

## Size dependent predation risk in cryptic and conspicuous insects

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**Abstract** It is not clear which selective pressures balance the strong fecundity advantage associated with large female body size in insects. A positively size-dependent mortality risk could provide a solution. In aviary experiments with artificial larvae, we studied if larger larvae of folivorous insects are more readily found (= detectability) and/or attacked (= acceptability) by birds. As size and colouration are likely to interact in determining birds' responses, both cryptic and conspicuous prey items were used. As detectability is likely to be context-dependent, both simple (smooth) and complex (plants) backgrounds were used in respective experiments. In the conspicuous larvae, acceptability correlated negatively with prey size. However, their detectability was context dependent, being positively correlated with size on the simple background, whereas no significant effect was found on the complex background. Surprisingly, cryptic larvae showed no correlation between detectability and size, and there was only a weak tendency for birds to attack large larvae more readily. On the basis of a quantitative model, we conclude that the effect of positively size dependent bird predation, as a single factor, is not likely to counterbalance the fecundity advantage in cryptic species, and may thus not be crucial in determining the optimum for body sizes in these insects. In conspicuous species, there is a potential for different outcomes, because detectability and acceptability affect survival in different directions. The net outcome is, therefore, likely to be highly context-dependent. Furthermore, our results provide an explanation for the recently reported absence of systematic body-size differences between cryptic and conspicuous Lepidopteran larvae: although conspicuous larvae benefit from increasing their warning signal when growing larger, they also suffer a much sharper rise in detectability.

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## Introduction

In many insect species, body size is a strong determinant of female fecundity (e.g. Honěk 1993). The consequent phenotypic selection for large adult size should lead to continuous evolutionary increase in insect body size, if it was not balanced by other selective forces (Endler 1986). In other words, to explain the lack of such trend, we need to assume substantial costs of large sizes. Locating these costs has turned out to be a surprisingly non-trivial question, however (Leimar 1996; Blanckenhorn 2000; Tammaru et al. 2002; Gotthard 2004).

An increase in development time forms an intuitive cost of larger adult size (Roff 1992; Stearns 1992). However, a constant, body-size independent mortality may not be sufficient to balance the fecundity advantage. This is particularly obvious when weight gain per time unit is high, as in many moth larvae (Tammaru 1998). However, *positively body-size dependent* mortality rates might prove to represent an ecological factor capable of balancing the advantages of large body size.

Bird predation could easily form the factor behind size-dependence in survival rates. Birds are typically the predominating cause of larval mortality in herbivorous insects, particularly for the latest instars (e.g. Baker 1970; Dempster 1984; Cornell and Hawkins 1995; Grushecky et al. 1998). Moreover, birds are known to discriminate between differently sized prey (Gamberale and Tullberg 1996, 1998; Grieco 2002).

It is reasonable to assume that birds might respond differently to the body size of cryptic versus warningly coloured prey. Conspicuous warning signals are typically used by aposematic animals (or their mimics) to advertise their unpalatability or toxicity to potential predators (Poulton 1890). Birds have been reported to show stronger aversion towards warningly coloured prey with larger body size (Gamberale and Tullberg 1996, 1998), or group size (Mappes and Alatalo 1997; Riipi et al. 2001). It has also been demonstrated that warning coloration is more effective when displayed on large areas, which implies that the signal strength is increased in insects with large bodies (Forsman and Merilaita 1999). The latter circumstance could significantly reduce, or even reverse, the positive correlation between size and mortality in conspicuous species. For the given reasons, it is often assumed that being large should be more profitable to conspicuously coloured insects than to cryptic ones (Forsman and Merilaita 1999; Nilsson and Forsman 2003). This is because the latter do not have warning signals that reduce the costs of a large body.

Prey size can affect predation risk in two different ways: (1) by larger prey being more easily *detected* by predators and (2) by predators preferentially *accepting* either smaller or larger prey after detection. The third potential component in determining predator's success is formed by the ability of the prey animals to *resist* the attack, thus surviving it with minimal damage (Vermeij 1982). Such ability may substantially contribute to differential mortality risk in the case of invertebrate predators (e.g. Dyer 1995), though its importance in the case of bird predation on Lepidopteran larvae is likely to be minimal.

To evaluate the power of bird predation to create size-dependent mortality patterns, and its potential to determine the optimum for body sizes thereby, we

conducted aviary experiments with artificial prey items, imitating folivorous Lepidopteran larvae. We asked if and how size affects detectability and acceptability of prey by insectivorous birds. Moreover, if the assumption of conspicuous species profiting more from larger body size holds, we should be able to demonstrate that both cryptic and conspicuous larvae are more easily found by birds when being large. On the other hand, the two colour types should show different correlations between size and acceptability by birds.

## Methods

### Rationale of the approach

Our intention was to measure the two components of size- and colour-dependent predation risk—detectability and acceptability—independently of each other. Therefore, in the detectability experiments, experimental birds were first trained to accept prey items with conspicuous (warning) colouration as readily as cryptic ones, after which they were allowed to search for hidden individuals of both. To test for the generality of the results, the prey items were to be found from two backgrounds differing in complexity: a smooth cryptic background in *detectability experiment I*, and potted plants in *detectability experiment II*. In the acceptability trials, on the contrary, the birds were offered novel prey. Both cryptically and conspicuously coloured prey items were easily distinguishable from the background. Note that the green prey items termed “cryptic” were actually cryptic against the background in the detectability experiments, but not in the acceptability trials. In the latter, “cryptic” refers to “cryptic under natural circumstances”, or “not warningly coloured”.

### Study species and the artificial prey

Great tits (*Parus major* L.) were used as predators in the aviary experiments. Great tits are common natural enemies of herbivorous insect larvae in Palaearctic temperate forests. The birds were used in experiments with the permissions from Central Finland Regional Environment Centre, the Ethical Committee of the University of Jyväskylä, and the Estonian Ministry of the Environment. The birds were captured singly in cage traps with commercial bird food as bait. In captivity, they were kept in individual cages for up to a month and provided with bird food containing fat and seeds, and fresh water ad libitum. Prior to the experiment, they were food deprived for about 2 h to increase their motivation to feed. Each bird was used only once, and released to the site of capture after the experiment.

In both detectability and acceptability experiments, we used artificial prey designed to imitate Lepidopteran larvae. However, the two experiments set different requirements to the design chosen. In the *detectability* experiments, it was necessary that all prey items had the same nutritive value, to prevent any motivational biases. Therefore, we used defrosted mealworms (darkling beetle larvae, *Tenebrio molitor* L.) of an approximately constant size (ca. 0.8 cm) glued under differently sized and coloured stripes of paper. Since the paper stripes were bended over the mealworms, the “larvae” had a three-dimensional shape, rather than being just flat images on the background. The three-dimensionality was considered to be important in

determining the detectability trends, as the shadows and profile views may well contribute to birds' searching efficiency. The paper stripes of four sizes ( $2 \times 0.4 \text{ cm}^2$ ,  $3 \times 0.5 \text{ cm}^2$ ,  $4 \times 0.65 \text{ cm}^2$  and  $5 \times 0.8 \text{ cm}^2$ ) were coloured either cryptically (green) or conspicuously (black with yellow dots, representing the typical warning colouration in insects), using non-toxic, non-smelling water based colours. The size of the yellow dots was proportional to the size of the artificial larvae, so that larger larvae also had a larger colour pattern. The colour of the cryptic larvae was selected to be close to the experimental backgrounds used. It was spectrophotometrically confirmed that the paint we used for colouring the cryptic larvae, and also the smooth background in *detectability experiment I*, had similar spectral composition to that of the plant leaves used in *detectability experiment II*.

In the *acceptability* experiment, it was necessary for the prey items to look reasonably natural (since the birds were not trained to eat them), and also for the prey size to reflect its nutritive value. For these reasons, we used edible pastry cylinders as prey items, consisting of lard and flour (Church et al. 1997). The artificial larvae were coloured with green food colour, or black and yellow non-toxic finger-paints, respectively. The sizes and colour patterns were matched with those used in the detectability experiments. The conspicuous "larvae" had black bristles, imitating the aposematic caterpillars of *Orgyia antiqua* (Lepidoptera: Lymantriidae). The colours of the cryptic "larvae" were tested for UV reflection to confirm their non-conspicuous nature.

## Detectability experiment

### *Predator training*

For detectability trials, we used birds caught at Konnevesi Research Station in Central Finland during February and March 2003. To break the innate (Schuler and Hesse 1985) or previously learned (Lindström et al. 1999a) avoidance of aposematic prey, as well as the possible neophobic reaction to the artificial prey items (Marples et al. 2005), each bird was trained to find mealworms attached under  $4 \times 0.65 \text{ cm}^2$  paper stripes of two different colours (the artificial larvae described above). The training consisted of four green and four black–yellow "larvae" offered to each bird simultaneously. The training was considered to be complete when the bird had found and consumed all eight mealworms. To confirm the efficiency of training, ten birds of the *detectability experiment II* were tested for colour preference after completing the training and before conducting the experiment. Five pairs of artificial larvae (one green and one black–yellow) were offered sequentially to each bird, and the time to attack the items of either colour was compared. No significant difference was found in the attacking time of green vs. black–yellow paper larvae (Wilcoxon matched pairs test:  $n = 10$ ,  $T = 18.5$ ,  $P = 0.36$ ). It can be concluded therefore that any possible initial preferences for particular colours had been effectively removed.

### *Detectability experiment I: the simple environment*

In this experiment, we asked how prey size and colour combine in their effect on the detecting efficiency by birds in a simple, uncomplex environment. The impact of size on detectability of different prey items was measured in a  $3.9 \times 3.5 \times 2.3$  (height)  $\text{m}^3$

aviary. The aviary floor was covered with green painted timber to form an experimental arena of  $3.6 \times 3.2 \text{ m}^2$ . On the green arena, four green and four black–yellow artificial larvae of different sizes (see the [Study species and artificial prey](#) section) were glued in random sites. To increase the crypsis, differently sized protrusive stripes of green colour resembling the larva imitations were painted to the surface. Both the stripes and the background were coloured with the same paint as the cryptic larvae. All of the 21 birds used had passed the training as described above.

During the experiment, each bird was allowed to seek food for 20 min, or until it had found all eight food items. If it had not found at least 50% of the items in 20 min, the experiment was terminated, and the particular replicate was excluded from the analyses. The time spent searching was measured from the moment when the bird started looking for food on the arena. The absolute, and ranked time to finding each item were recorded. The first item to be found was assigned rank value 1, and the last item found received rank value 8. Ranking was performed to standardize the time values within and between trials, thereby reducing the error variance caused by the high variation in the searching times of individual birds. The simultaneous choice set-up is effective for testing relative differences in the detectability of different prey types.

The differences in overall “mortality” between the artificial larvae of different colours and sizes were analysed by logistic regression. The dependence of the rank and time of being found on colour and size was analysed with type III repeated measures ANOVA (SAS PROC MIXED, Littell et al. 2002), size being treated as a continuous variable. The repeated design accounted for several measurements on a single bird. “Size” was standardized by subtracting the mean size, so that the main effect of “colour” could be interpreted as applicable to an average-sized larva in the resulting heterogeneous slopes model (Littell et al. 2002). The values of “time” were logarithmically transformed, to meet the requirement of normal distribution of residuals. Additionally, for the purpose of better visualisation, the size-dependence of detection rate was analysed separately for each colour type by repeated measures linear regression (SAS PROC MIXED), discarding the few larvae that were not found.

An additional control experiment was conducted to test for the possibility that the size-dependence detected in conspicuous larvae could have been caused by a preference bias of the birds, instead of different detectability. This could have occurred because the smooth green background may have allowed the birds to see several conspicuously coloured larvae at the same time. This was tested on 12 previously trained birds before they were used in the experiment, by offering 4 differently sized conspicuous larvae simultaneously to each of them, and measuring the time to attacking the larvae. The position of the differently sized larvae on the feeding tray was randomised; the results were analysed by type III repeated measures ANOVA.

### *Detectability experiment II: the complex environment*

The efficiency of finding hidden prey depends on the texture or complexity of the background (Endler 1978; Merilaita et al. 2001), which varies in nature. Therefore, the detectability experiment was repeated using a more complex background. Previously trained 37 great tits, one at a time, were allowed to seek for differently sized artificial caterpillars from potted plants (*Philodendron scandens* Baumfreund) in the

aviary. Sixteen potted plants (with up to 80 cm long repent shoots) were placed on the floor in four rows at a roughly constant distance (ca 75 cm) from each other. The four different sizes of both cryptic and conspicuous artificial larvae were glued to randomly selected plants, one per plant. Each larva was placed on the dorsal midrib of a randomly selected leaf on its plant. During the experiment, each bird was allowed to search for the hidden larvae for 30 min, or until it had found all eight larvae. The data were recorded and the results were analysed as in *detectability experiment I*.

### Acceptability experiment

The acceptability of differently sized and coloured artificial caterpillars was tested in cage experiments. The trials were carried out in Estonia, using 19 great tits caught in the town of Tartu during the winter of 2002, and 89 at Kabli Bird Station during the fall migration of 2003. The birds were trained to feed in individual cages (ca  $80 \times 80 \times 80 \text{ cm}^3$ ). During the experiment, each bird was offered four pastry caterpillars of different sizes, one at a time in a random order. Half of the birds received only cryptic, and the rest only conspicuous larvae. For both colours, all possible sequences of the four sizes were used with equal frequency to avoid imbalance in exposure orders. Larvae of both colours were clearly visible on the feeding tray, implying that none of them were actually cryptic. Each larva was offered to the bird together with a live mealworm; eating the mealworm indicated that the bird was motivated to feed. It was recorded if the bird did attack the larva in 10 min after eating the mealworm; the recorded “acceptability” constituted thus a binary variable (attack/no attack). If, however, the bird did not take either food item in 30 min, the experiment was postponed until the following day.

We used type III repeated measures logistic regression (GLIMMIX macro for SAS, Littell et al. 1996) to analyse the effects of size (standardised and treated as a continuous variable) and colour on the probability of accepting the pastry caterpillar. The repeated design accounted for several measurements on a single bird. Study site and presentation order of different sizes (*rank*) were included in the analysis as blocking factors.

## Results

### Detectability experiment I: the simple environment

The birds managed to find 95% of the 168 artificial larvae exposed on the green background. The conspicuous larvae were more likely to be found ( $n = 168$ ,  $\text{Chi-square}_{(1)} = 16.0$ ,  $P < 0.0001$ ), but size did not have an effect on the probability of finding the artificial larvae in the cryptic group: ( $n = 84$ ,  $\text{Chi-square}_{(1)} = 0.02$ ,  $P = 0.88$ ). No larvae remained undetected in the conspicuous group.

Conspicuous larvae were found faster than the cryptic ones (Table 1; Fig. 1a). There was also a significant interaction between size and colour in determining the order of detecting each food item (Table 1; Fig. 1a). This implies that the size-dependence of detectability differed between colours, with the conspicuous group experiencing a positively size-dependent detection order ( $n = 21$ ,  $F_{(1/62)} = 7.31$ ,

$P = 0.008$ ), while there was, quite unexpectedly, no size-dependence in the cryptic group ( $n = 21$ ,  $F_{(1/62)} = 2.47$ ,  $P = 0.12$ ). The pattern did not qualitatively differ with *time to detection* as the response variable (Table 1; Fig. 1c).

The additional control experiment revealed no significant size preference in conspicuous prey items ( $F_{(3/33)} = 0.53$ ,  $P = 0.66$ ). This shows that all initial preferences for prey size were successfully removed. We can therefore conclude that the trends found in the experiment were, indeed, derived from the detectability differences between sizes, not from the preferences of birds.

### Detectability experiment II: the complex environment

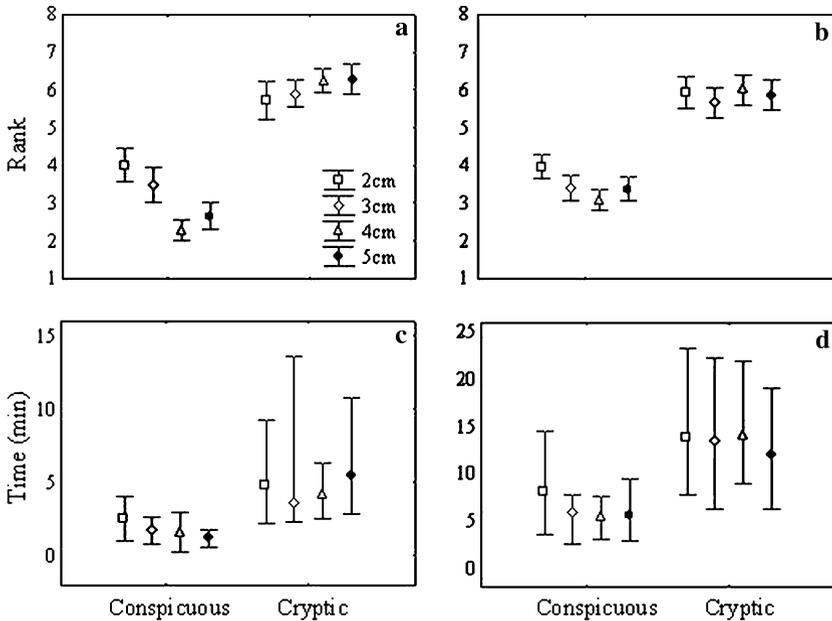
The birds managed to find 90% of the 296 hidden larvae, although it took ca 2.7 times longer on average to find them from the complex substrate as opposed to the smooth background. The variation in searching times was higher in this experiment (Fig. 1), possibly accounting for the average searching times being longer. Similarly with *detectability experiment I*, the conspicuous larvae were found with higher probability ( $n = 296$ ,  $Chi-square_{(1)} = 21.5$ ,  $P < 0.0001$ ). Size had no effect on the probability of being found for the cryptic larvae: ( $n = 148$ ,  $Chi-square_{(1)} = 20.1$ ,  $P = 0.77$ ). Too few conspicuous larvae remained undetected for a meaningful analysis.

The time of finding the larvae from plants depended on colour: conspicuous larvae were detected faster than cryptic ones (Table 1; Fig. 1b). Unlike in the

**Table 1** Repeated measures ANOVA results for the ranked and absolute time to being detected by birds from smooth and complex backgrounds

Effect	SS <sup>a</sup>	Num <i>d.f.</i>	Den <i>d.f.</i>	<i>F</i>	<i>P</i>
Ranked time					
<i>Smooth background</i>					
Colour	360.2	1	20	95.6	<0.0001
Size	5.19	1	144	1.38	0.24
Colour × size	27.5	1	144	7.30	0.0077
Error	548.2				
<i>Complex background</i>					
Colour	214.33	1	34	68.79	<0.0001
Size	1.27	1	225	0.65	0.41
Colour × size	4.05	1	225	0.68	0.38
Error	1045.03				
Absolute time					
<i>Smooth background</i>					
Colour	27.8	1	19	43.7	<0.0001
Size	0.55	1	133	0.98	0.32
Colour × size	3.65	1	133	5.74	0.018
Error	146.9				
<i>Complex background</i>					
Colour	13.67	1	34	37.25	<0.0001
Size	0.65	1	225	1.14	0.29
Colour × size	0.43	1	225	2.04	0.16
Error	117.35				

<sup>a</sup> As the MIXED procedure of SAS does not calculate sums of squares for repeated design, the SS were estimated using SAS PROC GLM



**Fig. 1** (a) Ranked time (mean  $\pm$  SE) to detecting artificial larvae from a smooth background or (b) from potted plants, as dependent on their size; (c), (d) absolute time elapsed until detecting the larvae (median & quartiles; the few larvae that remained undetected are excluded). In both backgrounds, the conspicuous larvae were found significantly faster than the cryptic ones; (positive) size-dependence was present only in the conspicuous group (see Table 1 for statistics)

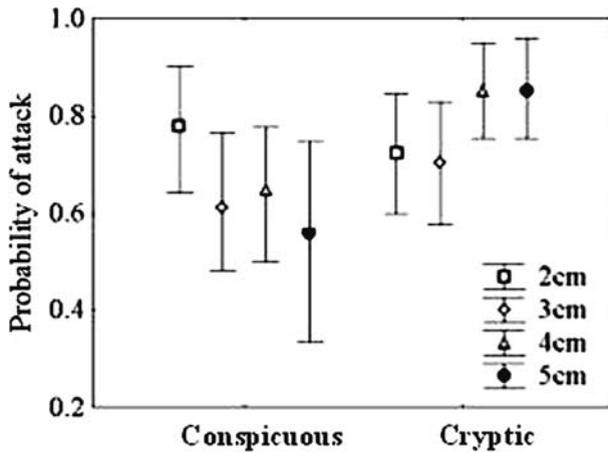
previous experiment, there was no size-dependence in the detection rate of either conspicuous ( $n = 37$ ,  $F_{(1/107)} = 1.48$ ,  $P = 0.23$ ), or cryptic larvae ( $n = 37$ ,  $F_{(1/84)} = 0.04$ ,  $P = 0.84$ ). Consistently, the interaction between size and colour was not significant in this experiment (Table 1). These results remained unchanged when analysing the absolute time needed to find each larva (Table 1, Fig. 1d).

### Acceptability experiment

Great tits attacked the pastry larvae of both colours (Fig. 2), although cryptic larvae were handled more readily than the aposematic ones (Table 2). This affirms the natural (innate or learned) preference for non-conspicuous prey in great tits. There was a strong interaction of colour and size in determining the probability of the birds to attack the prey items (Table 2). Large aposematic prey appeared to be unattractive to birds, whereas large cryptic prey was the most attractive (Fig. 2).

### Discussion

The results of our experiments show that body size does affect bird predation rates for both cryptic and conspicuous prey. The strength and direction of these effects, however, differed between the colour types. The conspicuously coloured larvae triggered the expected size-dependent response from birds: large artificial larvae



**Fig. 2** The probability of great tits to attack differently sized and coloured artificial larvae (mean; 95% confidence limits). The cryptic larvae were attacked significantly more often than the conspicuous ones. Birds avoided larger conspicuous prey, but preferred larger cryptic prey (see the text and Table 2 for statistics)

**Table 2** Results of the repeated measures logistic regression for the probability of a larva being attacked in the acceptability experiment

Effect	Num <i>d.f.</i>	Den <i>d.f.</i>	<i>F</i>	<i>P</i>
Rank	1	318	33.6	<0.0001
Site	1	105	3.12	0.08
Colour	1	105	8.1	0.0053
Size	1	318	0.08	0.78
Colour × size	1	318	17.4	<0.0001

“Rank” refers to the order in which a particular larva was presented to the bird

were more easily found, but treated with more caution, than small ones. This confirms an often-suggested trade-off in the evolution of conspicuous colouration: by increasing their warning effect, the conspicuous individuals also increase their risk of being detected and consumed by naïve predators (Endler 1988; Gamberale and Tullberg 1996; Lindström et al. 1999a).

In contrast, the results with cryptic larvae were rather unexpected: no correlation was found between body size and the risk of being detected. Birds attacked the larger cryptic prey slightly more readily, though. Our results suggest that even if there is a positively size-dependent predation risk for cryptic larvae, it is not likely to be strong enough to form the single factor able to counterbalance the remarkable fecundity advantage of large female size. This conclusion should hold, as a minimum, for capital breeding moths (i.e. relying on resources derived during larval period, Tammaru and Haukioja 1996), which display a strong dependence of fecundity on body size (Honěk 1993; Tammaru et al. 1996, 2002). Our argument is based on a simple life-history model, which will be formulated below.

Let us estimate costs and benefits of attaining large size in a typical capital breeding moth like *Orgyia*. The ratio of body lengths in successive larval instars corresponds closely to those between our 3 and 5 cm long models (Esperk and

Tammaru 2004). We can thus formulate the question in terms of a cost–benefit analysis of growing through an additional larval instar, i.e. to ask under which conditions it would pay off to grow to 5 cm instead of pupating at 3 cm. Assuming that fecundity is proportional to adult weight (Tammaru et al. 2002), the relative fitness benefit of growing through the additional instar is equal to the third power of the relative increase in the length, i.e. an adult formed from a 5 cm long larva is expected to be  $(5/3)^3 = 4.6$  times more fecund, as compared to a conspecific pupating at the length of 3 cm. To (over)compensate for such a fecundity advantage, i.e. to make adding an extra instar unprofitable, the survival rate through the extra instar should be lower than  $1/4.6 = 0.22$ . Assuming that going through an instar takes 7 days, a value typical for Lepidoptera, daily survival should remain below  $0.22^{1/7} = 0.8$ . This implies that we must assume at least a 20% daily mortality among large (3–5 cm) *Orgyia* larvae, to be able to explain the evolutionary stability of body sizes.

An analogous, empirically based (Varley 1973; Tammaru et al. 2002) calculation shows, however, that the daily mortality rate in the earlier instars cannot exceed 10%/day: otherwise, self-replacement of the population (2 adult recruits from 400 eggs laid by a female) would not be possible. The assumption of mortality rate of 10%/day representing the maximal sustainable value for folivorous insects is also well supported empirically (Cornell and Hawkins 1995, and references therein). In concert, these calculations imply that, if the size-dependence of bird caused mortality were the sole factor resisting the fecundity advantage, we should expect a twofold increase in mortality risk (i.e. from 10 to 20%) with larvae growing from 3 to 5 cm in length. Size-dependent averages of mortality rates found in our study, and confidence levels to them (Figs. 1, 2), safely allow to exclude effects of this magnitude for cryptic larvae.

The weakness of size-dependence in both detectability and acceptability of cryptic larvae would thus considerably impair the potential of bird predation as an agent behind size-dependent mortality. The notion that the discovered trends could be fairly general is supported by the results on the detectability of cryptic prey being consistent in the two experimental environments differing in complexity. However, naturally, it would be desirable to repeat this kind of study with different bird species.

In contrast, in conspicuous species, size dependent predation can play a number of different roles in affecting the optimum for body size. This is because both detectability and acceptability of the conspicuous larvae showed strong patterns of body size dependence. In particular, our results (Figs. 1, 2) allow to conclude that, unlike in cryptic larvae, the potentially crucial twofold (see above) size-dependent effects are well realistic for both detectability and acceptability. However, the strong size-dependence of detectability was only found in the experiment with a simple background. This can be explained by the necessarily more important role of random environmental effects in the complex background setting, which is therefore not as effective to test the effect of size per se. On the other hand, importantly, these results support the view that the effect of predation as a selective factor on the appearance of the prey is strongly environment-specific (see discussion in Mappes et al. 2005). For example, if the background is complex and the larvae tend to hide, their detectability is not likely to be strongly size dependent. However, in any case, our simple background setting should not be considered too unrealistic either. This is because conspicuously coloured larvae are, indeed, often found in exposed situations (e.g. Bernays and Singer 2002; our own observations).

As these two causal components of mortality risk—detectability and acceptability—show opposite patterns of dependence on body size, the net effect of size on mortality risk is likely to be strongly context-dependent, as well. In other words, both detectability and acceptability may depend on body size, but the way these two opposite effects combine under different conditions may well lead to both quantitative and qualitative differences in the correlation between body size and predation risk.

Most importantly, the outcome in the strength and direction of size dependence in conspicuous larvae must depend on the relative impacts of detectability and acceptability in determining mortality rates. The latter, in turn, may depend on the predator community and the prey species characters, e.g. repellent odours (Marples and Roper 1996; Rowe and Guilford 1996; Lindström et al. 2001) or movements (Myers and Smith 1978; Hunter 2000), as well as gregariousness (Gamberale and Tullberg 1996; Riipi et al. 2001) may affect the relative impact of acceptability. Moreover, the substrate inhabited by the prey species might alter the relative importance of detectability in determining the size-dependence of bird predation. Field experiments have to be performed to estimate the net effect of detectability and acceptability in natural conditions; such experiments are currently underway.

It should also be noted that in conspicuous species, the distance-dependence of detectability depends, in turn, considerably on the coarseness of their colour patterns. Interestingly, the pattern coarseness appears to become more important with increasing distance, while having minimal effect at close view (Tullberg et al. 2005). The stronger size-dependence of detectability in the conspicuous larvae can likely be related to this phenomenon. Since the pattern elements of our conspicuous baits were proportional to their body size (typical of Lepidopteran larvae), the smallest black–yellow baits were conspicuous only when viewed closely, appearing nearly cryptic at larger distances.

Notably, in the acceptability trials, the small conspicuous prey items were as likely to be attacked as the small cryptic ones, implying that warning colouration is not effective in small larvae. Similar trends have been described in poison frogs (Hagman and Forsman 2003) and vipers (Niskanen and Mappes 2005). Our acceptability experiments, however, cannot determine whether this was due to the small *body size*, or the small *pattern elements* of these larvae. There is evidence for both these components affecting birds' aversion for warningly coloured insects (Gamberale and Tullberg 1996; 1998; Forsman and Merilaita 1999), suggesting that these aspects combine in determining the acceptability of a conspicuous larva. Since the *detection risk* of small larvae was still considerably higher for the conspicuous individuals compared to the cryptic ones, this finding suggests that conspicuous colouration should be much less beneficial for small larvae as compared to crypticity. Possibly, this disadvantage can be reduced by gregarious life style that is, indeed, particularly common in aposematic species (Mappes and Alatalo 1997; Riipi et al. 2001).

Nevertheless, our results fail to fully support a prediction arising from the recognition that the repellence of conspicuous prey increases with its size (Gamberale and Tullberg 1996, 1998). In particular, it has been predicted that, since cryptic prey species do not have a warning signal balancing the disadvantage of higher detectability when being large, they profit less from growing large than do the conspicuous species. If so, one would expect cryptic species to evolve smaller body sizes on average, than do the conspicuous ones (Hagman and Forsman 2003). However, in an across-species comparison of Lepidoptera, recently performed by Nilsson and Forsman (2003), no such correlation was found. Partly, this result was due to the

tendency of conspicuous caterpillars to feed in aggregations more often than cryptic ones but further comparisons between solitary species similarly failed to show the expected differences.

Our results may shed some light to the causes of the lack of correlation between colour and body size. In particular, our results suggest that, with respect to bird predation, body size may be related to mortality risk in cryptic larvae less strongly than frequently thought. If so, the assumption of large body size being more costly to cryptic insects does not necessarily hold. At the same time, conspicuous species benefit, as predicted, from an increased body size via the enhanced warning signal (Forsman and Merilaita 1999; this study), but they also suffer a much sharper rise in detectability (see also Lindström et al. 1999b; Riipi et al. 2001), than do the cryptic species. Since conspicuous colouration does not provide a complete protection against all predators (Endler 1988; Endler and Mappes 2004; Mappes et al. 2005; this study), the increase in detectability forms a considerable cost of large body size in conspicuous species. Therefore, while the mechanisms leading to size-dependent bird predation are substantially different for these two colour types, our results leave the possibility open that its overall effect on them is not necessarily so different at all.

This study addressed bird predation as a possible driving force in the evolution of insect body size. Observably enough, other evolutionary forces must not be underestimated. It is way possible that other predators or parasitoids can inflict mortality with various degrees of size-dependence to the larvae (e.g. Weseloh 1990; Grushecky et al. 1998; Zaviezo and Mills 2000; Henry and Day 2001; Teder and Tammaru 2001; Cogni et al. 2002). Furthermore, various thermal constraints, as well as those related to flight physiology may be present in different species (e.g. Oliveira 2005). Additionally, we cannot ignore the phylogenetic constraints on body size, since, typically, closely related species of Lepidoptera appear to show only small differences in body size. However, there is no other way to understand the evolution of insect body size than to study the importance of each mechanism separately in an experimental setting. In this context, it has to be noted that, even if this study suggests that size-dependence in predation risk alone is unlikely to be the crucial factor in the evolution of body sizes at least in cryptic insects, it may well play an important role when acting in concert with other selective forces, and, perhaps, physiological constraints (e.g. factors determining the dependence of larval growth rates on body size).

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