



## Research

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# Parental risk management in relation to offspring defence: bad news for kids

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Do parents defend their offspring whenever necessary, and do self-sacrificing parents really exist? Studies recognized that parent defence is dynamic, mainly depending on the threat predators pose. In this context, parental risk management should consider the threat to themselves and to their offspring. Consequently, the observed defence should be a composite of both risk components. Surprisingly, no study so far has determined the influence of these two threat components on parental decision rules. In a field experiment, we investigated parental risk taking in relation to the threat posed to themselves and their offspring. To disentangle the two threat components, we examined defence behaviours of parent blue tits *Cyanistes caeruleus* towards three different predators and during different nestling developmental stages. Nest defence strategies in terms of alarm call intensity and nearest predator approach differed between the three predators. Defence intensity was only partly explained by threat level. Most importantly, parental risk management varied in relation to their own, but not offspring risk. Parent defence investment was independent of nestling risk when parents followed a high-risk strategy. However, parents considered nestling as well as parental risk when following a low-risk strategy. Our findings could have general implications for the economy of risk management and decision-making strategies in living beings, including humans.

## 1. Introduction

In the animal kingdom, parent–offspring solidarity can be considered an example of altruistic behaviour. We tend to sympathize with the idea that parent behaviour is always unselfish, putting the welfare of kids above all. Is this really the case? Offspring can be considered the currency for parental fitness [1]. During 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 [2–5], infectious diseases and parasites [6–8], or interspecific brood parasitism [9,10].

Another major factor known to have a significant impact on offspring survival is predation [11–14]. Therefore, offspring protection by parents is a key factor enhancing offspring survival and an individual's fitness [1,15–19]. One question in this context arises: do parents really defend their offspring whenever necessary?

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 [20–25]. Risk management and differential allocation into offspring defence are related to a variety of internal and external factors [17,26]. Consequently, the choice of the right defence strategy towards a threat is an important area of competence, influencing the survival and fitness of an individual involved in defending its offspring against predators [22,25,27–30].

As offspring defence can be dangerous [15,31,32], parents may face a trade-off between survival of the current brood and their own survival, and, as a consequence, that of their future broods [28,33,34]. This compromise between current and future reproduction may consequently influence risk-taking decisions and defence intensity towards a threat posed to the offspring [28].

Furthermore, the time and energy invested to replace a brood increases with offspring age [35], whereas the mortality rate declines and the probability that the young reach reproductive age is higher in older offspring [36]. As predicted by the brood value hypothesis, the value of a brood, in terms of offspring age or condition, has been recognized to play a role in parental risk management [15]. In fact, there is already certain evidence that parents invest more in the defence of older (and hence more valuable) offspring [37,38].

Finally, differential allocation in offspring defence is to a great extent related to the threat a predator poses. In line with this, parental risk management should take two major threat components into account, namely the threat to the parent and the threat for the offspring. Thus, the observed defence pattern should be a composite of both risk components. Surprisingly, there is no information so far on how these two threat components influence parental decision rules.

The threat that an individual faces can, in principle, be described as a gradient from no to high risk and be independent for parents and offspring. To understand parent decision rules in this context, the most explanatory study would be to investigate those cases, where the direction of the two gradients is reversed (e.g. when a certain threat bears a high risk for the offspring but a low risk for the parent, or vice versa). Such an example could be a brood parasite [39], which usually poses a high risk for the offspring, but is of low or no risk for the parents. In contrast, when the threat for the parents reaches a certain threshold and, for example, their own life is at stake, offspring risk might no longer be considered important for risk management and the choice of proper defence strategies. Alternatively, parental defence costs may, under certain circumstances, increase up to the level of a kamikaze response, sacrificing a parent's life. Such circumstances may include that offspring survive without parental care, and that parents have little opportunity for future reproduction [40].

The aim of our study was to demonstrate in a field experiment that both threat components are important for parent risk management. For this purpose, we used a passerine bird, the blue tit (*Cyanistes caeruleus*), as a model species to experimentally simulate situations of varying threat. For many passerine bird species, nest predation is the main cause for loss of the brood, and therefore has a significant impact on annual and lifetime reproductive success [13,15,41,42]. Therefore, active nest defence is a crucial reproductive strategy especially in altricial songbirds, where parents can significantly increase offspring survival [28]. By contrast, when performing nest defence, parents also face the risk of injury or death, which forces them into a compromise between current and future reproduction [28].

The specific level of threat posed by different predators may change with age and development of the brood [36,43]. In order to disentangle the two risk components, we would like to make use of this important aspect. Blue tits are particularly ideal for our investigation because (i) they are very common and breed in easy accessible nest-boxes [44], (ii) males and females invest in offspring care (including predator defence) and [45] (iii) they are short-lived [46]. 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 [47–49].

To investigate the importance of parental and nestling risk for decision making in regard to investment into

**Table 1.** Level of risk the three types of predators represent to parent blue tits and their young (5-day-old) and older (12-day-old) nestlings.

predator	parental risk	risk nestling young	risk nestling old
snake	medium	high	high
sparrowhawk	high	low	high
woodpecker	low	high	low

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. 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 [50]. Consequently, the choice of the right defence strategy towards a threat is an important area of competence that influences the survival and fitness of an individual involved in defending its offspring against predators [22,27–30]. For example, in order to attack, a predator might constitute a higher risk than alarm calling [28]. Thus, to accurately determine investment and risk taking, it might be necessary to examine different anti-predator behaviours. 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 with a response behaviour of low risk (e.g. alarm calling).

The questions we would like to answer are as follows. (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? (iv) How important is parental and nestling risk for parent risk management, and in particular investment into predator defence in relation to different defence behaviours?

## 2. Material and methods

### (a) General methods

The study was conducted in 2013, on a nest-box population in the Viennese forest near Vienna (48°18' N, 16°8' E; about 320 m a.s.l.) with 200 nest-boxes. The study area covers 60 ha of mixed deciduous forest of mainly hornbeams (*Carpinus betulus*) and European beeches (*Fagus sylvaticus*), and interspersed open areas. Nest-box design and placement can influence various aspects of reproductive behaviour [51,52]. To avoid the possible impact of variation in nest design, placement or nest-box manipulation on behaviour, we tried to provide equal conditions for all breeding pairs. Therefore, all nest-boxes are the same age, have a standard size of 26 × 14 × 17 cm and have an entrance hole-width of 2.5 cm with a metal plate attached. All nest-boxes have been installed at a height of approximately 2 m on beech trees with a diameter between 30 and 40 cm, pointing in the same direction, and are regularly cleaned out and maintained in autumn.

The experiments were carried out from late April until mid-June of 2012. Nest-boxes were controlled on a 2-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 5 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 in the nest-box. Adult birds were banded with aluminium rings and a unique Darvic colour ring combination for individual recognition during the experiments.

## (b) Study species and choice of predators

Blue tits (*C. caeruleus*) are common passerines that breed in cavities and readily accept nest-boxes, allowing frequent monitoring of the breeding activity (e.g. development of eggs and nestlings) [44,46]. Regular monitoring since establishment of the breeding population in 2008 revealed that pairs produce only one brood per year, and only rare cases of replacement clutches have been observed.

In order to simulate dynamic risk for the nestlings, models of three common different predators (one model per predator type) 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*) [45,50,53] as well as stuffed models of a great spotted woodpecker (*Dendrocopos major*) [49] and a female sparrowhawk (*Accipiter nisus*) [31]. The availability of only one specimen per predator type may not allow us to derive more general implications; however, a pre-study conducted in 2011, using different specimens, revealed that birds responded exactly in the same manner towards models of the three predator types (for details, see Discussion).

The three predators were chosen based on their abundance in the study area and varying threat they pose for nestling and adult blue tits. All three have been identified as predators on blue tits in our study site (unpublished data, 2008–2012).

A very important predator in our study area of in particular nestlings blue tits [45,53] is the Aesculapian snake, which is able to climb trees and enter natural cavities and nest-boxes (own observation, 2008–2012). When detected by an adult passerine, snakes, because they are less mobile, pose a minor threat and usually are not able to successfully prey on them [54]. Therefore, we predict the snake to represent a medium-level risk for the adults (table 1). However, 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 [44], 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 [55–57] (own observation, 2008–2012). 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 of being predated by a great spotted woodpecker, and therefore we predict that the woodpecker constitutes a minor threat for the parents and older chicks but represents a high risk for small nestlings (table 1).

The sparrowhawk is a common bird of prey in our study area [44]. It is specialized to prey on small passerines and poses the greatest threat for adult blue tits. A major part of a sparrowhawk's prey consists of small-to-medium-sized birds, and therefore they are well adapted for ambush predation [44]. We therefore predict

the sparrowhawk 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 sparrowhawk 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 nest-box. It is therefore considered to be a high risk for older nestlings (table 1).

## (c) Nest defence behaviour

Before the experiment started, we observed the surroundings of the nest-boxes for 5 min to ensure the adult birds were around and not distracted by our presence. The predator type was randomly selected for each experiment.

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 (sparrowhawk). 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 min; 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 (Swarovski 8 × 42) from a distance of 15–20 m.

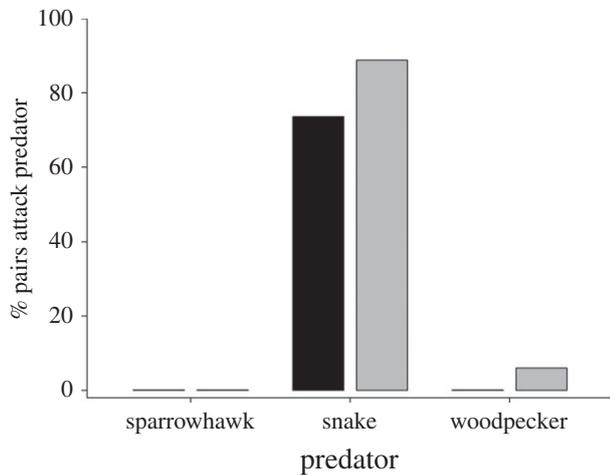
The behaviour was recorded in 10 s intervals, noting variables that represent different levels of risk: (i) the number of direct attacks towards the predator, which is an active nest defence strategy in passerines; (ii) 'rattling', which is a behaviour expressing excitement in combination with an alarm function; and (iii) attacks representing the highest possible intensity of parental nest defence behaviour [15,28,45,53]. 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 [58], 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 [59]. 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.

## (d) Statistical analysis

For statistical analyses, STATISTICA v. 7.1 (Statsoft Inc., Tulsa) was used. Our sample size involves a total of 50 breeding pairs. From 56 original pairs, we excluded four pairs owing to insufficient information gathered and two pairs because of brood loss before day 12.

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 × 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 univariate analyses of variance (ANOVA). To test whether 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 with a nestling age of 5 and 12 days. To compare the behaviour towards the three predators triggered by the experiments, we used repeated-measures ANOVA with parental nest defence level (rattling or adult minimum approach) as the dependent variable, predator type (sparrowhawk, snake and woodpecker) and their respective threat intensity (high, medium and low) as the



**Figure 1.** Maximum predator response. Percentage of blue tit pairs attacking experimentally placed predators (high risk, sparrowhawk; medium risk, snake; low risk, woodpecker) when nestlings are 5 (black bars) or 12 days old (grey bars).

independent factors, and experiments with 5- and 12-day-old chicks as repeated factors. For *post hoc* 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.

### 3. Results

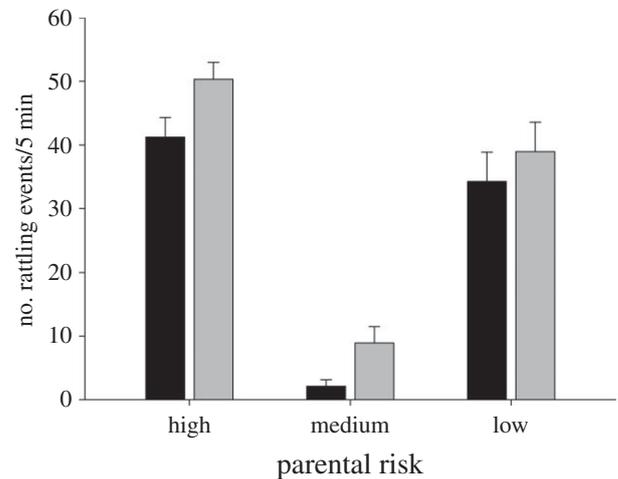
#### (a) Do blue tits perform risk assessment and adjust risk taking accordingly?

Examining whether pairs really attack a predator, a behaviour that poses a very high risk for the defender, significantly differs between the three different predator types for both chick ages (Freemant–Halton exact test for chicks aged 5 days:  $\chi^2 = 34.05$ ,  $p < 0.01$ ; for chicks aged 12 days:  $\chi^2 = 41.4$ ,  $p < 0.01$ ). The proportion of blue tit pairs attacking an Aesculapian snake is in both trials (with 5- and 12-day-old chicks) very high (figure 1): 73.6% and 88.8% of all pairs attacked the snake. Almost no pair attacked the great spotted woodpecker, and none of them attacked the sparrowhawk (figure 1).

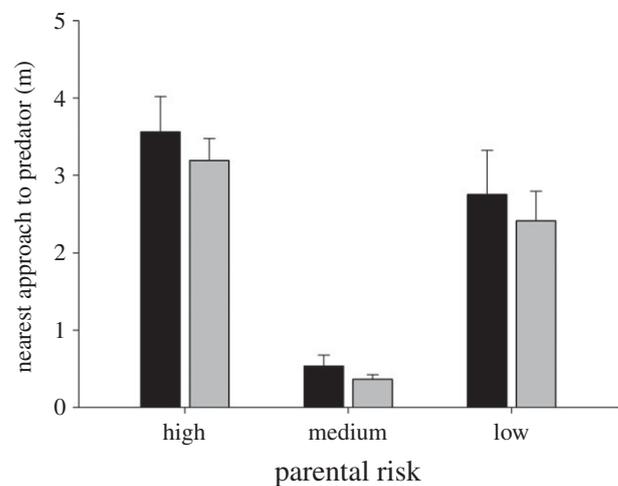
#### (b) Do blue tits differently use strategies reflecting varying risk?

Examining the low-risk behaviour in terms of rattling, parent birds respond significantly different towards the three types of predators (ANOVA:  $F = p < 0.01$ , d.f. = 2.49; figure 2). This difference is mainly due to the significantly reduced rattle frequency towards the snake model. The rattle frequency was highest towards the sparrowhawk and slightly lower towards the great spotted woodpecker (figure 2).

Examining predator approach, which reflects high-risk behaviour, again revealed a significant variation between predator types (ANOVA:  $F = 5.4$ ,  $p < 0.01$ , d.f. = 2.49). Blue tit pairs keep the greatest distance from the sparrowhawk (figure 3). Compared with 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 (figure 3).



**Figure 2.** Low-risk predator response. Number of rattling events per 20 min elicited against experimentally placed predators (high risk, sparrowhawk; medium risk, snake; low risk, woodpecker) when nestlings are 5 (black bars) or 12 days old (grey bars). Given are means and standard error.



**Figure 3.** High-risk predator response. Minimum distance (m) of the parental birds to experimentally placed predators—snake (medium risk),  $n = 16$ ; sparrowhawk (high risk),  $n = 18$ ; woodpecker (low risk),  $n = 16$ —when nestlings are 5 (black bars) or 12 days old (grey bars). Given are means and standard error.

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 sparrowhawk when chicks were older (paired *t*-test: snake:  $t = -2.32$ ,  $p = 0.035$ , d.f. = 30; sparrowhawk:  $t = -2.40$ ,  $p = 0.028$ , d.f. = 34; figure 2). However, rattling frequency did not significantly differ between younger and older nestlings in response to the great spotted woodpecker ( $t = -1.21$ ,  $p = 0.25$ , d.f. = 30; figure 2).

Taking a higher 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:  $t = 0.26$ ,  $p = 0.8$ , d.f. = 30; sparrowhawk:  $t = 0.13$ ,  $p = 0.9$ , d.f. = 34; woodpecker:  $t = 0.16$ ,  $p = 0.87$ , d.f. = 30; figure 3).

**Table 2.** The importance of parental and nestling risk with respect to rattling displays.

factors	d.f.	F	p
parental risk	2.47	57.78	<0.01
nestling risk (chick age)	1.47	11.29	<0.01
interaction		0.39	0.68

### (c) How important is parental and nestling risk for the application and intensity of low- and high-risk behaviour in offspring defence?

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 (table 2). A *post hoc* comparison suggests that the differences are significant among all three predator types (Fisher's least significant difference test: all  $p < 0.05$ ).

When the adult birds perform high-risk defence and actually approach the predator, the level of risk for their offspring no longer affects their response intensity, given as nearest approach towards the predator, in relation to the three threat levels reflected 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:  $p < 0.05$ ).

## 4. 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. It rather seems to be a complex process depending on internal as well as external stimuli [25,32,60–62]. According to our study, parent birds are obviously able to simultaneously assess and integrate different risk components based on immediate external stimuli such as the threat level reflected by a predator and other factors [28], including an adaptive nestling reaction towards a predator (as suggested by the chick reaction hypothesis) [25,63,64] or internal reference values (such as brood value or future reproductive success) in their decision-making process [32,60,61,65].

We are among the first to examine the two risk components in combination, and our results are consistent with the predictions proposed. In particular, we 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. However, the most exciting conclusion from our results is that their influence also depends on the defence strategy involved. When parents do not risk a lot, more specifically when they decide to invest in alarm calls, both parental and nestling risk seem to influence alarm call frequency (table 2). However, nestling threat does not influence parental defence intensity when parents perform high-risk behaviour in terms of predator approach. In other words, how close parents approach seems to solely depend on their risk.

**Table 3.** Importance of parental and nestling risk with respect to the 'nearest predator approach'.

factors	d.f.	F	p
parental risk	2.47	50.12	<0.01
nestling risk		0.09	0.77
interaction		0.003	0.99

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 [28].

Our results show that nest defence intensity varies between different predators, showing consistency with the results of many previous studies [47,66–69]. This indicates that parent blue tits perform dynamic risk assessment [50] and show an adaptive predator response.

Examining the reaction towards a predator in relation to the threat 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 sparrowhawk, because this aerial predator poses a crucial threat to them [44]. For the parental bird, the risk of attacking a sparrowhawk would be too high, and the nestlings in the nest-box are unattainable by the aerial raptor. By contrast, the highest attack probability towards a medium threat such as the Aesculapian snake is not necessarily expected but may be due to the fact that snakes are less mobile and usually are not able to successfully prey on adult passerines [54]. Therefore, closer approach against snakes does not necessarily mean higher risk taking. Furthermore, parent defence towards snakes might be more efficient and results in successfully deterring the snake from the brood. Surprisingly, and against the expectation, there were almost no attacks towards the great spotted woodpecker. Even though great spotted woodpeckers commonly prey on nestling tits, there is no evidence that woodpeckers prey on adult passerines, and therefore they pose no threat (or a very low one). The question that then arises is 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 [49], great spotted woodpeckers could possibly cause injuries in an attempt to fight it off [28] and additionally, a close approach might be less efficient. 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 alternative explanations for an adaptive 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 [15,16,36,70].

However, as already mentioned, there are other factors that may influence offspring defence intensity. One factor is related to the benefit for the current brood versus future costs [61,65]. These future costs are of course dependent on the survival of the parental birds [15]. However, blue tits

are short-lived, and individuals of our nest-box population can be seen as r-selectionists [71], because our monitoring data reveal that individuals of our study site produce not multiple broods but only one large brood per year [72]. Thus, year-to-year survival is low, and to save energy for future broods is a rather unlikely strategy. It is already demonstrated that parental re-nesting potential may play a major role for risk taking. 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 [60,73,74]. Unfortunately, we do not have any information about the age of our birds to draw any conclusions along this line.

Winkler [37] and Lambrechts *et al.* [38] 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 [75]. 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 later stage of the nestlings' development would be a severe setback. Regarding our experiments, we would expect stronger 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 sparrowhawk and the woodpecker, because nestling risk changes with the age of the nestlings (e.g. nestling risk increases with the sparrowhawk and decreases with the woodpecker; 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 (figures 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. Brunton [76] showed that 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 sparrowhawk and woodpecker (figure 2).

The choice of defence tactic seems also to be 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 as their offspring get older. If the parental risk is high, the intensity of nest defence does not increase with the developmental stage of the nestlings.

Our results have to be interpreted carefully, because the availability of only one specimen per predator type may

possibly restrict us to derive more general implications. However, a pre-study conducted in 2011, using different specimens, revealed that birds responded in exactly the same manner towards different model specimens of the three predator types. As in our study, blue tits kept the greatest distance to the sparrowhawk and approached closest to the snake. Similarly, alarm call intensity was higher for the sparrowhawk and the snake than for the woodpecker, and increased with nestling age for the sparrowhawk and the snake, but not for the great spotted woodpecker model. Thus, a predator-specific response rather than any other difference is very likely. Variation in defence behaviour owing to variation of individual predator characteristics should be minor, given the evolutionary cost of performing the wrong response to a given predator species. A general assumption is that prey might not be able to recognize individual predators, therefore less attention is given to replicas in predation experiments [28].

In conclusion, our results suggest risk assessment to be a dynamic process in the sense that it changes over time, but also in the choice of the defence strategy [50]. Blue tits have developed various strategies for nest defence against different predators. In a field experiment, we have been able to disentangle parental and 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. We think that our findings, based on our model system, have general important implications for the economy of risk management and decision-making strategies in living beings, including humans.

**Ethics statement.** The experiments reported in this paper comply with the current laws on animal experimentation in Austria and the European Union. The long-term nature of the study allowed us to confirm that handled birds and their offspring did not suffer any detectable reduction in welfare and survival. Permission for this study was approved by the government (licence number: RU5-BE-7/010-2011).

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