universität wien

DIPLOMARBEIT

Titel der Diplomarbeit

„Adjustment of Nest Defence Behaviour and Risk Taking Decisions in Blue Tits (*Cyanistes caeruleus*)“

verfasst von

Georg Friedrich Riegler

angestrebter akademischer Grad

Magister der Naturwissenschaften (Mag.rer.nat.)

Wien, 2013

Studienkennzahl lt. Studienblatt:	A 439
Studienrichtung lt. Studienblatt:	Diplomstudium Zoologie
Betreut von:	AO Univ. Prof. Hans-Christoph Winkler

Abstract

Background

Predation is one important evolutionary force of natural selection, influencing individual fitness. In order to reduce predation risk, individuals develop anti-predator tactics. Particularly interesting in this respect is offspring defence in passerines, because the nestlings are highly vulnerable and represent a special target for predation. Therefore, nest defence behaviour of altricial birds is crucial to enhance offspring survival and ideal to investigate factors influencing investment into brood defence. There are two major factors driving the decision that parents may invest in offspring defence when faced with a predator, namely, the risk to parents and the risk to the nestling. Consistent with this, the predator type is very much responsible for the strength of the threat it represents to parents as well as offspring. Hence, to maximise reproductive success, individuals should be able to precisely assess the risk posed by a predator and adjust their defence behaviour in an adaptive way. To determine the importance of parental versus nestling risk in the decision making process of investment and risk taking towards a specific threat, we conducted a field experiment examining defence behaviours towards different predators and different nestling developmental stages. We used blue tits (*Cyanistes caeruleus*) and tested the reaction of adults towards models of three different predators: (i) great spotted woodpecker (*Dendrocopus major*); (ii) aesculapian snake (*Zamenis longissimus*); and (iii) sparrowhawk (*Accipiter nisus*). Whereas the aesculapian snake represents a major risk for the nestlings during the whole nestling stage, it is less dangerous for the parents. The sparrowhawk is more likely to predate the defending parents or fledglings. The woodpecker is known to predate on very young nestlings, but is no threat to the parents. Each predator was tested twice on each nest, once during the early nestling phase and a second time shortly before fledging.

Results

Our results indicate that nest defence strategies differed strongly between the three predators. Defence intensity is only partly explained by the level of threat. The parental reaction was not influenced by nestling risk when parents followed a high-risk strategy. However, parents considered nestling as well as parental risk when following a low-risk strategy.

Conclusions

Our results suggest dynamic risk assessment in blue tits and suggest that, if adults' fitness costs are higher than the benefits, they would rather desert the brood than risking their own lives.

Introduction

Offspring can be considered as the currency for individual fitness (Montgomerie and Weatherhead 1988). During their early development, the offspring of any species are more or less vulnerable and may face a variety of threats, including adverse weather conditions or food shortage (Sheldon et al. 1998; Rytkönen and Orell 2001), infectious diseases (Pinowski et al. 1994) or brood parasitism (Campobello and Sealy 2011).

Another major factor known to have a significant impact on offspring survival is predation (Thompson and Burhans 2003; Zanette et al., 2006). Therefore, parental offspring protection may be one of the key factors that enhances the fitness of individuals (Montgomerie and Weatherhead 1988). Consistent with this, risk assessment and, consequently, the choice of the right defence strategy towards a threat are important areas of competence that influence the survival and fitness of an individual involved in defending its offspring against predators (Swaisgood et al. 2003; Zuberbühler 2009) (Caro 2005; Curio, Klump, and Regelmann 1983).

There is plenty of evidence that in many animals, including birds and mammals, individuals perceive and respond to different levels of threat in an adaptive way (Payne, Payne, and Rowley 1985; Owings et al. 2001; Weidinger 2002; Swaisgood et al. 2003; Krüger 2007; Langmore et al. 2009). However, this indicates that parental investment into offspring defence against a predator might not follow fixed patterns but is influenced by a variety of factors.

As offspring defence can be dangerous (Curio and Regelman 1985; Onnebrink and Curio 1991), parents may face a trade-off between survival of the current brood and their own survival and in consequence their future broods (Trivers 1972, 1974; Carlisle 1982; Winkler 1987) This compromise between current and future reproduction may consequently influence risk-taking decisions and defence intensity towards a threat posed to the offspring (Caro 2005).

The time and energy invested to replace a clutch increases with the age of the brood (Boucher 1977); whereas, the mortality rate declines and the probability that the young reach reproductive age is higher in older offspring (Patterson, Petrinovich, and James 1980).Therefore, the value of the brood, in terms of age or condition of the offspring, might play a role in parental anti-predator investment (Montgomerie and Weatherhead 1988). In fact, there is already certain evidence that parents invest more in the defence of older and, hence, more valuable offspring (e.g., Winkler 1987, Lambrecht 2000).

With regard to the threat posed by a predator, there is one rather unrecognised element of variance; namely, the risk assessment in relation to a predator usually consists of two components: (i) the risk for the defending parent and (ii) the risk to the offspring of being predated (Greig- Smith 1980; Montgomerie and Weatherhead 1988). These two risk components are not necessarily correlated and, therefore, the observed defence behaviour, investment and risk taking towards a specific predator consists of both risk components. When the predation threat for defending parents is very high, and when parental death would result in the loss of the dependent offspring, the parental risk taking should account for parental survival. In contrast, parental risk taking may increase up to the level of a Kamikaze response where parents may sacrifice their lives. This behaviour occurs only if offspring have a chance to survive without parents or with the parental support of only one remaining parent, and when parents may have little opportunity for future reproduction (Lehmann and Keller 2006).

For many passerine bird species, nest predation is the main cause for loss of the brood and, therefore, has a significant impact on the annual and lifetime reproductive success (Ricklefs 1969; Nilsson 1984; Montgomerie and Weatherhead 1988; Martin 1993). Previous studies suggest that active nest defence is a crucial reproductive strategy especially in songbirds, since offspring are typically highly altricial, and parents can increase the viability of the young by defending the contents of the nests (Caro 2005). In contrast, throughout the nesting period they also face the risk of injury or death (Montgomerie and Weatherhead 1988), which forces parents into a compromise between current and future reproduction (Caro 2005). The specific level of threat posed by different predators may change with age and development of the brood (Verbeek 1972; Patterson, Petrinovich, and James 1980). This is one important aspect we want to make use of in order to investigate the two risk

componants. Blue tits are particularly ideal for our investigation because they are (i) very common and breed in easy accessible nest boxes (Svensson 1999), (ii) males and females invest in offspring care including predator defence and (iii) are short-lived (Cramp and Perrins 1994). Therefore, parental age and consequently future reproductive success should be less important in the decision-making process of how much to invest in nest defence (Curio 1975; Weatherhead 1989; Radford and Blakey 2000). In order to investigate the importance of parental and nestling risk for decision-making in regard to investment into predator defence, we recorded the response of parental blue tits towards three different types of predators constituting different threats for the parents as well as for the nestlings, during two stages of offspring development. The nestling age was included in the experiments because we assume that the level of threat to the nestlings changes over time and depends on the predator (Table 1). Furthermore, the use of different anti-predator strategies may pose a different threat to the parents and reflect variation in risk taking (Kleindorfer et al. 2005). For example, to attack a predator might constitute a higher risk than alarm calling (Caro 2005). Thus, to accurately determine investment and risk taking, it might be necessary to examine different anti-predator behaviours. Thus, in these experiments in relation to parental and nestling risk, we separately examined the role of a defence response considered as posing a high risk (e.g., predator approach) in comparison to a response behaviour of low risk (e.g., alarm calling). The questions we would like to answer are: (i) Do blue tits perform dynamic risk assessment? (ii) Do they respond in an adaptive way? (iii) Are low- and high-risk behaviours used differently? and (iv) How important is parental and nestling risk for investment into predator defence in relation to different defence behaviours? The aim of our study was to determine the role of parental and nestling risk for parental anti-predator investment. For this purpose, we used a passerine bird known as the blue tit (*Cyanistes caeruleus*) as a model species to experimentally simulate situations of varying threat.

Material and methods

General methods

The study was conducted on a nest-box population established in 2008 in an area near Vienna in Pressbaum (48° 18' N, 16° 8' E; about 320 m asl) and covered by mixed forests and open areas. The experiments were carried out from late April until mid-June of 2012. Nestboxes were controlled on a two-day basis to gain sufficient information about breeding effort and nestling development. Because the relevance of the three predators for the nestlings is supposed to change with age (Table 1), brood defence behaviour was tested at two different stages of nestling development. The first experiment took place five days post-hatching, and the second experiment was carried out 12 days post-hatching.

Before the behavioural observation trials started, parent blue tits were captured on day 3 post-hatching (± 1 day) in the nest box. Adult birds were banded with aluminum rings and a unique Darvic colour ring combination for individual recognition during the experiments.

Study species and choice of predators

Blue tits (*Cyanistes caeruleus)* are common passerines that breed in cavities and readily accept nest boxes, which allows frequent monitoring of the breeding activity (e.g., development of eggs and nestlings). Our observations of the population revealed that one brood per year is common and that replacement clutches are very rare. In order to simulate dynamic risk for the nestlings, models of different common predators were exposed in close proximity to the nest box. To simulate different levels of parental and nestling risk, we used a rubber model of an Aesculapian snake (*Zamenis longissimus*)(Kleindorfer et al 2005; Johnsen et al., 2005; Mahr et al., 2012) as well as stuffed models of the great spotted woodpecker *(Dendrocopus major*)(Radford and Blakey 2000) and a female sparrow hawk (*Acciper nisus*) (Curio et al. 1983). As a known predator of nestlings in the study area (Johnsen et al. 2005), the Aesculapian snake is able to climb trees and enter natural cavities and nest boxes. When detected by an adult passerine, the snake poses a minor threat and usually is not able to successfully prey on them (Colombelli-Negrel et al. 2010).

Therefore, we predict the snake to represent a medium-level risk for the adults (Table 1). Aesculapian snakes easily manage to enter a nest box and predate the whole brood, therefore, we predict that they represent a very high risk for young and older nestlings (Table 1). Whereas great spotted woodpeckers, the most frequent woodpecker species in the study area, commonly feed on insects, grubs, seeds and fruits (Svensson et al. 1999), there is no evidence that woodpeckers prey on adult passerines; therefore, we predict that they are of little relevance as a predator for adult blue tits (Table 1). However, woodpeckers are able to make their way into a nest box and feed on the eggs and small chicks of other birds (Table 1) (Dale, Gustavsen, and Slagsvold 1996; Hudson and Newborn 1990; Wheelright, Lawler, and Weinstein 1997; own observations). After the nestlings have reached a certain size, they are no longer suitable as prey for the woodpecker. They are too big to be swallowed whole, and the woodpecker is missing the tools to dissect larger prey. Thus, the bigger the offspring the lower the probability to get predated by a great spotted woodpecker and, therefore, we predict that the woodpecker constitutes a minor threat for the parents and older nestlings but a high risk for small chicks (Table 1).

The sparrow hawk is specialised to prey on small passerines and poses the greatest threat for adult blue tits (Svensson et al. 1999). A major part of a sparrow hawk's prey consists of small-to-medium size birds and, therefore, they are well adapted for ambush predation. We, therefore, predict the sparrow hawk to represent the highest parental risk. However, nestlings in a nest box are unattainable for the aerial raptor and, thus, represent a low risk (Table 1). However, the sparrow hawk is more relevant as a predator when nestlings become older and are about to leave the nest box and display clearly visible begging behaviour at the entrance of the nestbox. It is, hence, considered as high risk for older nestlings (Table 1).

Table 1. Level of risk three types of predator represent to parents, young- and old nestlings

Predator	Parental Risk	Risk Nestling young	Risk Nestling old
Snake	Medium	high	high
Sparrow hawk	High	low	high
Woodpecker	Low	high	low

Nest defence behaviour

Before recording data during each experimental predator challenge, we observed the surrounding of the nest boxes for 5 minutes to ensure the adult birds were not distracted by our presence. We altered the predators randomly. For the trials, models of the three different predator types were exposed either on top of the nest box (snake and woodpecker) or close on a branch (sparrow hawk). The trial started when the first bird was detected within 15 m of the nest box. The experiment was discarded from our sample when the time until the first parent appeared exceeded 15 minutes; this guaranteed a minimum disturbance and sufficient food provisioning for the nestlings. To prevent any influence on the birds' behaviour by the observer, the defence behaviour of the blue tits was observed with binoculars from a distance of 15–20 meters. The behaviour was recorded in 10-s intervals, noting variables that represent different levels of risk: (i) the number of direct attacks towards the predator, which is an active nest defence strategy in passerines (Montgomerie and Weatherhead 1988), (ii) “rattling” which is a behaviour expressing excitement in combination with an alarm function and (iii) attacks representing the highest possible intensity of parental nest defence behaviour. An attack is defined by a swooping approach towards a predator resulting in an approach nearer than 0.1 m or body contact. Attacks were recorded as present or absent data. Rattling resembles typical alarm calls of longer duration used over longer distances (Winkler 2001) and represents the lowest risk of an anti-predator tactic we tested and is expressed as the number of rattles per 5 min. Another variable representing high-risk behaviour was the minimum approach distance (e.g., Kleindorfer, Fessl and Hoi 2003). The minimum approach distance towards a predator was noted to the nearest 0.1 m. We considered this variable to be of higher risk than rattling but of lower risk than attacks.

After 5 min, the predator model was removed. In the following 5 min, we observed the nesting area to make sure that the parents would return to feed their offspring.

Statistical analysis

For statistical analyses, Statistica7.1 (Statsoft Inc., Tulsa) was used. Data were tested for normality and if necessary adequate data transformations were conducted (log-transformed). However, absolute values were used for graphical presentation.

To compare the number of attacks per experiment (present/absent) between different predators, a 2 x 3 Freeman-Halton contingency table was used. To determine parental risk taking dependent on the three predators, the nest defence behaviour for each predator was tested using a univariate analyses of variance (ANOVA). To test if the behaviour of the parental birds changed with the age of their offspring, we used a paired t-test because each nest box was tested for the same predator at two occasions, namely experiment 1 with a chick age of 5 days and experiment 2 with a chick age of 12 days. To compare the behaviour towards the three predators triggered by the experiments, we used repeated measures ANOVA. We used the parental nest defence level (rattling, minimum distance) as the dependent variable, predator type (snake, sparrow hawk and woodpecker) and threat intensity (high, medium and low) as the independent factors and experiments with 5 and 12 day old chicks as repeated factors. Sample sizes slightly differed ($\pm$ 1) for the t-test and the ANOVA because in some cases we could only test the birds in one trial. To examine single comparisons in a multiple design, e.g., whether there is a significant difference between all three levels of risk for the parental birds in the rattling behaviour and minimum distance, we used a post-hoc analysis (Fisher's Least Significant Difference test). P-values < 0.05 are considered to be significant. For visual representation of our results, bar charts using means and standard errors were applied.

Results

Do blue tits perform risk assessment and adjust risk taking accordingly?

Examining whether pairs attack a predator, a behaviour that poses a very high risk for the defenders, revealed a significant variation between the three different predator types independent of chick age (Freemann Halton exact test for chicks with 5 days: $\chi = 34.05$, $p < 0.01$; for chicks with 12 days $\chi = 41.4$, $P < 0.01$). Our results suggest that the proportion of blue tit pairs attacking an Aesculapian snake is in both trials (with 5 and 12 day old chicks) very high (Fig. 1). Out of all the pairs, 73.6 and 88.8% attacked the snake, whereas almost no pair attacked the great spotted woodpecker and none of them attacked the sparrow hawk (Fig. 1).

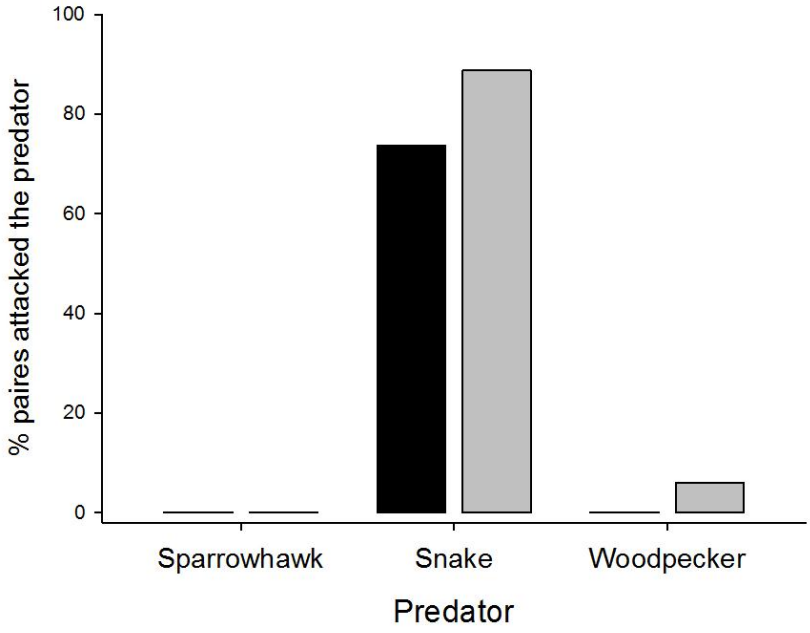

Fig. 1: Percentage of blue tit pairs attacking experimentally placed predators (high risk = sparrow hawk, medium risk = snake, and low risk = woodpecker) with 5 (experiment 1= black bars) and 12 day old chicks (experiment 2 = grey bars).

Do blue tits use different strategies depending on their risk?

Examining a low-risk behaviour like rattling, parent birds respond significantly differently towards the three types of predators (ANOVA: $F = p < 0.01$, Fig. 2). This result is mainly due to the reduced rattle frequency towards the snake model. The rattle frequency was highest towards the sparrow hawk and slightly lower towards the great spotted woodpecker (Fig. 2), whereas the snake did not elicit a strong rattle response (Fig. 2).

Examining a high-risk behaviour, e.g., in terms of the nearest distance they approach towards a predator, again revealed a significant variation between predator models (ANOVA: $F = 5.4$, $p < 0.01$). It turns out that blue tit pairs keep the greatest distance to the sparrow hawk (Fig. 3). Compared to the aerial raptor, the snake did not prevent the parents from getting very close, whereas the approach towards the great spotted woodpecker lies between the other two predators (Fig. 3).

Examining the application of low- and high-risk behaviour in relation to brood value reflected as nestling age (5 or 12 days old), we again found significant differences in defence intensity. Comparing the low-risk behaviour between 5- and 12-day-old nestlings revealed that adults rattled significantly more frequently against the snake as well as the sparrow hawk when chicks were older (paired t-test: snake t = -2.32; p = 0.035, n = 16; sparrow hawk: t = -2.40; p = 0.028, n = 18, Fig. 2). However, rattling frequency did not significantly differ between younger and older nestlings in response to the great spotted woodpecker (t = -1.21; p = 0.25, n = 16, Fig. 2).

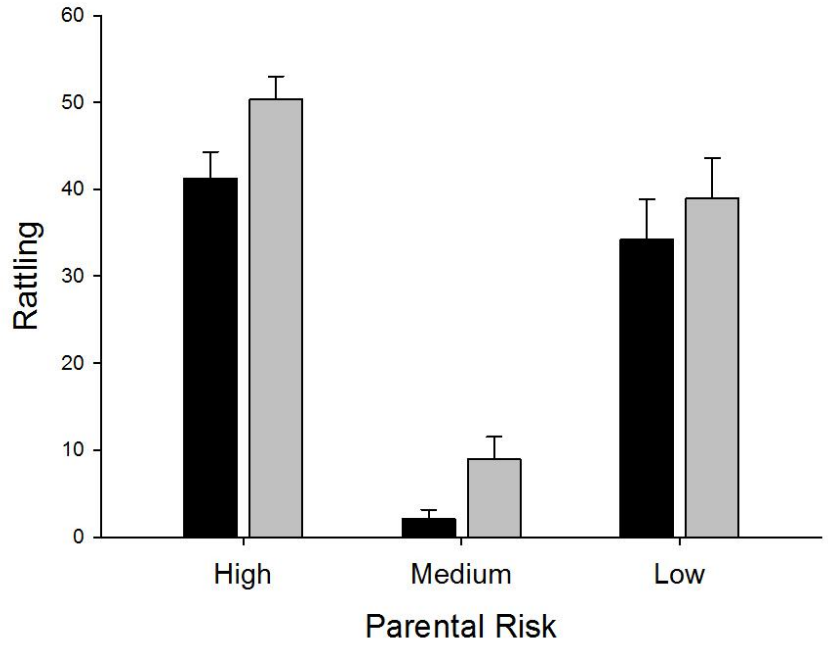

Fig. 2: Number of rattling events/5 min elicited against experimentally placed predators (high risk = sparrow hawk, medium risk = snake, and low risk = woodpecker) with 5 (experiment 1= black bars) and 12 day old chicks (experiment 2 = grey bars). Given are means and standard error.

In terms of taking a high risk – nearest approach towards a predator, there was no significant difference in this response between the experiments with young and older nestlings for any of the three predator types (snake: t = 0.26; p = 0.8, n = 16; sparrow hawk: t = 0.13; p = 0.9, n = 18; woodpecker: t=0.16; p=0.87, n = 16). (Fig. 3).

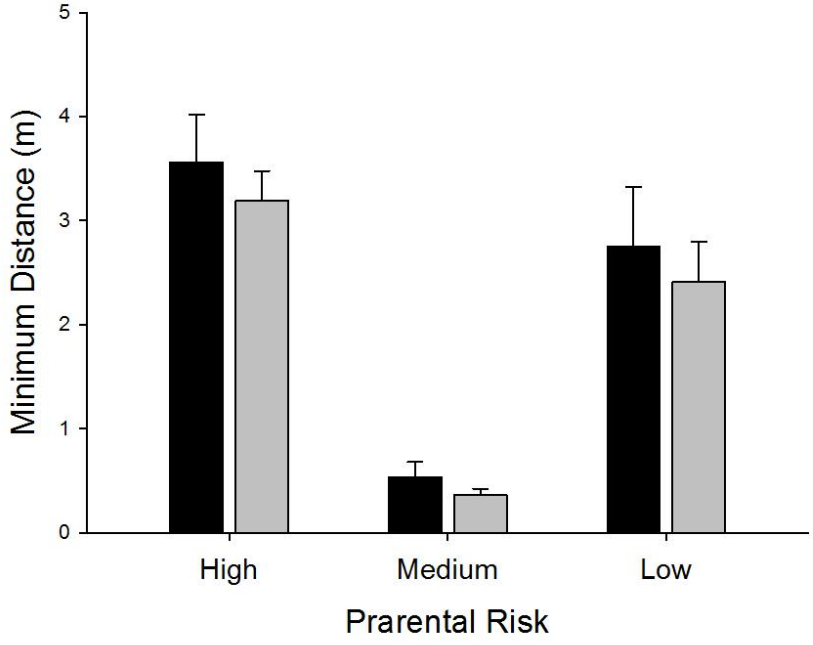

Fig. 3: Minimum distance (m) of the parental birds to experimentally placed predators (snake [medium risk] N= 16, sparrow hawk [high risk] N=18, woodpecker [low risk] N=16) in trial 1 (black bars) and trial 2 (grey bars). Shown are means and standard error.

How important is parental and nestling risk for the application and intensity of low and high risk behaviour in offspring defence?

The results show that defence adjustment varies for the low- and high-risk behaviour. Examining the low-risk strategy, and including parental and nestling risk in the model, revealed a significant effect of both—parental and nestling risk (see Table 2). A post-hoc comparison suggests that the differences are significant among all three predator types (Fisher's Least Significant Difference test: for all $p < 0.05$)

Table 2. The importance of parental and nestlings' risk with respect to rattling displays

Factors	FG	F	P
Parental risk (A)	**2,47**	**57.78**	**<0.01**
Nestling risk (chick age) (B)	**1,47**	**11.29**	**<0.01**
Interaction (AB)		0.39	0.68

When the adult birds performed high-risk defence – approach the predator - the level of risk for their offspring no longer affects their response intensity (nearest approach towards the predator) in relation to the three threat levels demonstrated by the three predators (Table 3). Post-hoc analysis revealed that there is a significant difference between all three levels of risk for the parental birds in terms of the nearest distance they approach towards the threat (for all predator types: $p < 0.05$).

Table 3.The importance of parental and nestlings' risk with respect to "minimum distance"

Factors	FG	F	P
Parental risk (A)	**2,47**	**50.12**	**<0.01**
Factor (nestling risk) (B)		0.09	0.77
Interaction (AB)		0.003	0.99

Discussion

Our results suggest that risk assessment is not just a simple rule of thumb like using a rough estimate for the perceived risk posed by a predator and reacting accordingly, but rather seems to be a complex routine. According to our study, parent birds are obviously able to simultaneously asses and integrate different risk components and other factors, including brood value, future reproductive success and nestling reactivity (Montgomery and Weatherhead 1988) in their decision making process.

We are among the first to examine the two risk components in combination with each other and our results are consistent with the predictions we proposed. In this study we in particular demonstrated that when trying to determine the importance of both factors—the threat a predator poses to the parent and/or to the nestlings—both factors are of importance for parental investment into offspring defence. In this

respect, the most exciting conclusion from our results is that their influence depends also on the defence strategy involved. When parents follow a low-risk strategy, more specifically when they give alarm calls, both parental and nestling risk seems to influence alarm call frequency (Table 2). However, when parents approach a predator, which means they take a higher risk, nestling threat no longer influences parent defence intensity. In other words, how much parents invest varies with different offspring defence strategies. This, on the other hand, indicates that parents would rather desert the brood than risk their own lives. From the theoretical point of view, the decision to desert the nestlings would mean that parent fitness costs are higher than the benefits (Caro 2005).

Our results show that nest defence intensity varies between different predators, which is consistent with the results of previous studies (Kruuk 1964; Curio 1975; Veen 1977; Buitron 1983; Kryštofková 2011). This may indicate that parental blue tits perform dynamic risk assessment (Kleindorfer et al. 2005) and raises the question of whether predator response is really adaptive?

Examining the reaction towards a predator in relation to the threat or risk they pose, the response intensity, however, only partly explains the different levels of defence behaviour, but supports the idea of adaptive predator response. As expected, adult blue tits did not attack the sparrow hawk because this aerial predator poses a crucial threat to them (Svensson et al. 1999; Stichmann et al. 2005). For the parental bird, the risk of attacking a sparrow hawk would be too high, and the nestlings in the nest box are unattainable by the aerial raptor. In contrast, the highest attack probability towards a medium threat like the Aesculapian snake is not necessarily expected but may be due to the fact that snakes usually are not able to successfully prey on adult passerines (Colombelli-Negrel et al. 2010), and parents might be able to successfully deter the snake from the brood. Therefore, higher risk taking against snakes might be reasonable as well. Surprisingly and against the expectation, there were almost no attacks towards the great spotted woodpecker. There is no scientific evidence that woodpeckers prey on adult passerines and, therefore, pose no or a very low threat. The question arises, why they do not attack more frequently when their nestlings might be at risk. One explanation could be that great spotted woodpeckers are much bigger than our study species, have a strong beak and are more agile than a snake. Therefore, although they do not prey on adults (Radford and Blakey 2000), great

spotted woodpeckers could possibly cause injuries in an attempt to fight it off (Caro 2005). Consequently, to avoid unnecessary investment by the display of costly attacks the parental birds may have restricted their nest defence to a certain distance. Thus, even when the relation between predator threat and parent defence response is not clear cut there are possible explanations for an adpative response. For example, “defence efficiency”, the probability that a predator can be driven away combined with “parent vulnerability,” e.g., the risk of the parent to get injured or killed may explain the results of our experiment (Greig-Smith 1980; Patterson, Petrinovich, and James 1980; Knight and Temple; Montgomerie and Weatherhead 1988).

However, there are other factors that may influence offspring defence intensity. One factor is related to the benefit for the current brood versus future costs (Redondo 1989). These future costs are of course dependent on the survival of the parental birds (Montgomerie and Weatherhead 1988). However, blue tits can be seen as r-selectionists (Pianka 1972) having only one very large brood per year and they are rather short lived (Cramp and Perrins 1994). Thus, year-to-year survival is low and it is rather unlikely that saving energy for future broods, either in the same or next year, is an important strategy in this species. It is already demonstrated that parental re-nesting potential may play a major role. Furthermore, there is evidence that an adult that is more likely to nest again should risk less for its current brood than a bird with a lower re-nesting potential (Curio, Regelmann, and Zimmerman 1984; Ghalambor and Martin 2000, 2001). Unfortunately, we do not have any information about the age of our birds to draw any conclusions along this line.

Winkler (1987) and Lambrechts et al. (2000) found evidence that parental birds invest more in the defence of an older brood, suggesting that another factor influencing parent offspring defence would be the brood value (Curio and Regelmann 1982). This predicts an increasing defence investment with offspring age because with nestling age, the time and energy parents have invested increases. Therefore, the loss of the brood at a higher stage of the nestlings’ development would be a severe setback. Regarding our experiments, we would expect a higher response intensity in the second experiment when nestlings were older. However, our results do not support the brood value hypothesis. Brood value cannot be examined in relation to the sparrow hawk and the woodpecker since nestling risk changes with the age of the nestlings, e.g., nestling risk increases with the sparrow hawk and decreases with the

woodpecker (see Table 1). Only the snake constitutes a stable threat level, and the threat stays the same for young and older nestlings. Consistent with this, however, our results (Figs. 2 & 3) do not suggest a change in offspring defence in relation to brood value (nestling age).

Organisms may also have to develop predator-specific defensive strategies. As Brunton (1990) showed, predators of a different nature may demand specific response tactics and, therefore, are deterred by different types of nest defence. In line with this, our results show that birds use specific tactics in specific contexts or with specific predators. Distinguishing low- (rattling) and high-risk behaviours (predator approach), we found clear differences in the application against specific predators. Interestingly, almost no alarming behaviour was observed towards the snake. This lack may have to do with the fact that snakes cannot hear and indicates that rattling is addressed towards the predator. In contrast, rattling is the main response towards the sparrow hawk and woodpecker (Fig. 2).

The choice of defence tactic seems to be also related to nestling age, which seems to affect the intensity of the nest defence, if the parental risk is low. The parents' reaction on the source of threat gets stronger the older their offspring gets. If the parental risk is high, the intensity of the nest defence does not increase with the developmental stage of the nestlings.

In conclusion, our results correspond with our predictions. Risk assessment is dynamic in the sense that it changes over time but also in the use of the strategies (Kleindorfer et al. 2005). Blue tits have developed various strategies for nest defence against different predators. We have been the first to analyse parental vs. nestling threat and their influence on risk taking and response intensity. Our findings suggest that the intensity of the nest defence is affected by parental as well as nestling risk, but only if the defence behaviour poses a low risk. If the strategy poses a high risk for the defending individual, their own wellbeing seems to have priority over offspring risk—defence behaviour seems not effected by nestling risk.

Acknowledgements

This research was financially supported by the Sparkling Science Foundation of the Bundesministerium für Wissenschaft und Forschung, Vienna.
I especially thank my supervisors Dr. H. Hoi, Prof. Dr. H. Winkler and Mag. K. Mahr for their great support, time and patience. I thank the Sacre' Coeur School in Pressbaum for the collaboration in this study. I am grateful to the students who built and installed the nest boxes and participated in field work. Special thanks also to the Biology teachers (M. Mahr and R. Freimann) for their support. I also thank Johanna Aman and Alexandra Molling for helping us with the field work. All observations conducted were in line with the Austrian law.

References

Boucher, D. H. 1977. On wasting parental investment. *Am Nat* 111:786-88.

Brunton, D. H. 1990. The effects of nesting stage, sex, and type of predator on parental defense by killdeer (Charadrius vociferous): testing models of avian parental defense. *Behavioral Ecology and Sociobiology 26*:181-190.

Buitron, D. 1983. Variability in the responses of black-billed magpies to natural predators. *Behaviour* 87:209-36

Campobello, D., and S. G. Sealy 2011. Use of social over personal information enhances nest defense against avian brood parasitism. *Behavioral Ecology* 22: 422-428.

Carlisle, T. R. 1982. Brood success in variable environments: Implications for parental care allocation. *Anim Behav* 30:824-36.

Caro, T., 2005. *Antipredator defenses in birds and mammals*. University of Chicago Press.

Cramp, S., and C. M. Perrins (Eds.). 1994. *The birds of the Western Palearctic*. Oxford University Press.

Colombelli-Négrel, D., J. Robertson, and S. Kleindorfer. 2010. Nestling presence affects the anti-predator response of adult superb fairy-wrens (Malurus cyaneus). *acta ethol* 13:69-74.

Curio, E. 1975. The functional organization of anti-predator behaviour in the pied flycatcher: A study of avian visual perception. *Anim Behav* 23:1-115.

Curio, E., and K. Regelmann 1982. Fortpflanzungswert und „Brutwert “der Kohlmeise (Parus major). *Journal für Ornithologie 123*:237-257.

Curio, E., G. Klump, and K. Regelmann. 1983. An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? *Oecologia* 60:83-88.

Curio, E., K. Regelmann, and U. Zimmermann. 1984. The Defence of First and Second Broods by Great Tit (Parus major) Parents: A Test of Predictive Sociobiology1. *Zeitschrift für Tierpsychologie 66*:101-127.

Curio, E., and K. Regelmann. 1985. The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Z Tierpsychol* 69:3-18

Dale, S., R. Gustavsen, and T. Slagsvold. 1996. Risk taking during parental care: A test of three hypotheses applied to the pied flycatcher. *Behav Ecol Sociobiol* 39:31-42.

Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Animal Behaviour 60*:263-267.

Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science 292*:494-497.

Greig-Smith, P. W. 1980. Parental investment in nest defence by stonechats (Saxicola torquata). *Animal Behaviour 28*:604-619.

Hudson, P. J., and D. Newborn. 1990. Brood defence in a precocial species: Variations in the distraction displays of red grouse *Lagopus lagopus scoticus*. *Anim Behav* 40:254-61.

Johnsen, A., K. Delhey, E. Schlicht, A. Peters, and B. Kempenaers. 2005. Male sexual attractiveness and parental effort in blue tits: a test of the differential allocation hypothesis. *Anim Behav* 70:877-88.

Kleindorfer, S., B. Fessl, and H. Hoi. 2003. The role of nest site cover for parental nest defence and fledging success in two *Acrocephalus* warblers. *Avian Sci* 3:21–29

Kleindorfer, S., B. Fessl, and H. Hoi. 2005. Avian nest defence behaviour: Assessment in relation to predator distance and type, and nest height. *Anim Behav* 69:307-13.

Krüger, O. 2007. Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. *Philosophical Transactions of Royal Society B* 362:1873-1886.

Kruuk, H. 1964. Predators and antipredator behaviour of the black-headed gull (*Larus ridibundus* L.). *Behaviour* Suppl. 11:1-129.

Kryštofková, M., M. Haas, and A. Exnerová. 2011. Nest defense in blackbirds Turdus merula: effect of predator distance and parental sex. *Acta Ornithologica* 46:55-63.

Lambrechts, M. M., B. Prieur, A. Caizergues, O. Dehorter, M. J. Galan, and P. Perret. 2000. Risk-taking restraints in a bird with reduced egg-hatching success. *Proc R Soc Lond Ser B. Biol Sci* 267:333-38.

Langmore, N. E., A. Cockburn, A. F. Russell, and R. M. Kilner. 2009. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behavioral Ecology* 20:978–984.

Lehmann, L., and L. Keller. 2006. The evolution of cooperation and altruism – a general framework and a classification of models. *Journal of Evolutionary Biology* 19:1365-1376.

Martin, T.E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.* 141:897-913.

Montgomerie, R. D., and P. J. Weatherhead. 1988. Risks and rewards of nest defence by parent birds. *Q Rev Biol* 63:167-87.

Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. *Ornis Scand* 15:167-75.

Onnebrink, H., and E. Curio. 1991. Brood defense and age of young: a test of the vulnerability hypothesis. *Behavioral Ecology and Sociobiology 29*: 61-68.

Owings D. H., R. G. Coss, D. McKernon , M. P. Rowe, and P. C. Arrowood. 2001. Snake-directed antipredator behavior of rock squirrels (*Spermophilus variegatus*): Population differences and snake-species discrimination. *Behaviour* 138:575-595.

Patterson, T. L., L. Petrinovich, and D. K. James. 1980. Reproductive value and appropriateness of response to predators by white-crowned sparrows. *Behav Ecol Sociobiol* 7:227-31.

Payne, R. B., Payne L. L., and Rowley I. 1985. Splendid Wren *Malurus Splendens* Response to Cuckoos - an Experimental Test of Social-Organization in a Communal Bird. *Behaviour* 94:108-127.

Pianka, E. R. 1972. r and K selection or b and d selection?. *American Naturalist* 581-588.

Pinowski, J.,M. Barkowska, A. H. Kruszewicz, and A. G. Kruszewicz. 1994. The causes of the mortality of eggs and nestlings of Passer sp. *Journal of Biosciences* 19:441-451.

Radford, A. N., and J. K. Blakey. 2000. Intesity of nest defence is related to offspring sex ratio in the great tit *Parus major. Proc R Soc Lond Ser B Biol Sci* 267:535-38.

Redondo, T. 1989. Avian nest defence: Theoretical models and evidence. *Behaviour* 110:161-95.

Ricklefs, R. 1969. An analysis of nesting mortality in birds. *Smiths. Contr. Zool*. 9:1-48.

Rytkönen, S., and M. Orell. 2001. Great tits, Parus major, lay too many eggs: experimental evidence in mid-boreal habitats. *Oikos*, *93*:439-450.

Sheldon, B. C., J. Merilä, G. Lindgren, and H. Ellegren. 1998. Gender and environmental sensitivity in nestling collared flycatchers. *Ecology 79*:1939-1948.

Svensson, L., P. J. Grant, K. Mullarney, and D. Zetterström. 1999. *Der neue Kosmos-Vogelführer. Alle Arten Europas, Nordafrikas und Vorderasiens*. Stuttgart: Franckh-Kosmos Verlags-GmbH & Co. S. 92, 226

Swaisgood, R. R., M. P. Rowe, and D. H. Owings. 2003. Antipredator responses of California ground squirrels to rattlesnakes and rattling sounds: the roles of sex, reproductive parity, and offspring age in assessment and decision-making rules. *Behav Ecol Sociobiol* 55:22-31.

Thompson III, F. R., and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. *The Journal of wildlife management* 67:408-416.

Trivers, R. L. 1972. Parental investment and sexual selection. In *sexual selection and the descent of man*, ed. B. Campbell, 136–79. Chicago: Aldine.

Trivers, R. L. 1974. Parent-offspring conflict. *Am Zool* 14:249-65.

Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the sandwich tern (*Sterna s. sandvicensis*, Lath). *Behaviour* Suppl. 10:1-193.

Verbeek, N. A. M. 1972. The exploitation system of the yellow-billed magpie. *Univ Calif Publ Zool* 76:1-58.

Weatherhead, P. J. 1989. Nest defence by song sparrows: Methodological and life history considerations. *Behav Ecol Sociobiol* 25:129-36.

Weidinger, K. 2002. Interactive effects of concealment, parental behavior and predators on the survival of open passerine nests. *J Anim Ecol* 71:424-37.

Wheelwright, N. T., J. J. Lawler, and J. H. Weinstein. 1997. Nest-site selection in Savannah sparrows: using gulls as scarecrows?. *Animal Behaviour 53*:197-208.

Winkler, D. W. 1987. A general model for parental care. *Am Nat* 130:526-43.

Winkler, H. 2001. The Ecology of Avian Acoustical Signals. *Ecology of Sensing* 79-104 Springer Berlin Heidelberg.

Zanette, L., M. Clinchy, and J. N. Smith. 2006. Combined food and predator effects on songbird nest survival and annual reproductive success: results from a bi-factorial experiment. *Oecologia 147*:632-640.

Zuberbühler, K. 2009. Survivor signals: the biology and psychology of animal alarm calling. *Advances in the Study of Behavior* 40:277-322.

Zusammensfassung

Eine der häufigsten Ursachen in der Natur für den Verlust der Nachkommen ist Predation durch Raubtiere. Bei einigen Tierarten haben sich daher unterschiedlichste Strategien entwickelt, um die Fitness durch das Überleben der eigenen Jungen zu steigern. Man unterscheidet hier zwischen Prozessen, welche die Wahrscheinlichkeit auf ein Raubtier zu treffen verringern und andere, die aktiv Predatoren vertreiben sollen. Bei der Wahl und Intensität der Strategien zur Verteidigung des Nachwuchses spielen mehrere Faktoren, wie Art des Fressfeindes, das Risiko für die Eltern und der Brutwert eine entscheidende Rolle. Die Art des Räubers und somit die Gefahr die von ihm ausgeht haben einen ziemlich großen Einfluss auf das Risiko, das die Eltern bereit sind einzugehen. Sie sind somit in einem Zwiespalt zwischen dem eigenen und dem Risiko der Jungen. Ist der Nachwuchs also in Gefahr, müssen die Eltern abwägen, wie viel sie zur Verteidigung riskieren, ohne dass sie selbst verletzt werden beziehungsweise dem Räuber zum Opfer fallen.

Besonders bei Sperlingsvögeln sind Verhaltensweisen, die der Nestverteidigung dienen weit verbreitet. Aus früheren Studien ist bekannt, dass die Elternvögel mitunter ein sehr weites Spektrum an Verhaltensweisen entwickelt haben, um unterschiedlichste Arten von Räubern aus der unmittelbaren Nestumgebung zu vertreiben. Dabei spielt nicht nur die Art des Raubtieres eine Rolle, sondern auch die Verwundbarkeit der Jungvögel, die sich während ihrer Entwicklung stetig ändert.

Unsere Studie befasst sich mit dem „ dynamic risk assessment“. Wir untersuchen die unterschiedlichen Reaktionen auf drei Raubtiertypen, die jeweils einen bestimmten Risikofaktor darstellen. Dabei wird nicht nur das Risiko, das die Predatoren für die Altvögel darstellen berücksichtigt, sondern auch das für die Nestlinge. In der Konsequenz sollte sich der elterliche Aufwand zur Verteidigung des Nestes nicht nur aufgrund der Art der Räuber unterscheiden, er sollten auch durch frühe und spätere Entwicklungsstufen der Jungvögel beeinflusst werden. Die adulten Tiere müssten ihr Verhalten einem mit dem Alter der Jungen ab- bzw. zunehmenden Risiko für ihre Nachkommen anpassen. Es sollte also zu erwarten sein, dass die Eltern bei zu hohem Eigenrisiko eher das Nest aufgeben, als ihr Leben zu riskieren. Wenn jedoch das Risiko für die Jungen hoch ist und das der Eltern eher gering, wäre eine hohe Verteidigungsbereitschaft zu erwarten.

Um zu überprüfen, ob es dynamic risk assessment unter Sperlingsvögeln gibt, führten wir eine Studie im Frühling 2012 an frei lebenden Blaumeisen (*Cyanistes caeruleus)* durch. Wir testeten dabei die Reaktion der Altvögel auf drei verschiedene Arten von Räubern (Äskulapnatter, Sperber und Buntspecht). Dabei wurde pro Nistkasten nur ein Typ der Attrappen verwendet (Sperber: n = 18, Schlange: n = 17, und Buntspecht: n = 16), wobei die Nistkästen per Zufall ausgewählt wurden. Nach der Anbringung der Attrappe am Nistkasten wurden unterschiedlich risikoreiche Verhaltensweisen wie: Attackieren (sehr hohes Risiko), Rattling (Alarmrufe, niedriges Risiko) und die minimale Distanz (hohes Risiko) zu dem potentiellen Räuber protokolliert. Die Eltern, die mit der Sperberattrappe konfrontiert wurden, führten keine direkten Attacken auf den vermeintlichen Fressfeind durch. In beiden Versuchsdurchläufen attackierten die Altvögel die Modellschlange am häufigsten. Die Wahrscheinlichkeit für einen Angriff auf den Buntspecht war hingegen eher gering. Somit sind hier schon starke Unterschiede aufgrund der unterschiedlichen Risikofaktoren, die diese drei Räuber für die Elternvögel darstellen erkennbar. Ähnlich starke Differenzen gab es bei der minimalen Distanz zu den Attrappen zu beobachten. Dabei war die Distanz zur Schlange am geringsten, zum Sperber am größten. Die Untersuchung der Alarmierung (Rattling) ergab wieder starke Unterschiede zwischen den einzelnen Risikofaktoren, wobei diesmal der Sperber die stärkste und die Äskulapnatter die schwächste Reaktion auslöste. Außerdem bestätigen die Ergebnisse der Änderungen der Beobachtungen zwischen ersten und zweiten Versuch unsere Erwartung, dass die Intensität der risikoärmsten Verteidigungsmaßnahme mit dem Alter der Jungvögel zunahm. Das war zumindest bei den Trials mit Schlangen- und Sperberattrappe der Fall. Der Buntspecht löste wie erwartet durch seine abnehmende Relevanz als Nesträuber keine signifikant stärkere Reaktion aus. Übereinstimmend mit unserer Voraussage riskierten die Eltern auch mit dem höheren Entwicklungsstadium der Jungen nicht mehr, wenn das Eigenrisiko durch minimalen Abstand zum Fressfeind zu hoch war.

Unsere Studie ist mitunter eine der ersten, die sich mit dynamic risk assessment unter Rücksichtnahme mehrerer Faktoren beschäftigt. Die Ergebnisse lassen darauf schließen, dass Blaumeisen variable Strategien für die Nestverteidigung gegen verschiedene Räuber entwickelt haben. Die Intensität der Nestverteidigung steigt mit dem Alter der Nestlinge, wenn das elterliche Risiko dabei gering ist. Wenn das

elterliche Risiko jedoch hoch ist, hat ihr Überleben Priorität und der Brutwert scheint keinen Einfluss auf ihr Nestverteidigungsverhalten zu haben.

Curriculum Vitae

Name:	Georg Friedrich Riegler
Adresse:	2860 Kirchschlag, Mühlgasse 6/7
e-mail:	a0601132@unet.univie.ac.at
Geburtsdatum:	27.10.1986
Geburtsort	Oberpullendorf, Niederösterreich

Bildungsweg

03/2012 – 08/2013	Diplomarbeit am KLIVV (Konrad Lorenz Institut für Vergleichende Verhaltensforschung) und Department of Animal Biodiversity der Universität Wien.
10/2006 – 09/2013	Studium der Biologie mit Fachbereich Zoologie
09/2001 – 05/2005	AHS BORG Wiener Neustadt Abschluss: Matura
09/1997 – 06/2001	Hauptschule Kirchschlag
09/1993 – 06/1997	Volkschule Kirchschlag

Berufliche Erfahrung

03/2012 -	Mitarbeit bei Projekten von „*Sparkling Science*“ (BMWF) „Die Auswirkungen des Klimawandels auf unsere heimische Vogelwelt“; „Vögel als Bioindikatoren“: - Organisation und Durchführung der Freilandarbeit - Betreuung von Schulklassen
03/2012 -	Mitarbeit am Projekt „*Science twins*“ im Rahmen von „*Sparkling Science*“ einem Projekt des BMWF (Bundesministerium für Wissenschaft und Forschung): - Betreuung von Fachbereichsarbeiten (Datenaufnahme, Auswertung, wissenschaftliches Schreiben)

Poster

J. Amman, K. Mahr, G. Riegler, A. Molling, H. Hoi (2013) **The effect of surplus food on reproductive behaviour and success in various tit species** 8th Conference of the European Ornithological Union, Norwich, UK (submitted, in revision)

Sprachkenntnisse

Englisch: sehr gute Kenntnisse