driven by factors other than an anti-predator response, such as minimising the risk of brood parasitism or poor nest site selection.

To further investigate nesting strategies, I determined how nest site selection might be influenced by neighbouring conspecific nest sites and nest stages. Neighbour nest stage did have an influence on nest site distance to a neighbour, while the fate of the focal birds' previous nest did not. These results suggest that the choice of nest placement by re-nesting Grey Fantail pairs is partially influenced by the nest stage and behaviours of neighbouring pairs. The choice offers two important benefits for the re-nesting pair: to minimise wasted time and energy on territorial disputes and to benefit from nest clustering with birds engaged in similar activities.

My thesis lays the groundwork for further exploration of on-nest vocalisation and nesting behaviours in relation to predation risk. This foundation is essential to chart future research, such as 1) investigation into the function of on-nest vocalisations and song types, 2) studying song learning and any potential effects of senescence on song type diversity, 3) examining nest abandonment rates in response to cuckoos, and 4) determining the distance at which sound around the nest increases nest predation risk in Grey Fantails. Overall, my thesis suggests that Grey Fantails strategically vocalise on the nest and make nesting decisions to save time and energy. These seemingly risky behaviours have underlying functions that relate to specific nest stage, suggesting a trade-off between when the behaviours are used and when they are not in relation to predation risk. This research contributes to an increased understanding of seemingly costly behaviours in relation to nest predation risk and provides further insight into the evolutionary strategies of nest abandonment and on-nest vocalisations. It is my hope that these findings will guide future research direction to further investigate these behaviours andsimilar behaviours.

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