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Getting Informed in a Risky World

Risk Assessment, Predator Information
& Parental Decisions

NICOLE A. SCHNEIDER



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& Parental Decisions

Nicole A. Schneider

*Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala*

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Cover: Pencil drawing, brown thornbill breeding pair and a grey currawong
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Abstract

Predation ultimately affects the fitness of individuals. In nest building species like birds, the predation of dependent offspring is the most important source of reproductive failure, favouring the selection of parental adaptations to enhance offspring survival. However, environmental heterogeneity hampers individuals of having an accurate knowledge of perceived current risks. Consequently, individuals have to acquire information about their environment to optimise their nest site selection, antipredation responses, and parental investment decisions. Thus, individual reproductive decisions should be dynamic and depend on the availability and reliability of environmental information, as well as a species life-history strategy.

This thesis examines the effect of individual risk assessment and antipredation strategies on parental investment in brown thornbills *Acantiza pusilla*, as well as the reliability of landscape features in predicting nest predation patterns in northern wheatears *Oenanthe oenanthe*.

During incubation brown thornbill females used dynamic risk assessment to evaluate the risk different predators posed. Decreased environmental information via greater nest concealment increased female vigilance, with greater vigilance tending to increase brood survival. Within the breeding season, parental risk sensitivity increased and decreased for consecutive breeding attempts. Feeding rates in the presence of a predator of adults and a brood predator decreased, while risk taking increased by approaching predators more closely. When facing predators, brown thornbills used two alarm vocalisations, with alarm call rate denoting the degree of danger a predator posed to the adult birds. Parental alarm calls only silenced nesting begging over short time periods. In northern wheatears, predation increased for birds breeding closer to agricultural field and woodland habitat interfaces. This was only the case during incubation but not during nestling feeding, indicating that seasonal changes in ground vegetation structure and a change in predator composition can result in highly variable predation patterns.

Overall, this thesis shows that antipredation responses and predation patterns can be dynamic and change within time and space, and thus influence the breeding success of bird species in general.

Keywords: alarm calls, antipredation strategies, habitat edges, nestling begging, nest predation, parental investment, predator occurrence, risk assessment

Author's address: Nicole A. Schneider, SLU, Department of Ecology,
P.O. Box 7044, 750 07 Uppsala, Sweden
E-mail: Nicole.Schneider@slu.se

Dedication

To the birds,
those fascinating creatures.

To my dear
friends and family,
who make life smile.



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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Nicole A. Schneider, Michael Griesser (2012). Incubating females use dynamic risk assessment to evaluate the risk different predators pose. *Behavioral Ecology* (early online).
- II Nicole A. Schneider, Michael Griesser. Re-nesting opportunities affect parental antipredator investment in a long-lived bird species. (manuscript).
- III Nicole A. Schneider, Michael Griesser. The function of alarm calls in breeding brown thornbills – self-defence or warning offspring? (manuscript).
- IV Nicole A. Schneider, Matthew Low, Debora Arlt, Tomas Pärt (2012). Contrast in edge vegetation structure modifies the predation risk of natural ground nests in an agricultural landscape. *PLoS ONE* 7(2), e31517.

Papers I and IV are reproduced with the permission of the publishers.

The contribution of Nicole A. Schneider and the co-authors to the papers included in this thesis was as follows:

- I Concept and design together with MG. Field work. Data analysis. Wrote paper as main author together with MG.
- II Concept and design together with MG. Field work. Data analysis. Wrote paper as main author together with MG.
- III Concept and design together with MG. Field work. Data analysis. Wrote paper as main author.
- IV Concept and design together with TP. Contribution to collection of long-term dataset. Data analysis together with ML. Wrote paper as main author together with DA, ML, TP.

1 Introduction

“To be, or not to be – that is the question.” While Shakespeare’s intentions will have been of more philosophical nature, this question represents one of the key challenges for all organisms. Every individual strives to increase its fitness – to survive, to reproduce and to leave offspring (Darwin, 1859). This is where predation enters the stage. Predation has been described as one of the ultimate fitness affecting factors (Lima & Dill, 1990). An individual that does not survive long enough to reproduce or is not successful in rearing offspring to independence and to reproduce themselves will suffer great fitness impacts, and may even irreversibly set its fitness to zero. In birds, the predation of dependent offspring is the most important source of reproductive failure (Martin, 1995; Ricklefs, 1969; Skutch, 1949). Yet already the mere perception of an increased predation risk can greatly reduce reproductive prospects (Zanette *et al.*, 2011; Eggers *et al.*, 2006). Thus, predation is an important evolutionary force that favours the selection of adaptive strategies in prey to survive predator encounters.

1.1 Mitigating predation

Given the large impact of predation on reproductive success, the question arises which strategies individuals can employ to counteract predation. One of the main currencies to mitigate predation is the acquisition of biological information, such as on the density or distribution of predators (Dall *et al.*, 2005). Environmental heterogeneity and variability hamper individuals of having complete knowledge of the state of their current surroundings (Schmidt *et al.*, 2010). This particularly applies to the perception of actual predation risks (Bouskila & Blumstein, 1992). Consequently, to overcome the uncertainty of predation hazards, individuals have to acquire information about their environment to increase their likelihood of making informed, optimal

decisions. Information use thus is a key feature of adaptive behaviour and has been described as a ‘fitness enhancing resource’ (McNamara & Dall, 2010; Dall *et al.*, 2005).

To acquire information individuals can use two different channels. They can interact with their environment via trial-and-error tactics, thus gaining personal information, or they can gain information from observing and interacting with conspecifics or heterospecifics (Danchin *et al.*, 2004). The latter includes social and public information –information potentially accessible to all individuals– which comprises signals, such as the intentional communication between individuals, but also eavesdropping, the gaining of information by intercepting on communications or interactions of others (Wagner & Danchin, 2010; Danchin *et al.*, 2004). This information needs to be spatially and temporally correlated to have any proximate value for the decisions of individuals (Seppänen *et al.*, 2007), as certain information, such as an alarm signal for example, might be limited to a specific location and time point.

In the case of breeding birds, the strategies individuals can take to alleviate predation impacts can be divided into two broad categories (Figure 1):

- (a) Antipredation measures *prior* to breeding, and
- (b) Antipredation measures *during* breeding.

(a) Antipredation measures prior to breeding

The choice of breeding habitat and nest location can greatly influence reproductive output. On a larger scale, the spatial distribution and composition of habitat types within the landscape can influence the distribution of predators (Nour *et al.*, 1993; Andrén & Angelstam, 1988). Breeding at habitat interfaces for example can increase nest predation risk (Batáry & Báldi, 2004; Winter *et al.*, 2000; Donovan *et al.*, 1997), which in the case of ground nests can be a result of that habitat interfaces are preferred foraging and movement areas for mammalian predators (Söderström *et al.*, 1998; Nour *et al.*, 1993). Given that birds are able to assess such spatial differences in predator distributions (Schmidt *et al.*, 2006; Lloyd *et al.*, 2005), landscape structures should provide readily available cues for improving breeding site selections (Figure 1).

Before selecting a nesting site, individuals can also draw on social and public information, such as the presence of conspecifics during habitat establishment, or personal or conspecific reproductive success from the prior breeding season (Doligez *et al.*, 2004; Doligez *et al.*, 2002). Whereas these cues sometimes may be misleading (i.e. lack of temporal correlation) (Safran, 2004), individuals can use predator vocalisations as direct cues of risk to select safer nesting sites (Emmering & Schmidt, 2011; Eggers *et al.*, 2006).

During nest site selection another factor that individuals have to consider is the degree of nest concealment. Well concealed nests may provide better protection from visually oriented predators, but also pose a greater danger to incubating individuals as an obstructed view may allow to be ambushed by a predator (Lima, 2009; Götmark *et al.*, 1995). This information deficit is aggravated in species breeding in cavities or closed nests (Collias, 1997), and exemplified by higher female mortality rates during reproduction compared to open-cup nesters (Low *et al.*, 2010; Moorhouse *et al.*, 2003). Incubating individuals using these nest types thus should have evolved behavioural adaptations that reduce their information deficit and their risk of being predated.

(b) Antipredation measures during breeding

The measures that breeding birds can take to reduce predation impacts after nest site selection and nest construction involve direct behavioural adjustments and investment decisions at the level of the individual. When being exposed to a greater perceived predation risk individuals can reduce their clutch size, as it has been shown in a diverse range of species such as song sparrows (*Melospiza melodia*), Siberian jays (*Perisoreus infaustus*), or rufous-bellied thrushes (*Turdus rufiventris*) (Zanette *et al.*, 2011; Eggers *et al.*, 2006; Ferretti *et al.*, 2005). Moreover, individuals can avoid feeding young in the presence of a predator or during periods of the day when nest predation risk is high to reduce the risk of disclosing the nest location (Eggers *et al.*, 2008; Eggers *et al.*, 2005).

During breeding individuals can also minimise predation via the giving of alarm calls on predator detection. Alarm calls can either be directed at the predator, to harass it and drive it off (Curio, 1978), or at conspecifics to warn them about danger and reduce the likelihood of predation (Caro 2005). The antipredator communication of breeding birds can be elaborate (i.e. referential and escape urgency calls) and elicit behaviours in offspring –like ceasing to beg or escaping from the nest– that reduce the risk of being taken by different types of predators (Suzuki, 2011; Platzen & Magrath, 2004) (Figure 1).

1.2 Direction of antipredation and investment decisions

Given breeding individuals have attained information and are bound to take decisions, a new question arises: How will they adjust their investment and reproductive decisions, and what will determine the direction of their decisions? One central aspect exerting a strong influence on individual investment and antipredation responses is a species' life-history strategy

(Martin & Briskie, 2009). Generally, parents have to balance their investment between current and future reproductive events, as an increased investment into current offspring reduces a parents' residual reproductive value (Trivers, 1974; Williams, 1966). Life-history theory predicts that parents adjust their reproductive investment according to their life-span (Martin, 2004; Ricklefs, 1977; Williams, 1966). In long-lived species with a slow life-history parents trade off current versus future reproduction, given that the fitness value of the current brood is low compared to future reproductive prospects. In contrast parents of short-lived species are predicted to have a high investment into current reproduction (Ghalambor & Martin, 2001; Williams, 1966).

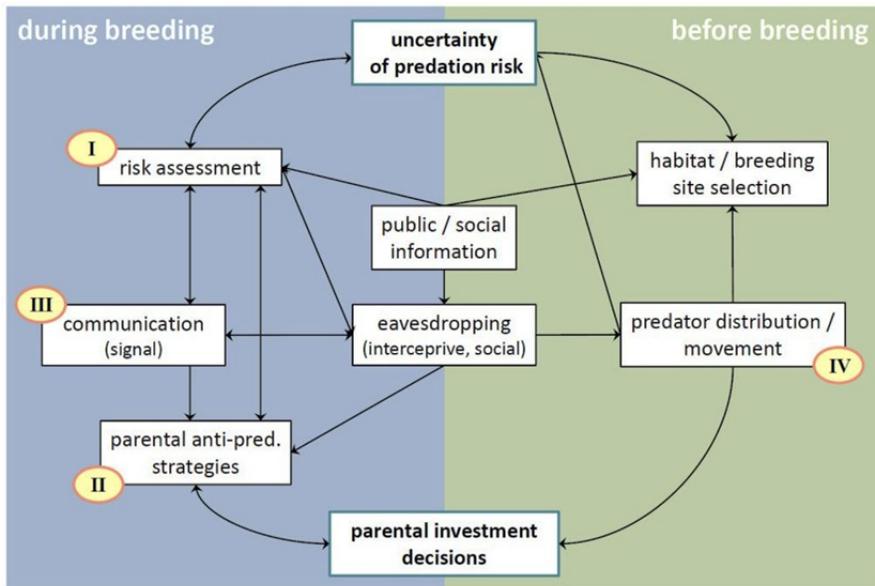


Figure 1. Simplified conceptual diagram of how individuals can gain information to reduce their uncertainty about predation risks to adjust their investment decisions. Roman numbers indicate the topics addressed in Papers I-IV in this thesis.

Breeding individuals that are exposed to different predation threats –a predator posing only a danger to the adult birds or towards their brood– have been shown to adjust parental investment and antipredation responses according to the above life-history theory predictions. In a large scale comparative experiment Ghalambor and Martin (2001) showed that long-lived southern hemisphere bird species reduced feeding rates more strongly in the presence of a predator of adults than in the presence of a brood predator, whereas the opposite pattern was prevailing in short lived northern hemisphere species. Another parental strategy under strong life-history selection is the investment female birds accrue into clutch size and clutch mass; with high nest

predation rates and longevity favouring small clutch sizes that allow individuals to spend less energy per clutch, thus allowing for more nesting attempts per reproductive season (Martin *et al.*, 2006; Roper, 2005). However, it remains largely unknown how parental antipredation investment changes between repeated nesting attempts over a breeding season (but see Chalfoun & Martin, 2010; Paper II).

Another tool breeding individuals can use to adjust their investment and antipredation responses, as surprising as it may sound, is predation per se. Using information such as prior predator encounters or nest predation events, individuals are able to refine their estimates of the chance to lose their brood to a predator (i.e. Bayesian updating) and can adjust their investment decisions accordingly (Schmidt & Whelan, 2010; Valone, 2006). Especially in correlated environments prior nest predation thus may provide reliable clues on the survival value of a brood (Schmidt & Whelan, 2010; Martin *et al.*, 2000). As a consequence, parental investment into offspring and antipredation responses is predicted to decrease with an increased accuracy of higher nest predation prospects.

In this thesis I try to shed new light on certain aspects of individual antipredation responses and investment, while also taking one step back to look at the 'larger picture' and the reliability of landscape features in predicting predation patterns.

2 Thesis Aims

There is currently a spread of the notion that research in the field of antipredation responses or ‘classical’ behavioural research has been exhausted. However, when taking a closer look it becomes evident that this is not the case. The current evidence on detailed behavioural processes linked to predation mainly stems from a relatively small number of species. Also, many studies on large scale predation patterns were conducted on either artificial nests or nest-boxes, although both have been questioned to produce patterns of general validity (Moore & Robinson, 2004; Purcell *et al.*, 1997). Moreover, it has been criticised that a large proportion of our current knowledge originates from short-lived northern hemisphere bird species, whose life-histories are known to deviate from the majority of the world’s avifauna (Robinson *et al.*, 2010; Martin, 2004).

In this light this thesis pursued two general aims. Firstly, to investigate individual antipredation mechanisms and investment strategies at the example of a long-lived southern hemisphere bird species, the brown thornbill *Acanthiza pusilla* (Paper I-III). Secondly, to investigate larger scale predation patterns on natural nests in a dynamic landscape, at the example of northern wheatears *Oenanthe oenanthe* (Paper IV).

The specific aims of the individual papers that make up this thesis were as follows (Figure 1):

Paper I

To explore the mechanisms closed nesting species can apply to assess predation danger during incubation. Females of closed nesting species only have limited information on their surroundings during incubation and thus should have evolved behavioural mechanisms to reduce this information deficit

and their risk of being trapped in the nest by a predator. This question until now remained unstudied.

Paper II

To explore how parental investment and antipredation strategies differ between different nesting attempts within a breeding season. Parental investment is predicted to differ depending on prior nest predation events and a species life-history strategy, although evidence from long-lived species is limited.

Paper III

To examine in more detail (building up on the experiment of Paper II) the vocal system of breeding individuals and to whom alarm calls are directed.

Paper IV

To explore if nest predation on a landscape scale is predictable by habitat structures (habitat edges, ground vegetation structure), which are linked to greater predator abundance or activity. Particularly in heterogeneous landscapes, which undergo seasonal changes in habitat structure (agricultural landscapes), the reliability of indicators for safer breeding sites may be fleeting. This question was addressed using a unique long-term data set of natural ground nests.

3 The Study Systems

3.1 Brown Thornbills

Study species

Brown thornbills are small (6-9 g), sexually monomorphic passerines endemic to the forests of south-eastern Australia (Figure 2). Brown thornbills are typical for the Australian passerines (Corvida) whose life-history traits are characterised by small clutch sizes, long breeding seasons with multiple nesting attempts, an extended period of post-fledgling care and high juvenile and adult survival. Despite their small size brown thornbills have a long lifespan with up to 17 years (Green & Cockburn, 1999). The clutch size is 3 ± 1 eggs, incubations lasts for about 18 days, nestlings remain in the nest for about 16 days and are dependent on their parents for about 6 weeks after fledging (Higgins & Peter, 2002; Green & Cockburn, 2001; Green & Cockburn, 1999).



Figure 2. Brown thornbill, left (Photo: Steve Igie). Closed dome nest with incubating female, right (Photo: Catherine Young).

Female brown thornbills build a closed dome nest typically in dense vegetation and incubate the eggs without assistance of the male (Figure 2), which contributes to territory defence and the rearing of nestlings and fledglings (Green & Cockburn, 1999). Brown thornbill pairs defend permanent, year-round territories (0.4 - 3.1 ha) and are extremely philopatric, rarely switching territories following divorce or death of a mate (Green et al., 2004; Green & Cockburn, 1999).

Study area

I studied brown thornbills at the Trevallyn Nature Recreation Area (41°26' S, 147°05' E) close to Launceston, Tasmania, Australia (Figure 3). The vegetation of the study area consists of native woodland with mainly eucalypt (*Eucalyptus* spp.) and wattle (*Acacia* spp.) stands and an understory of large tussock grasses and bracken ferns. While on the mainland the breeding season lasts from about July - November (Green & Cockburn, 1999), the breeding season on Tasmania, due to the higher latitude, lasts from about September - January. Between early October 2010 and early January 2011 brown thornbill nests were located and the birds of 75 breeding pairs individually colour ringed. We found nests primarily during the building, laying or egg stage (N = 61), and a smaller proportion during the nestling stage (N = 24).

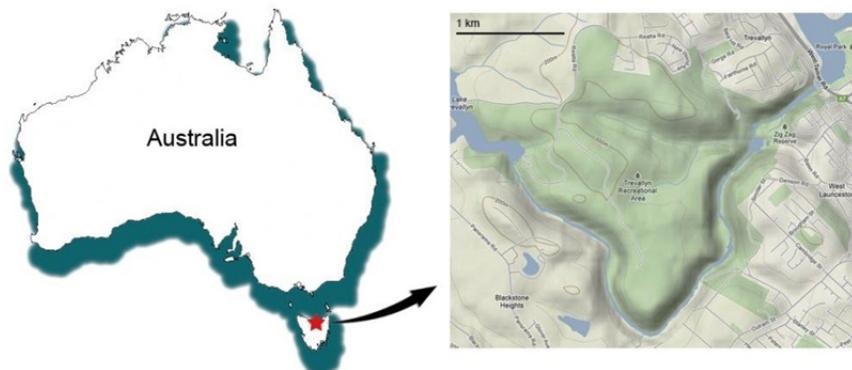


Figure 3. Location of the study area, Trevallyn Nature Recreation Area, next to the city of Launceston, Tasmania, Australia.

Nest predation

The major cause of nesting failure in brown thornbills is nest predation by other bird species such as Currawongs *Strepera* spp. (Higgins & Peter, 2002; Green & Cockburn, 1999). The overall nest predation rate in my study population was 51% (20% during incubation). After a failed nesting attempt females take longer to re-nest with the amount of time they had invested into

the previous attempt (Green & Cockburn, 1999). As a consequence of predation failures brown thornbills can initiate up to three clutches during a breeding season, though they rarely fledge more than one brood. After a successful attempt females are less likely to re-nest because of the long period of post-fledging care and the costs associated with caring for fledglings.

3.2 Northern Wheatears

Study species

Northern wheatears (wheatear hereafter) are small (ca. 25 g), sexually dimorphic passerines (Figure 4). Wheatears are long-distance migrants that breed in the warm temperate and boreal climate zones of the northern hemisphere and winter south of the Sahara (Cramp, 1988). The species is a ground foraging insectivore with a preference for open habitat with short ground vegetation (Cramp, 1988). In Sweden a large part of the wheatear population breeds in tundra habitats, but also frequently in other open habitats such as farmlands. Wheatears nest in different types of cavities, mainly on the ground (Cramp, 1988). Females build the nest and incubate the eggs, whereas males contribute to the rearing of the offspring. The clutch size is 5 ± 1 eggs, incubation lasts for about 13 days and nestlings spend about 15 days in the nest before fledging (Pärt, 2001a).



Figure 4. Male northern wheatear, left (Photo: Adrian Foster), and female northern wheatear, right (Photo: Arie Ouwkerk).

Study area

The study area (ca. 40 km²) was situated in a heterogeneous agricultural landscape south-east of Uppsala (59°50' N, 17°50' E), Sweden (Figure 5). The landscape consists of a mosaic of crop fields (~65%), woodlands (~20%), grazed and ungrazed grasslands (~10%) as well as farmyards and human

settlements (<5%). From 1993 - 2008 all territories which were previously occupied or suitable for wheatears (N = 161 territories) were monitored throughout each breeding season (mid April to the end of June) and classified according to land-use, ground vegetation height and breeding success (Arlt et al., 2008; Arlt & Pärt, 2007). Wheatears return to the study area in early spring (mid-April) and select territories and nest sites when ground vegetation is generally sparse and short. The majority of nests in the study area are on the ground under stones (~80% in stone piles), while a smaller proportion of birds nest under the roof tiles of farm buildings. Ground vegetation height is a good indicator of territory quality, as previous studies have shown that territories with a permanently short ground vegetation have a higher reproductive success because of higher food availability, lower nest predation risk (Pärt, 2001a; Pärt, 2001b), and higher adult survival (Low et al., 2010).

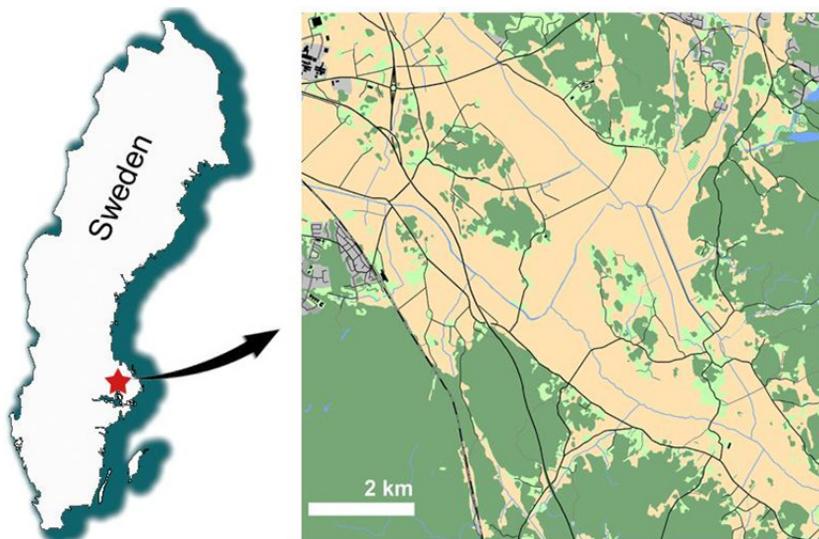


Figure 5. Location of the study area south-east of the city of Uppsala, Sweden. Dark green: forests and woodlands, light green: pastures, beige: areas under agricultural land-use.

Nest predation

Nest predation is the major cause of reproductive failure in wheatears in the study population, with approximately 85% of nest failures caused by predation (Pärt, 2001a), and >20% of nest predations resulting in the death of the resident female (Low et al., 2010). The key nest predators in the system are ground-living predator species (i.e. stoat *Mustela erminea*, weasel *Mustela nivalis*, red fox *Vulpes vulpes*, Eurasian badgers *Meles meles*, domestic cats *Felis catus*, and snakes) but not birds (Low et al., 2010; Pärt & Wretenberg, 2002). The

majority of nests (70%) were depredated by mustelid or snakes (leaving an empty but otherwise untouched nest) with the remaining 30% being taken by large mammals (fox, badger and domestic cat; nest usually dragged or dug out; T. Pärt unpublished data). The proportion of nests being dragged or dug out is higher during the nestling period as compared to the incubation period (50% vs 10%, T. Pärt unpublished data). The small species among the predator species (i.e. mustelids, snakes) show a preference for tall ground vegetation and linear habitat structures, where their primary prey is more abundant (e.g. voles *Clethrionomys* spp. and *Microtus* spp. (Salek et al., 2009; Weatherhead & Blouin-Demers, 2004).

4 Methods

In this chapter I present the key methods of the individual papers under the headings of the main thesis aims. First, for the experiments conducted to investigate individual antipredator responses during the incubation and nestling period (Papers I-III), and second, for the effects of habitat structure on predation patterns (Paper IV).

4.1 Individual antipredator responses

4.1.1 Incubation experiment on risk assessment mechanisms

I experimentally investigated risk assessment in incubating female brown thornbills (Paper I). Females (N = 23) were exposed to the territorial calls of two different predators, one posing a threat to eggs and nestlings (brood predator, grey currawong *Strepera versicolor*) and one posing only a risk to the female (predator of adults, collared sparrowhawk *Accipiter cirrhocephalus*). As a control females were exposed to the calls of an insectivorous passerine (dusky woodswallow *Artamus cyanopterus*) that neither poses a risk to adult thornbills nor their nest contents. The experimental setup, illustrated in Figure 6 below, was as follows: (i) The nest entrance was filmed with a camouflaged camera from ca. 2 m distance. (ii) A speaker with built-in amplifier (2 Watt output) connected to an MP3-player was set up in ca. 8 m distance from the nest, so that it could not be seen from the nest entrance. (iii) After the female returned to the nest from foraging a playback was started that consisted of 10 min silence, followed by 5 min of calls (15-20 s of calls interspersed with 30 s silence) of one of the predator species or the control. (iv) This setup was repeated for the following on-nest incubation intervals for the two remaining types of calls. For each experiment I used unique call sequences and randomised the treatment order between territories.

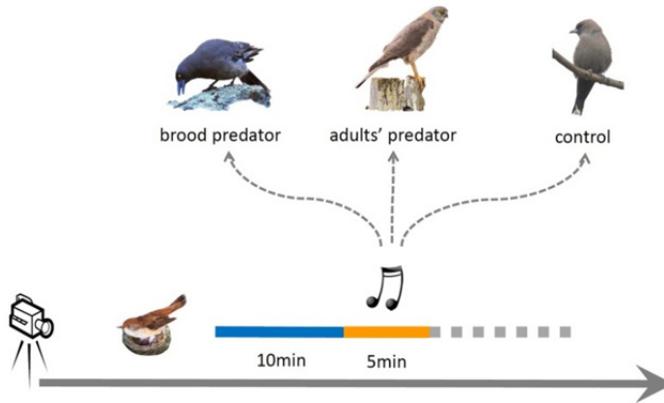


Figure 6. Graphical description of the experimental setup to assess female risk assessment during incubation.

From the video files the duration females showed alert behaviour before, during, and after the call exposure was extracted, as well as the female's immediate response to the different call types. The latter one could consist of one of three mutually exclusive response types: head out, look up, or no noticeable reaction (Figure 7). In addition to these variables, nest concealment was measured in the field as the amount of vegetation by which the nest was covered. This provided a measure of both, the information level incubating females can have on their surroundings and the visibility of the nest to predators.

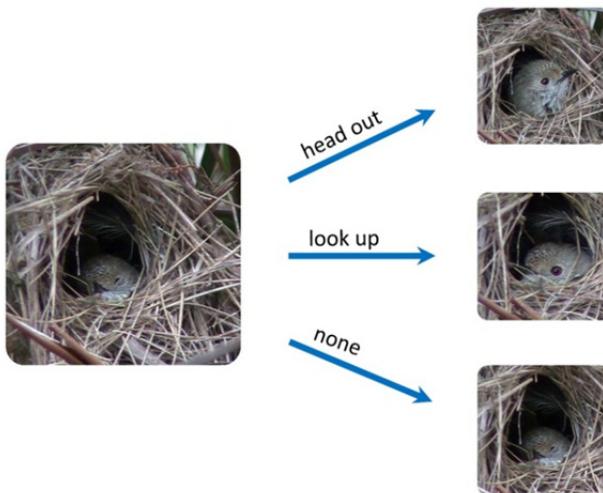


Figure 7. The three types of mutually exclusive immediate response incubating female brown thornbills showed. From top to bottom: response head out, look up, and no noticeable reaction.

In the consecutive statistical analyses I investigated the influence of the different call types and the degree of nest concealment (i) on the type and duration of immediate response, and (ii) on the degree of alertness females showed before compared to during and after the calls. Moreover, I investigated if the survival probability of broods was affected by female behaviour (alert behaviour, type of immediate response) and nest concealment. Analyses were done using general linear mixed models (for details see Paper I).

4.1.2 Nestling experiment on antipredation investment and communication

I experimentally investigated parental antipredator investment in relation to breeding attempt number (Paper II). I exposed 23 breeding pairs with approximately 10 day old nestlings to the perched models of a predator of adult birds (collared sparrowhawk), a brood predator (grey currawong), and a non-predatory control species (dusky woodswallow).

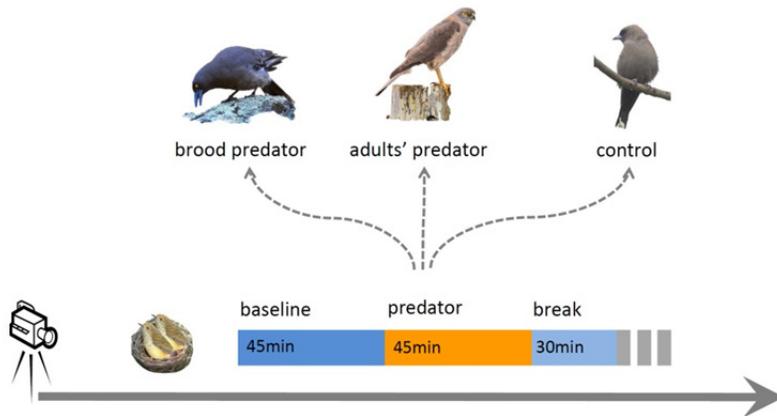


Figure 8. Graphical description of the experimental setup to assess parental antipredator investment

The experimental setup, illustrated in Figure 8, was as follows: (i) The nest entrance was filmed with a camouflaged camera from ca. 1-2 m distance. (ii) Parental baseline feeding behaviour was filmed for 45 min. (iii) One of the models was positioned 8-10 m from the nest. Next to the model I placed an MP3-player connected to a speaker with built-in amplifier (2 Watt output) and started a playback with social territorial calls of the respective model species. (iii) After 45 min the model and the speaker were removed and the breeding pair received a 30 min break. (iv) The same set-up was repeated for the two remaining stimuli. The presentation order of the models was randomised between territories and I used unique call sequences for each experiment to

avoid the possibility of pseudoreplication. All experiments were carried out in the mornings, with an entire experimental block taking 5.5 h.

During the model exposure bouts I collected the following variables in the field: (i) minimum distance of the breeding pair to the model, and (ii) the number of aggressive *tzzt* calls (Higgins & Peter, 2002) thornbills give when mobbing predators. From the video files the additional variables of (iii) the number of parental feeding visits and their food load size was extracted.

In the consecutive statistical analyses I investigated in separate statistical models how the response variables (i) parental feeding investment, (ii) approach distance to the predator models, (iii) parental mobbing investment were affected by breeding attempt number and the type of predator model. Analyses were done using general linear mixed models and AIC model selection to find the best-fitting model (for details see Paper II).

To examine the function of antipredator calls in brown thornbills I collected the following data in the above experiment (Paper III). During each model exposure period, and the 45 min of baseline behaviour, I counted the number of different calls given by the breeding pair. I recorded sound samples of the calls with the help of a Telinga Pro5PIP parabolic directional microphone and an Olympus LS10 digital recorder, sampling wave files at 44.1 kHz and 16 bits.

Brown thornbills are known to utter a variety of vocalisations that are either given during social interactions (e.g. song, *sooee* calls) or towards predators (*tzzt* call) (Higgins & Peter, 2002). Field observations in our population showed that it is possible to distinguish 5 different calls in the field (visualised in Figure 9):

1. Intense *tzzt*: in the field recognised as intense sounding *tzzt* call in which the individual syllables appear to nearly merge one another, long individual call elements, given during predator encounter.
2. Short *tzzt*: in the field recognised as briefly or rapidly given *tzzt* call, short individual call elements, given during predator encounter (the two types of *tzzt* calls were previously not distinguished in the literature (see Higgins & Peter, 2002)).
3. Contact: social calls given between the partners of the breeding pair or towards thornbills in neighbouring territories (*tchit*, *sooee* and *peep* calls) (Higgins & Peter, 2002).
4. Song: vocalisation given by males and females to signal territorial ownership towards neighbouring pairs (Higgins & Peter, 2002).
5. *tshurp*: call given by the individuals of a breeding pair predominantly during territorial disputes with neighbouring breeding pairs (a possible

functional similarity to *pee-orr* call of mainland brown thornbills (Higgins & Peter, 2002)).

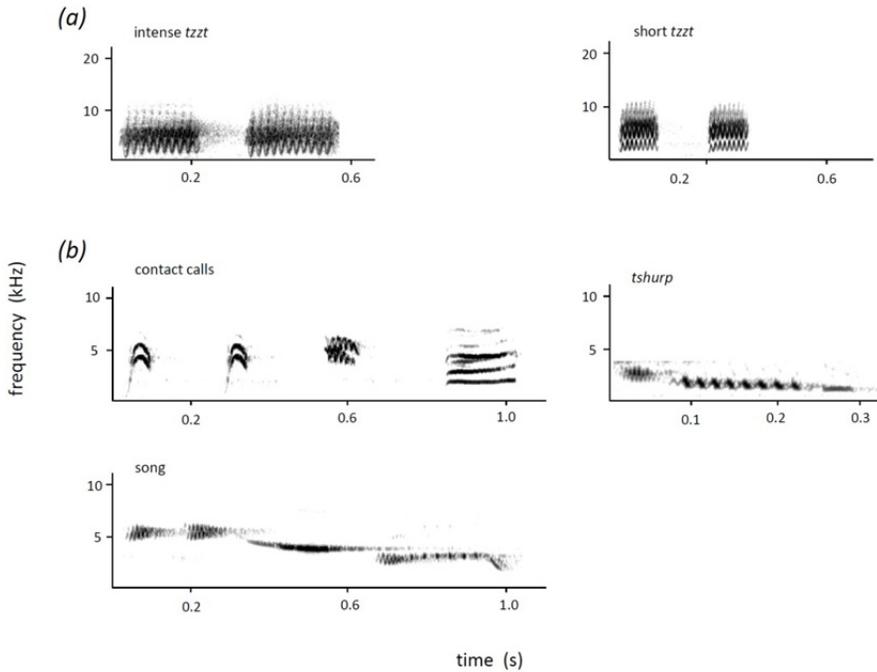


Figure 9. Calls given by brown thornbills (a) aggression calls given in an antipredator context and (b) social-territorial calls. Spectrograms produced in Raven Pro 1.4 using a 512-sample fast Fourier transformation, 256-sample Hann window and a 90% window overlap.

To test whether this field categorisation of calls was objective, I compared the two most similar calls –intense and short *tzzt* calls– as the other call types are acoustically very different and without doubt distinguishable in the field. To quantify the difference between the two *tzzt* calls I used spectrographic analyses methods in Raven Pro 1.4 (www.birds.cornell.edu/raven). Spectrograms were generated using a 512-sample fast Fourier transformation, 256-sample Hann window and a 90% window overlap. I randomly selected the elements from calls that had a sufficient signal-to-noise ratio and were free of background sounds. Subsequently, I defined a range selection around each element on the spectrogram and measured: element duration (ms), number of frequency cycles, modulation rate (number of frequency cycles per second, Hertz (Hz); counted at the bottom most frequency band), minimum frequency (kHz), maximum frequency (kHz), and peak frequency (the frequency at

greatest amplitude, kHz). Measurements were averaged across all element samples of a call type for each breeding pair, to account for variation in call properties within a breeding pair, as it was not possible to make individual specific recordings (mean number (\pm SE) of the randomly selected calls per breeding pair: intense *tzzt* 7.3 ± 1.2 , short *tzzt* 8.4 ± 1.6).

Moreover, I assessed the level of nestling begging intensity from the video recordings. Nestling begging can consist of two different call types (Magrath *et al.*, 2010): (i) repeat calls which are given in the time periods between parental visits seemingly without prompt. In brown thornbills repeat calls were shorter, quieter and given at a rate of approximately one call per second (average duration 138 ± 6.7 ms, max amplitude 66.8 ± 2.3 dB, peak frequency 8.6 ± 0.06 kHz). (ii) parent-present/-absent begging calls given at parental arrival at the nest or to other stimuli. In brown thornbills parent-present/-absent begging calls were longer, louder and given at a rate of approximately 2-3 calls per second (average duration 227 ± 6.7 ms, max amplitude 86.3 ± 1.9 dB, peak frequency 8.3 ± 0.04 kHz).

In the consecutive statistical analyses I tested if the two *tzzt* alarm calls statistically differ in their acoustic properties. I further investigated in which context the different call types described above were predominantly given, and which effect parental alarm calls have on nestling begging behaviour, over a longer time period (an entire 45 min exposure period) and within a short time frame in which parents were giving alarm calls (1 min). Analyses were done using principal component analysis (PCA), multinomial and binomial generalized linear mixed models (for detail see Paper III).

4.2 Habitat structure and predation risk

I investigated the occurrence of nest predation in relation to habitat structure, habitat edge type and nest conspicuousness at the example of northern wheatears (Paper IV). Wheatears breed in different types of farmland habitat and at a large range of distances from habitat edges. Habitat edges occur where two different habitat types meet, with habitats often differing in vegetation structure. In the course of the breeding season the ground vegetation in many places, like ungrazed areas, grows tall and changes from good to poor habitat. Nest predator behaviour likely differs according to the contrast in vegetation height and density between adjacent habitat types. Differences in a predators edge response thus will be due to differences in the permeability of the edge (Ries *et al.*, 2004), with weaker effects near 'soft' (low-contrast) edges than near 'hard' (high-contrast) edges. I therefore categorised habitat edges in this study according to the edge contrast concept (Ries *et al.*, 2004). Soft or low-

contrast habitat edges were defined as adjacent habitats that both feature either tall or short ground vegetation; e.g. mature crop field (tall) – ungrazed pasture (tall), or grazed pasture (short) – farmyard (short). Hard or high-contrast habitat edges were defined as adjacent habitats where one habitat has short and the other tall ground vegetation; e.g. grazed pasture (short) – mature crop field (tall), grazed pasture (short) – woodland (tall).

I examined the spatial and temporal nest predation patterns of 923 natural nests over a time period of 16 years (1993-2008). I did this by digitalising the distribution of land-use patterns in the study area (i.e. grassland, crop, woodland, buildings, roads and pathways) based on aerial photographs (Lantmäteriet 1999) in ArcGIS 9.2 (ESRI 2006). I also digitised the location of all ground-level nests where the exact location of the nest and the outcome of the breeding attempt was known. From this the distances from each nest, and the habitat type (short/tall vegetation) the nest was located in, to the next habitat edge (e.g. woodland or crop) or linear element (roads) could be calculated.

In the consecutive statistical analyses I investigated the relationship between nest predation risk (brood surviving or failing) and the habitat variables by looking at (i) the entire breeding season and (ii) separately at the incubation (N = 923) and nestling stage (N = 839). Analyses were done using binomial generalized linear mixed models (for details see Paper IV).

5 Results and Discussion

5.1 Individual antipredator responses

5.1.1 Risk assessment during incubation

Gathering information is essential for decision making and adaptive behaviour in individuals (Dall *et al.*, 2005). Until now previous studies on information acquisition and risk assessment by breeding individuals mainly focused on breeding site selection and benefits gained by using conspecific or heterospecific cues (e.g. Emmering & Schmidt, 2011; Doligez *et al.*, 2002). Our study showed that incubating female brown thornbills use two risk assessment responses during incubation to avoid predation. On hearing calls of predators close to the nest females could show the mutually exclusive immediate reactions (i) head out, looking with the head out of the nest entrance to scan the surroundings, or (ii) look up, looking up with the eye fixed on the nest entrance (see also Figure 7). Females reacted longest, with the strongest immediate response (head out) to the predator of adult birds (Figure 10), especially in fully concealed nests where females have a larger information deficit than females in less concealed nests (Figure 11). Although females reacted most strongly to the predator of adults, the calls of a non-predatory control species also elicited a risk assessment reaction in some individuals. This finding goes along with the theoretical predictions of predation risk assessment, as overestimating a potential danger will increase the female's information level and allow her to minimize her mortality risks (Bouskila & Blumstein, 1992). This is further underlined by the effect of nest concealment on female alertness. A better concealment of the nest can reduce the distance or the general ability of females to detect approaching predators (Magana *et al.*, 2010; Eggers *et al.*, 2008). All of this can increase female mortality (Öst & Steele, 2010; Miller *et al.*, 2007), and particularly in species breeding in cavities or closed nests (Low *et al.*, 2010; Moorhouse *et al.*, 2003; Collias,

1997). Incubating females in closed nests generally face a higher information deficit through the structure of the nest itself, especially when nests are located in dense vegetation.

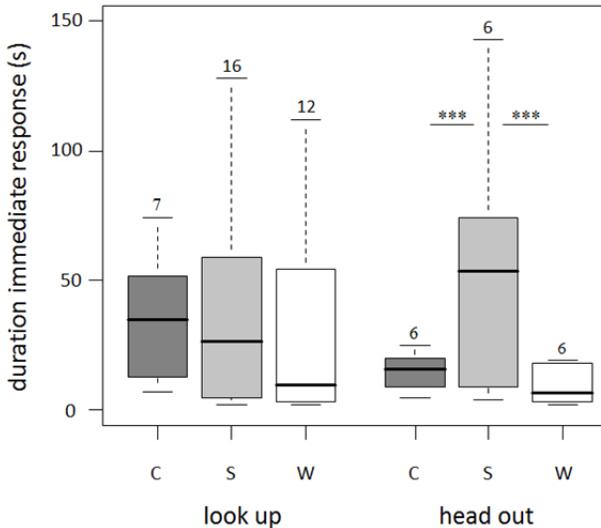


Figure 10. Duration (s) of the mutually exclusive immediate response behaviours head out and look up females showed on exposure to the calls of a nest predator (currawong = C), a predator of adults (sparrowhawk = S), and a non-predatory species (woodswallow = W). Numbers above the boxes show sample size (N = 35 look up, N = 18 head out). Statistically significant differences denoted by ***: $p < 0.0001$. Information shown in boxplot: thick black line = median, lower/upper box borders = first/third quartile, whiskers = min/max data values.

The higher information deficit of females is further highlighted by the finding that females maintained a higher level of alertness after hearing the calls of both predatory species. That individuals remain alert after the exposure to a predator previously was mainly investigated in the foraging context, where individuals with incomplete information about a predator are more vigilant and resume their previous behaviour later (van der Veen, 2002; Lima, 1987). In the case of incubating females of closed nest species this continued alertness may be important for gaining vital escape time.

The importance of the results above is further mirrored by the finding that brood survival was influenced by both nest concealment and female alert behaviour. Less concealed nests had a higher risk of being predated than nests with a higher degree of concealment ($F_{3,99.2} = 2.7$, $p = 0.04$), whereas female alert behaviour tended to be associated with a greater brood survival probability (although differences were non-significant $F_{1,100} = 3.2$, $p = 0.07$).

This highlights the trade-off between having a well concealed nest and a good view of the surroundings (Götmark *et al.*, 1995). Dense vegetation around the nest site can influence brood survival in two non-mutually exclusive ways: (i) Predators most likely detect poorly concealed nests more easily, as they faced a higher predation probability. (ii) Females breeding in well concealed nests have to engage in more risk assessment to scan the surroundings. These females thus might respond more appropriately and increase the survival of their brood.

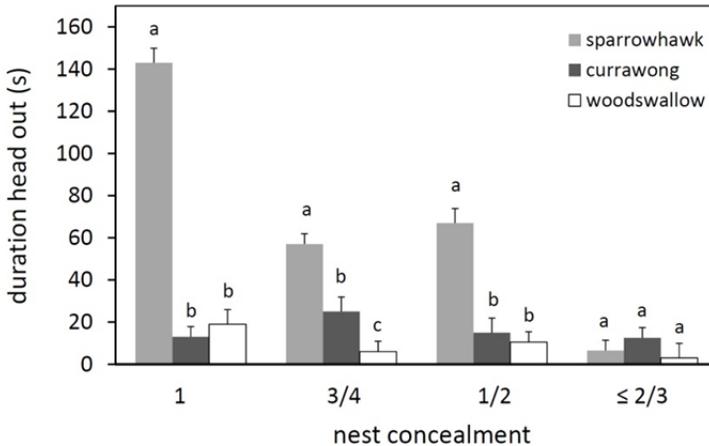


Figure 11. Duration of the immediate response head out by predator type in relation to nest concealment. Different letters above the bars indicate statistically significant differences within each nest concealment category. Nest concealment categories represent, 1: the nest is fully concealed by vegetation, $\frac{3}{4}$: around three-quarters of the nest are concealed, $\frac{1}{2}$: half of the nest is concealed, $\leq \frac{2}{3}$: nearly the entire nest is visible with two-thirds or less of the nest being concealed.

5.1.2 Renesting probability and antipredation investment

Within a breeding season parental antipredation investment and risk sensitivity should differ between different breeding attempts depending on a species life-span (life-history strategy), the level of brood predation, and the within-season renesting potential (Schmidt & Whelan, 2010; Martin, 2004; Andersson *et al.*, 1980). However, this remained largely unstudied, particularly in long-lived species. Our study showed that in a long-lived species parents with dependent young change the magnitude of their response and their risk sensitivity between breeding attempts. Parental risk sensitivity was much higher in second breeding attempts and feeding investment significantly decreased during the presence of both predator types (Figure 12) (LS means \pm SE: 1st nest before 3.8

± 0.8 vs model 2.2 ± 0.8 , $p = 0.02$; 2nd nest before 7.1 ± 0.7 vs model 1.9 ± 0.7 , $p = <0.0001$). This suggests that parents try to maximise both, adult and brood survival, by exposing themselves and the nest less to predators. However, avoiding to feed in the presence of a nest predator can be costly to offspring, as reduced provisioning can impact growth rates and have a negative influence on offspring quality (Martin *et al.*, 2011; Metcalfe & Monaghan, 2001). Nonetheless, limiting the number of temporally separate feeding visits by breeding individuals has been shown to directly affect fitness by increasing brood survival (Raihani *et al.*, 2010).

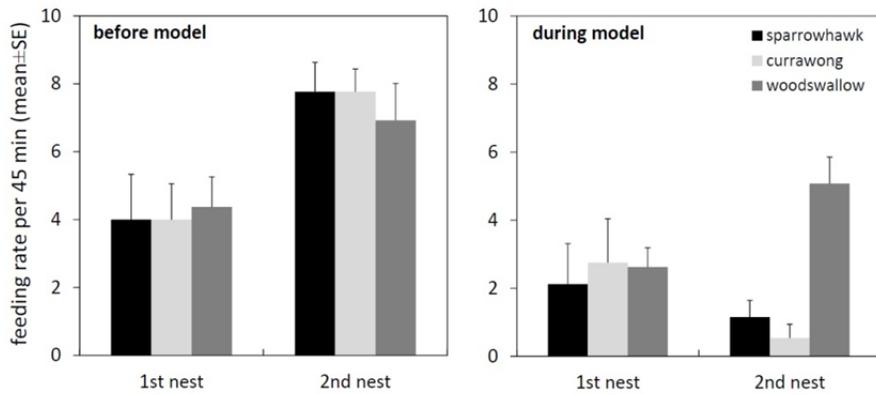


Figure 12. Number of feeding visits (mean±SE) in the 45 min before and during model exposure in relation to breeding attempt number.

When avoiding to feed in the presence of predators brown thornbill parents engaged in other antipredator behaviours, such as approaching and mobbing calling towards the predator models. Parental approach distances to the predators showed that, although parents were more careful during their first breeding attempts, they exposed themselves to more risk in the second attempt by approaching closer to the predator of adults (Figure 13). While approaching a predator can accrue costs (Dugatkin & Godin, 1992), there exists evidence that approaching and mobbing predators can provide direct fitness benefits as it not only increases the survival of mobbing individuals, which are less likely to be attacked by the predator, but also by driving off the predator (Zuberbühler *et al.*, 1999; Pavey & Smyth, 1998; Godin & Davis, 1995; Curio, 1978). Mobbing can be a part of nest defence, even though it can be costly and reveal the nest location to other eavesdropping predators and thus increase the probability of nest predation (Krama & Krams, 2005). However, this should favour reduced mobbing in nest vicinity irrespective of predator type. It can therefore be

suspected that the high mobbing intensity of brown thornbills reflects parental self-defence rather than nest defence.

Overall, the risk sensitivity of parents towards predation increased during later breeding attempts (lower feeding rates during predator exposure). Such an increase in risk sensitivity is in line with individuals using Bayesian updating and the information of prior nest predation events to adjust their behavioural strategies (Schmidt & Whelan, 2010). However, contrary to this, brown thornbill parents also tended to invest more and expose themselves to greater risk during later breeding attempts (approaching closer to predators, partial clutch size increase in 18% of breeding pairs). These findings suggest a more complex parental investment pattern, with Bayesian updating and a within-season ‘terminal investment’ effect interacting to influence parental investment into offspring and antipredation strategies.

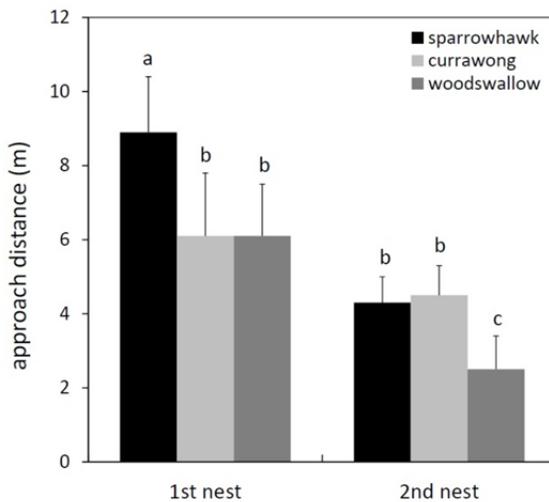


Figure 13. Minimal approach distance (mean±SE) of parental birds to the models dependent on breeding attempt number. Different letters above bars indicate statistically significant differences.

5.1.3 The function of alarm calls

Encoding information about predator type, predator behaviour or the degree of escape urgency has been shown to be an important antipredator strategy in birds (Griesser, 2008; Leavesley & Magrath, 2005; Templeton *et al.*, 2005), which can increase the survival of callers and recipients alike (Caro, 2005). The investigation of the alarm calls of breeding brown thornbills showed that individuals used two structurally different *tzzt* alarm calls, intense and short *tzzt* calls (two sample t-test: $F_{13,15} = 9.2$, $p = 0.0001$; see also PCA analysis in

Paper III). Although these two types of alarm calls were not predator specific, the rate at which calls were given depended on predator type (Figure 14, Table 1). Call rate in general seems to be an important feature to communicate different levels of threat. Studies on different species groups that use predator specific calls have shown that individuals respond to high-risk situations, or to the presence of a more dangerous predator, with increased calling rates (mammals: Lemasson *et al.*, 2010; e.g. birds: Griesser, 2009; Evans *et al.*, 1993). The collared sparrowhawk, the predator posing a direct threat to the survival of the breeding pair, was addressed with a higher call rate and thus can be seen as a higher risk situation. This result goes along with life-history theory, which predicts that species with high adult survival should respond stronger to risks that may impact their own survival as compared to the survival of their brood (Ghalambor & Martin, 2001).

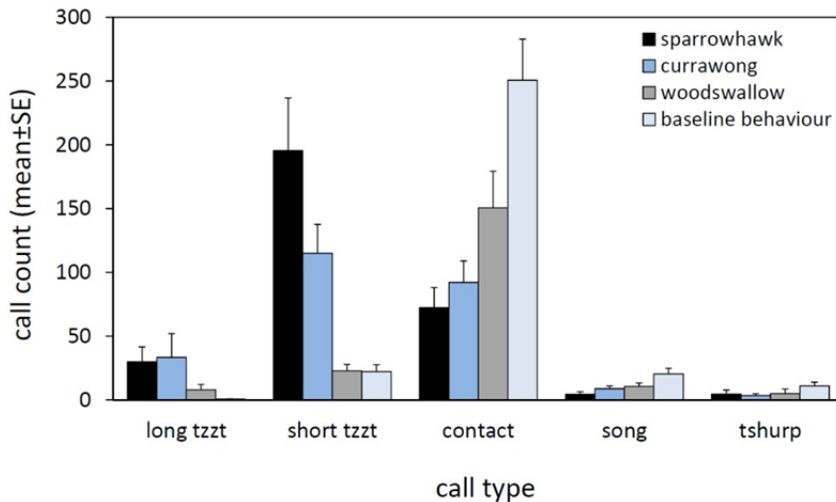


Figure 14. Amount of the different calls (mean±SE) given towards the different model types during the 45 min of model exposure.

Parental alarm calls also affected nestling behaviour by suppressing begging vocalisations over short time periods (1 min) (adjusted mean ± SE of parental calls per minute: 50.0 ± 4.5 vs 31.4 ± 6.7 (no begging vs begging); $p = 0.03$), whereas nestling begging over longer time periods (45 min) remained unaffected (call rate: $F_{1,62} = 0.05$, $p = 0.8$). Hence, parental alarm calls also seem to contain information directed to the nestlings, or information nestlings can eavesdrop on and respond accordingly. Nestlings going quiet following parental alarm calls has been shown in other bird species such as southern house wrens *Troglodytes musculus*, red-winged blackbirds *Agelaius*

phoeniceus, and white-browed scrubwrens *Sericornis frontalis* (Serra & Fernandez, 2011; Platzen & Magrath, 2004; Knight & Temple, 1988). However, in the case of brown thornbills the question remains whether nestlings ceasing to beg during higher parental alarm call rates actually promotes brood survival, as over longer time periods the level of nestling begging was unaffected by parental alarm calls. Given that parents reduce the number of feeding visits when predators are present (Eggers *et al.*, 2008; Paper II), and that it has been shown that begging varies in response to the state of hunger (Maurer *et al.*, 2003), this will most likely affect the longer term begging behaviour of nestlings and cancel out any short term effects of parental alarm calls. Still, to fully tease apart how nestling begging varies depending on parental alarm calls or nestling hunger in brown thornbills would require further playback experiments.

Table 1. Multinomial model (type III tests) for the effect of model type on the number of calls given towards the perched sparrowhawk, currawong and woodswallow model as well as during baseline behaviour (no model presented). Breeding territory was entered as a random variable into the model. *d.d.f.* = denominator degree of freedom, *n.d.f.* = nominator degree of freedom. Contrasts for the model specific call types are given in the second table section. Significant contrasts are highlighted in bold.

Effect	n.d.f.	d.d.f.	F-value	p-value	
Model	3	303	1.91	0.12	
Call type	4	303	76.27	<0.0001	
Model × Call type	12	303	10.87	<0.0001	

Model \ Call type	intense <i>tzzt</i>	short <i>tzzt</i>	contact	song	<i>tshurp</i>
Sparrowhawk vs Currawong	0.03	0.03	0.22	0.01	0.90
Sparrowhawk vs Woodswallow	0.002	<0.0001	0.002	0.003	0.54
Sparrowhawk vs Baseline	<0.0001	<0.0001	<0.0001	<0.0001	0.01
Currawong vs Woodswallow	0.30	<0.0001	0.05	0.67	0.62
Currawong vs Baseline	0.008	<0.0001	<0.0001	0.09	0.008
Woodswallow vs Baseline	0.08	0.77	0.004	0.21	0.002

5.2 Habitat structure and predation risk

The study on spatial and temporal nest predation patterns showed, that nest predation risk is higher closer to woodland and crop field edges, but only when these were hard edges in terms of ground vegetation structure (clear contrast between short ground vegetation surrounding the nest site vs tall ground vegetation in the adjacent woodland or crop field; Figure 15). No such edge effect was observed at soft edges where adjacent habitats had tall ground vegetation (crop, ungrazed grassland). Previous studies investigating the predation on artificial nests suggest higher predation risks along hard as compared to soft habitat edges (e.g. Malt & Lank, 2009), most likely because predator activity is spatially more concentrated along hard edges. Such a pattern is in agreement with the behaviour of the most common predators of wheatear nests (mustelids), which show higher density and activity along habitat edges (Brandt & Lambin, 2007). Mustelids prefer tall vegetation and rarely travel far from linear elements because of the higher abundance of their primary prey (i.e. voles) and greater cover from intraguild predation by aerial hunting raptors (Brandt & Lambin, 2007; MacDonald *et al.*, 2004). In the study area vole abundance and activity is higher along hard habitat edges and linear structures (footprint tracking tunnel study (Öberg, 2009)). Thus, the activity of the main nest predators is most likely concentrated in habitats with tall ground vegetation and along hard edges.

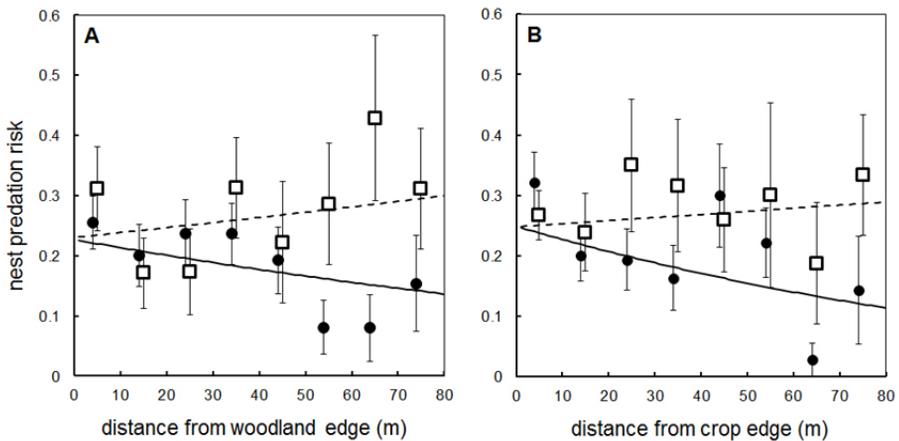


Figure 15. Nest predation risk during the breeding season (incubation + nestling stage) in breeding territories with short (black line, filled dots) and tall (dashed line, open squares) ground vegetation in relation to (a) distance from woodland edges, and (b) distance from crop field edge. Lines show model predictions; points raw data (mean \pm SE)

Table 2. Model (binomial GLMM) on nest predation risk during the incubation ($N = 923$) and nestling stage ($N = 839$) in relation to different habitat structures. Significant effects are highlighted in bold.

Fixed effects	Estimate	SE	z-value	p-value
Incubation period				
Intercept	1.712	0.496	3.4	0.0005
Woodland distance	-0.009	0.005	1.7	0.092
Crop distance	-0.017	0.006	2.9	0.004
House distance	0.005	0.005	-0.9	0.323
Road distance	-0.002	0.004	0.4	0.718
FLH	-1.248	0.523	2.4	0.011
FLH × woodland distance	0.019	0.008	-2.3	0.023
FLH × crop distance	0.020	0.008	-2.5	0.013
Nestling period				
Intercept	2.417	0.457	5.3	<0.0001
Woodland distance	-0.002	0.004	0.5	0.61
Crop distance	-0.003	0.004	0.7	0.46
House distance	0.004	0.005	-0.9	0.36
Road distance	0.003	0.004	-0.7	0.46
FLH	0.502	0.235	-2.1	0.03

Habitat structures = distance from the nest to woodland or crop edge, and field layer height (FLH) around the nest site (tall or short; reference category = short). Year and territory identity were included as crossed random effects (Incubation: variance year = 0.14, territory = <0.0001; Nestling: variance year = 0.31, territory = 0.38). Dropped non-significant interaction terms incubation stage model: FLH×house distance $p = 0.85$; FLH×road distance $p = 0.44$. Dropped non-significant interaction terms nestling stage model: FLH×woodland distance $p = 0.65$; FLH×crop distance $p = 0.35$; FLH×house distance $p = 0.13$; FLH×road distance $p = 0.55$.

An edge effect on nest predation risk was evident during the incubation stage but not the nestling feeding stage (Table 2). This absence of an edge effect during the nestling stage can be due to two mutually non-exclusive explanations. (i) A change in predator composition that goes along with a change in spatial predator activity. As wheatear nests are very cryptic during incubation, with only very few cues for active nest detection, nest predation during incubation is mainly caused by predators like mustelids which find nests incidentally. In the nestling period parental feeding activity expands the spatial range at which nests can be detected. As a consequence, small scale patterns of edge-related predation risk are likely to disappear. (ii) Seasonal growth of the ground vegetation transforms a proportion of initially hard edges into soft edges when wheatears are feeding nestlings. Thus, edges that soften through the growth of adjacent vegetation can cease being edges at all (Batáry & Báldi, 2004; Ries *et al.*, 2004). From the perspective of many ground predator species

a lack of change in the ground vegetation structure at habitat interfaces may therefore not represent edges at all but a continuous landscape of tall vegetation cover (Brandt & Lambin, 2007).

This study demonstrates that the relationship between nest predation risk and habitat edges can be highly variable and depend on the ‘hardness’ of the edge and the stage of the breeding cycle.

6 Conclusions

The findings of Paper I illustrate the value and the importance of environmental information. Female risk assessment during incubation was dynamic, with stronger responses and higher vigilance towards more dangerous predators (from the perspective of female survival) and in nests with a higher information deficit. Most importantly, this study highlights the trade-off between nest concealment and the degree of environmental information, as both the degree of concealment and female vigilance tended to influence brood survival. Thus, individual risk assessment behaviours may reflect life-history decision, as greater vigilance most likely will also promote female survival. Hence, risk assessment is likely to be an important proximate mechanism linking parental investment decisions to life-history strategies both across and within species.

Paper II highlights the temporal dynamics of parental investment responses in the face of predation. Parental antipredation investment in a long-lived species significantly changed during consecutive breeding attempts within a breeding season. However, parental investment patterns showed neither a clear increase nor decrease, suggesting that prior nest predation events (Bayesian updating) and a with-season ‘terminal investment’ effect interact in influencing parental antipredation strategies. This raises the importance of taking breeding attempt number into account when investigating parental investment and antipredation strategies, particularly since a large part of our current knowledge on this topic is based on single breeding events.

Looking in more detail at a specific antipredator response –alarm calling– and its function and potential information value (Paper III) showed that breeding brown thornbills use two different types of alarm vocalisations, but that the danger a predator poses is encoded in the alarm call rate. Given that the predator posing a threat towards the survival of the parents was addressed with

higher call rates, one could conclude that alarm calls primarily function as a means of promoting adult survival. This moreover is supported by that parental alarm calling only reduced nestling begging over short time periods.

Regarding larger, landscape scale predation patterns linked to habitat structure Paper IV revealed that predation risk patterns can be highly variable in space and time, and depend on the ground vegetation structure at habitat interfaces (hard vs soft edges) and the stage of the breeding cycle. This study hence suggests limitations in approaches that only look at habitat interfaces without accounting for predator behaviour or only one breeding stage. Since mammals largely contribute to the nest predation of ground nesting birds in fragmented, agricultural landscapes, the effects of ground vegetation edge contrast on predation risk should be of relevance for the breeding success of ground nesting birds in general. Moreover, the results further pinpoint the importance of reliable information for mitigating nest predation impacts during nest site selection. Particularly, that in dynamic landscapes seasonal changes can quickly alter the structure of habitats and thus override any landscape level indicators usually associated with lower predation risk.

All in all, the studies in this thesis demonstrate that both individual antipredation responses and larger scale predation patterns can be dynamic and change within time and space. Consequently, individual behaviour has the potential to influence the breeding success of bird species and affect population level dynamics.

7 Future Perspectives

An interesting aspect of future investigation, in light of Paper I and II, would be a comparative study to compare (i) the risk assessment mechanisms of species nesting in different nest types (cavity, closed, open-cup), and (ii) how both risk assessment and within-season parental antipredation investment differ in species with different life-history strategies.

The latter point would be particularly interesting as currently only comparisons between first within-season breeding attempts exist (Ghalambor & Martin, 2001), yet it appears that the findings of Paper II might be generally applicable across species as additional data from the study by Ghalambor & Martin (2001) suggests a trend of an even stronger response of parents with second breeding attempts (C. Ghalambor, personal communication).

Given that the results of Paper II suggest parental within-season investment to change depending on both, Bayesian updating of predation prospects and within-season ‘terminal investment’, our next step is to examine with a statistical model (in collaboration with Alejandro Ruete) how Bayesian updating influences the direction of parental investment decisions. Integrating further individual information in this model, such as age, and thereby integrating life-history effects would be particularly intriguing if the data would permit it.

In respect of the vocal system of brown thornbills, it would be interesting to build up on the findings on Paper III and conduct playback experiments to further disentangle the parent-offspring communication properties of parental alarm calls. Moreover, since the antipredator communication between brown thornbills on Tasmania and in Canberra seems to differ (discussion with Branislav Ijic who also works on brown thornbill), it would be intriguing to

make across-population investigations to find out which factors are driving these differences and thus influence communication system development.

Regarding the links between habitat structures and nest predation risk (Paper IV), it would be interesting to investigate how much the found patterns are linked to artificially fragmented, dynamic landscapes by comparing them to those in a landscape which naturally consists of a mosaic of habitats. Or otherwise, by investigating in greater detail the movement patterns and home ranges of predators to better understand and link their impacts on species of conservation concern, such as farmland birds.

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Tack! Thanks!

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