

Effect of sex and bright coloration on survival and predator-induced wing damage in an aposematic lantern fly with startle display

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Abstract. 1. Aposematic coloration in prey promotes its survival by conspicuously advertising unpalatability to predators. Although classical examples of aposematic signals involve constant presentation of a signal at a distance, some animals suddenly display warning colours only when they are attacked.

2. Characteristics of body parts suddenly displayed, such as conspicuous coloration or eyespot pattern, may increase the survival of the prey by startling the predator, and/or by signalling unpalatability to the predators at the moment of attack.

3. The adaptive value of such colour patterns suddenly displayed by unpalatable prey has not been studied. We experimentally blackened the red patch in the conspicuous red–white–black hindwing pattern displayed by an unpalatable insect *Lycorma delicatula* White (Hemiptera: Fulgoridae) in response to predator's attack.

4. There was no evidence that the presence of the red patch increased prey survival over several weeks. We hypothesise that predators generalised from the red–white–black patches on the hindwings of unpalatable *L. delicatula* to any similar wing display as a signal of unpalatability. Because a higher proportion of males than females stay put at their resting sites, displaying their wings in response to repeated attacks by predators, wing damage was more frequent in males than in females.

5. To our knowledge, this is the first experimental test of an adaptive role of aposematic signals presented by unpalatable prey during sudden displays triggered by direct predatory attack.

Key words. Aposematism, hindwing coloration, mark recapture, startle display, survival.

Introduction

Insects evolved a variety of adaptations to avoid predation (Cott, 1940; Edmunds, 1974a; Evans & Schmidt, 1990). Some of these adaptations involve sudden movements of conspicuous body parts, which elicit startling response in the predator. Eyespots, novel patterns, and bright coloration on insect hindwings are potentially effective adaptations to avoid predators through such a 'startle effect' (Schlenoff, 1985; Ingalls, 1993; Vallin *et al.*, 2005). Displaying these parts may decrease the risk of predation when sudden nature of the

'fearful' display causes predator to hesitate and to be more careful in handling the prey (Edmunds, 1974a). The startle effect of such sudden displays has indeed been shown in palatable prey species (Blest, 1957; Sargent, 1973; Ruxton *et al.*, 2004; Ruxton, 2005; Vallin *et al.*, 2005; Langridge *et al.*, 2007; Edmunds, 2008; Langridge, 2009), and it does not assume any effect on predator's learning to avoid certain prey. However, a possible aposematic function (signalling unpalatability to predators that learn to avoid unpalatable prey) of sudden displays of conspicuous coloration in prey has been largely neglected (Guilford & Cuthill, 1989; Ruxton *et al.*, 2004; but see Gamberale-Stille *et al.*, 2009).

Aposematic coloration is another example of insect adaptations to avoid predation. It is well documented that bright, aposematic coloration, which indicates prey unpalatability,

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may increase prey survival because it aids predators in learning to avoid unpalatable prey (Poulton, 1890; Edmunds, 1974a; Alatalo & Mappes, 1996; Gamberale & Tullberg, 1996; Gamberale-Stille & Guilford, 2003; Ruxton *et al.*, 2004). Most studies on aposematic coloration have focused only on those prey species in which the bright signal is constantly displayed regardless of the presence or absence of the predatory threat. However, a number of unpalatable prey species remain cryptic unless they are attacked by a predator, to which they respond by displaying warning coloration. Although the role of this behaviour in helping unpalatable prey to survive the attacks of predators has been largely ignored, some hypotheses have been proposed to explain this phenomenon (Ruxton *et al.*, 2004). For example, if cryptic coloration of prey decreases the risk of being detected by the predators that are resistant to the chemical defence of the prey (i.e. unpalatability or distastefulness), then it is beneficial for the prey to be cryptic and to display only at the moment of attack. This strategy would be effective against the predators that are susceptible to the prey defence, because the predators will be able to learn to avoid the prey based on the displays at the moment of predator's approach/attack. Another hypothesis proposes that the surprise effect due to sudden, unexpected display contributes to faster learning by predators to avoid unpalatable prey (Guilford & Cuthill, 1989; Ruxton *et al.*, 2004). Regardless of the hypothetical mechanism, the suddenly displayed conspicuous patterns in unpalatable prey should contribute to prey survival, and experimental colour alteration (Blest, 1957) can help to determine the survival value of the displayed pattern.

One of the chemically defended insects that perform sudden conspicuous wing display (deimatic display/startle display) in response to a predator's attack is a lantern fly *Lycorma delicatula* White (Hemiptera: Fulgoridae; Fig. 1). Its cryptic forewings appear to be an adaptation to decrease detection by predators on the bark of host trees. In response to tactile stimuli, such as initial pecking or grabbing by birds, the insect either instantly jumps away or suddenly opens its hindwings that have conspicuous red–white–black markings

(Fig. 1a; Video S1). The insects' body contains chemical defence substance (Xue & Yuan, 1996), and avian predators vomit after consumption of *L. delicatula* (C.-K. Kang, S.-I. Lee & P. G. Jablonski, unpublished observations on Magpies, *Pica pica* L.). Therefore, the sudden wing opening display appears to have an aposematic function. In this study, we manipulated hindwing coloration of *L. delicatula* to test whether coloration, presented during sudden aposematic displays of wing opening, affects survival of *L. delicatula* in a natural population. Predators have to learn and re-learn the association between the bright coloration and unpalatability, and this process causes observable wing damage in many aposematically coloured unpalatable species (Smith, 1979). The damage indicates that the prey was rejected by the attacking predator after being handled or that the prey managed to escape. If the damage in prey indicates the severity of non-lethal handling by the predators (Carpenter, 1941; Edmunds, 1974b; Shapiro, 1974), then any association between the intensity of aposematic signal and wing damage can reflect the efficiency of the signal to deter severe handling by the predators during non-lethal attacks. Therefore, we were also interested whether there is an association between coloration, presented during sudden aposematic displays, and wing damage in the prey. Additionally, we determined if sex differences in antipredatory behaviour, and in abdomen coloration, may contribute to prey survival and wing damage.

Materials and methods

Capture–mark–recapture procedure

We used the capture–mark–recapture method to compare survival of two classes of *L. delicatula* with different, experimentally altered, hindwing coloration. For the capture–mark–recapture experiment to be successful in indicating survival levels, the animals should show substantial level of sedentary rather than dispersal tendencies. We do not have direct data on when and how *L. delicatula* changes dispersal tendencies.

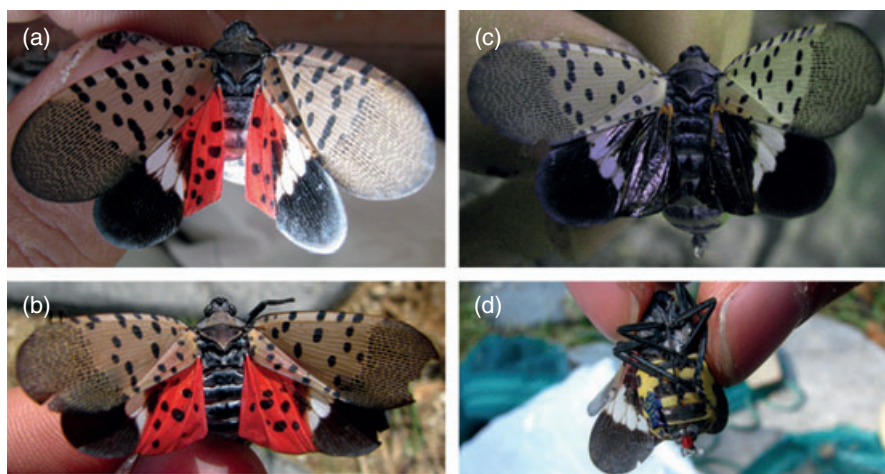


Fig. 1. Photographs of a female *Lycorma delicatula* with no wing damage (a), a male with wing damage (b), a black painted (treatment group) *L. delicatula* (c), and abdominal part of *L. delicatula* with blue marking on one side used to indicate wing damage (d).

However, typically in insects, dispersal, as well as noticeable sex differences in dispersal tendencies, occurs soon after emerging and before reproduction (Dingle, 1972; Harrison, 1980), and this corresponds to July/August in *L. delicatula*. Thus, we conducted the experiments in September and October, when the insects have already settled on the host trees. During this time the flight of the insects was only observed in response to human disturbance or predation attempts by birds (C.-K. Kang, S.-I. Lee & P. G. Jablonski, unpublished).

The study plot (about 120 × 120 m) was located in a mixed forest in Mt Soori, South Korea (37°21.95'N, 126°54.28'E). We collected every *L. delicatula* that we could catch with insect nets at the study site. We intensively searched most of the tree trunk of host trees in our study plot and collected them by hand or using an insect net. Using this method we collected most of *L. delicatula* on the lower parts of the tree trunks (up to about 3 m). We collected and marked 506 individuals (232 females and 274 males), similar numbers per day, over a period of 5 days: 22, 23, and 24 September, and on 1 and 2 October 2009. During the marking procedure, we avoided collecting from the same tree twice to prevent disturbance of the marked individuals.

We experimentally created two groups of insects with different coloration of the hindwings. For the treatment group (253 insects), the conspicuous red part of both hindwings was totally covered with a non-toxic black marker (MORRIS permanent marker) and the black part was untreated (Fig. 1c). For the control group (253 insects), the red part of each hindwing was untreated, but the black part was painted with the same black marker. Insects were assigned to either group in an alternating manner, which resulted in the balanced assignment of the two treatments on each marking day. Additionally, we applied non-toxic blue marker (MORRIS permanent marker) to the ventral surface of the abdomen in order to identify marked individuals during recapture. After marking, we held an insect by its body for at least 15 s. This caused an insect to keep its wings open, which facilitated drying out of the dye. Both, the black pigment of insect wings and the black coloration of the marker, similarly exhibited less than 3% of total reflectance from the white standard (measured with the Ocean Optics USB 2000 Portable Spectrophotometer, Dunedin, Florida) over the range between 300 and 700 nm, suggesting that our blackening treatment properly matched the natural black coloration. Marked insects were released on the same host tree where they were collected.

Some proportion of the *L. delicatula* had wing damage at the moment of capturing (Fig. 1b). We separately marked these insects by putting a different type of blue marking on the ventral surface of their abdomens (Fig. 1d) and did not include these individuals in the wing damage analysis. Occasionally we found insects with wing damage that apparently occurred during development (such as rolled up wings), and they were not included in the study. A few insects with severe wing damage, to the extent that they could not effectively display hindwing coloration to the predators, were also excluded from the study. We did not observe any noticeable effect of the wing treatment on the insects' ability to display, jump away, or fly away. Recapture procedure was conducted between 20 and

23 October 2009, which was 3–4 weeks after the initial capture. We used the same method as described above to collect insects and did not release marked individuals once they were caught. Although the individuals captured at the earliest date were exposed to potential predation for at least 10 more days than the individuals captured at the last capture date (assuming that they might have been recaptured at the first recapture date), the marking procedure resulted in a balanced sampling scheme, where the same number of control and treatment individuals were released on each capture date. Hence there was no difference between the control and treatment group in the duration of exposure to factors affecting survival (e.g. predators).

Comparing body length and yellow-striped area in each sex

In *L. delicatula*, sex difference in survival or the degree of wing damage could be related to differences between sexes in the body size or in the size of yellow coloration on the abdomen, which may serve as an additional warning signal. Therefore body lengths (tip of head to tip of genitalia) of 274 males and 232 females were measured. In order to compare males and females with respect to the surface area of the yellow stripes visible on the abdomen from above (the typical view by a predator), we randomly chose 10 individuals of each sex. Forewings and hindwings were removed and photo was taken from a dorsal view of each insect put on a paper with 1 × 1 cm grid (using a Canon PowerShot S5 IS). The surface area of the yellow colour in each picture was measured using ImageJ 1.43u (<http://rsbweb.nih.gov/ij/>). The difference between sexes in the size of the red patch was not considered because the presence of red patch did not affect survival or wing damage (see Results).

Sex difference in responses towards simulated predatory attacks

Sex difference in the display or jumping behaviour may lead to sex difference in the degree of wing damage and differential survival. Therefore, it is important to examine sex differences in antipredatory behaviour in response to predatory attacks. Experiments were conducted in October 2008 at Olympic Park, Seoul, South Korea. To standardise experimental conditions, *L. delicatula* were collected from the host trees (*Ailanthus altissima*) and released on the ground. After an insect settled on the ground in a non-displaying posture, an experimenter provided a tactile stimulus that mimics pecking by a predatory bird. Since *L. delicatula* is insensitive (in terms of releasing jump escape) to visual or vibratory stimuli, but it is sensitive to tactile stimuli (C.-K. Kang, S.-I. Lee & P. G. Jablonski, unpublished), we mimicked predatory attack by pecking the insects once with the tip of tweezers, observed their reaction and repeated this procedure once more. The antipredatory responses of the *L. delicatula* were categorised as two types: instantly jumping (without any preceding startle display) or staying put and displaying. A total of 40 females and 11 males were collected and tested.

Table 1. The explanatory variables, response variables, and model selection methods used for each GLMs analysis.

Response variables	Explanatory variables in full model	Model selection methods
Recapture rate (binary response)	Sex, treatment, presence of wing damage, their two-way interactions	Backward elimination based on both AIC and <i>P</i> -values
Presence of wing damage (binary response)	Sex, treatment, their interaction	Backward elimination based on both AIC and <i>P</i> -values

Statistical analysis

We used generalised linear models (GLMs) in order to identify the effect of sex, the treatment, and the presence of wing damage at initial capture on the probability of the insect being recaptured (binary variable: insect being recaptured or not). We also used GLMs to identify the effect of sex and the treatment on the presence of wing damage in the recaptured animals among those individuals that did not have wing damage at the initial capture (binary variable: wing damage present or absent). Binomial error distribution and logit link function were used. We conducted backward elimination starting from the full model containing sex, treatment, the presence of wing damage, and their two-way interactions using 'step' function in R (<http://www.r-project.org/>). We used two types of statistical modelling. First, we used the Akaike information criterion (AIC) to choose the most acceptable model (Quinn & Keough, 2002). Additionally, we also used the *P*-value as the criterion of significance of a given effect (Sokal & Rohlf, 1995). Some of the models chosen by the AIC contained all non-significant effects and the second approach removed the nonsignificant effects. The variables and model selection procedure are summarised in Table 1. Because body length and yellow stripe area did not match any of the distributions offered in the GLM analyses, we used Wilcoxon's rank sum test to compare between sexes. Continuity correction was applied to Wilcoxon's rank sum test and χ^2 test to compensate for small sample size and to obtain conservative results. All statistical analyses were conducted with software R 2.12.1.

Results

Recapture probability

Out of 506 individuals that were captured, 71 individuals (14%; 34 out of 253 individuals in the treatment group, and 37 out of 253 individuals in the control group) were recaptured. We did not find any effect of the experimental treatment (blackening of the hindwing red patch), sex, the presence or absence of wing damage at initial capture or any of the two-way interactions between these three factors, on the probability of insect recapture. In the best model based on AIC value, three explanatory variables remained with non-significant effects: treatment (GLMs, $\chi^2 = 0.16$, d.f. = 1, *P* = 0.69), presence of wing damage at initial capture (GLMs, $\chi^2 = 0.94$, d.f. = 1, *P* = 0.33), and their interaction (GLMs, $\chi^2 = 2.36$, d.f. = 1, *P* = 0.12). A similar result was found from an additional model selection based on *P*-values where all the explanatory variables, as they were not significant, were deleted. These

results suggest that presence of red patch in hindwings did not affect survival of the insects over the experimental period of 3–4 weeks.

Wing damage

At the stage of initial capture, more males had wing damage than females (185 out of 274 males vs. 124 out of 232 females; GLMs, $\chi^2 = 4.56$, d.f. = 1, *P* = 0.03, Fig. 2a). At the stage of recapture, wing damage was also found significantly more often in males than in females among the individuals that had no wing damage at the initial capture (*n* = 24; GLMs, $\chi^2 = 6.17$, d.f. = 1, *P* = 0.01, Fig. 2b). The effects of treatment and the interaction between sex and treatment on the wing damage were eliminated by model selection procedure (all *P* > 0.5), regardless of the model selection criteria (AIC or *P*-value).

Comparing body length and yellow-striped area in each sex

On average, females were 26% larger than males [19.9 ± 0.13 mm (mean \pm SE), *n* = 228 for females; 15.8 ± 0.06 mm, *n* = 269 for males; Wilcoxon's rank sum test with continuity correction, *W* = 59 462, *P* < 0.001]. Females had larger yellow-striped area than males on dorsal part of their abdomen

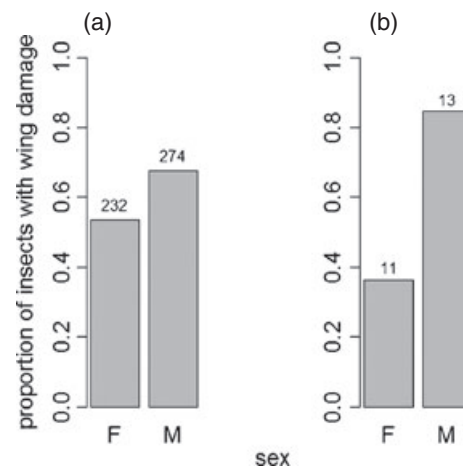


Fig. 2. Comparison of proportion of wing-damaged individuals between male and female *Lycorma delicatula* at the marking stage [(a) *P* = 0.03], and at the recapture stage for individuals who carried no wing damage at the marking stage [(b) *P* = 0.01]. The number above each bar represents the total sample size (i.e. the number that corresponds to 100%).

in terms of absolute area ($n = 20$, $W = 100$, $P < 0.001$, Fig. 3) or relative area (i.e. proportion of total abdominal surface area; $n = 20$, $W = 100$, $P < 0.001$).

Sex difference in responses towards simulated predatory attacks

There was no sex difference in the probability of jumping away in response to the first peck that imitates the very initial attack by the predator (χ^2 with continuity correction, $\chi^2 = 0.01$, d.f. = 1, $P = 0.94$; Fig. 4). However, in response to the second peck, imitating a continued attack of the predator, females jumped away significantly more often than males

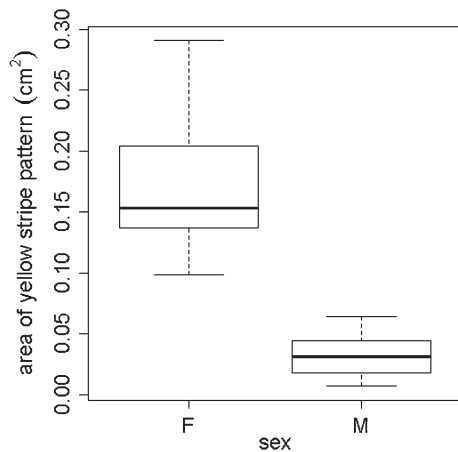


Fig. 3. Comparison of yellow-striped area between male and female *Lycorma delicatula* ($n = 10$ for each sex; $P < 0.001$). The thick black line indicates the median, the box indicates the first and third quartiles, the dotted line shows the minimum and maximum values.

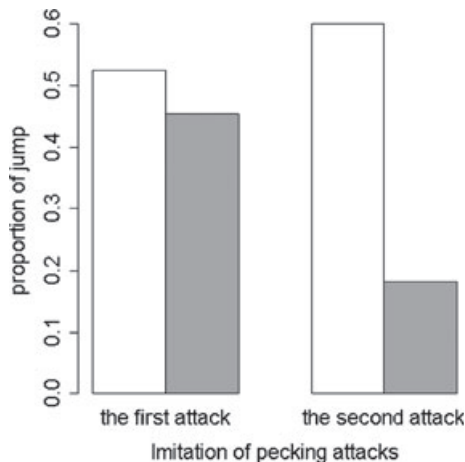


Fig. 4. Effect of sex (33 females and 11 males) on the response of *Lycorma delicatula* to tactile stimuli imitating pecks by predators. The bars (open bars for female, filled bars for male) represent the proportions (among males and females separately) of individuals who jumped in response to the first peck (difference between sexes, $P = 0.93$) and in response to the subsequent second peck ($P = 0.03$).

(χ^2 with continuity correction, $\chi^2 = 4.48$, d.f. = 1, $P = 0.03$; Fig. 4).

Evidence of predation on *Lycorma delicatula*

After marking the insects at the study site, we did not make attempts to detect predation on the marked insects. However, during experiments at the study site we found several dead *L. delicatula* under tree trunks. Their wings were still attached to the remains but abdominal and thorax parts were destroyed or missing. Based on the appearance of the dead insects, we suspected that they were predated by birds. Several species of insectivorous and omnivorous birds can attack *L. delicatula* in our study area: magpies (*Pica pica*), jays (*Garrulus glandarius* L.), bulbuls (*Ixos amaurotis* Temminck), great tits (*Parus major* L.), marsh tits (*Parus palustris* L.), varied tits (*Parus varius* Temminck & Schlegel), and rufous turtle dove (*Streptopelia orientalis* Latham). In summer 2007, one of the authors (PGJ) observed a great tit (*P. major*) and a jay (*G. glandarius*) attempting to attack *L. delicatula* at Ewha Womans University campus in Seoul (insects were pecked at, but not consumed).

Discussion

From classical studies on aposematism (Cott, 1940; Edmunds, 1974a; Guilford & Dawkins, 1991) we predicted that conspicuous traits in *L. delicatula* may facilitate learning by the predators to avoid this unpalatable prey. Additionally, we expected that the sudden display of bright colours may simply startle the predator contributing to the survival of the prey in accordance with the classical startle effect (Edmunds, 1974a; Vaughan, 1983). Since *L. delicatula* presents an aposematic signal, which is displayed in a startling manner, we predicted that *L. delicatula* enjoys the benefit of both strategies of aposematism and startling for deterring predators. Furthermore, one of the hypothetical explanations of sudden conspicuous displays by chemically defended animals proposes that the surprise effect due to sudden, unexpected display contributes to faster learning of prey avoidance by predators (Guilford & Cuthill, 1989; Ruxton *et al.*, 2004). However, in contrast to these predictions and what has been found in laboratory studies (Vaughan, 1983; Schlenoff, 1985; Ingalls, 1993), our results suggest no effect of conspicuous red coloration on survival of *L. delicatula* – an unpalatable prey that performs startle display.

Why haven't we observed the predicted effects? Possible, mutually non-exclusive, reasons include the following: (i) the predators are not startled by the wing display of *L. delicatula*; (ii) the startle effect might not have depended on the hindwings' red coloration (for example, the black and white wings may be as efficient as the black, white and red wings in their effect on the predators) or (iii) after 2 months of learning and memorising the association between prey unpalatability and sudden display of red–white–black patches on prey hindwings, the predators generalised to any conspicuous wing display, including white–black patches that lacked the red colour. Among these possibilities, we think that the third one

is more plausible than the others because, to our knowledge, no unpalatable insects of similar size performing similar wing displays are common at the study site. *Catocala* sp. moths in Korea bear a red–white–black hindwing pattern, albeit different than the pattern on *L. delicatula* hindwings (Shin, 2001). These moths also produce startle displays, but they are palatable, larger in size and far less common than *L. delicatula*, which occurs at high densities. We did not observe any *Catocala* moths disturbed by our activities during the capturing, marking, and recapturing at the study site. Thus, it is possible that predators may generalise and treat any wing display by an insect of the size similar to *L. delicatula* (regardless of the detailed hindwing pattern) as a signal specific for chemically defended prey. The experiments were conducted about 2 months after the emergence of adult *L. delicatula*, which approximately coincides with 2 months after fledging of young insectivorous birds from their nests (June and July). Hence, at the time of the experiments (October), even the young birds were no longer naive and might have learned to generalise the sudden wing display of *L. delicatula* as an indicator of the prey to avoid.

Based on our results, we cannot exclude the possibility that red coloration on the hindwings is an effective antipredatory adaptation only earlier in the season. For example, it is possible that sudden display of the red patch may enhance only the initial learning process of the naive predators to recognise unpalatable *L. delicatula*. Since aposematic coloration accelerates learning (Gittleman & Harvey, 1980; Roper & Wistow, 1986; Johnston & Burne, 2008) and delays forgetting (Speed, 2000) in predators, hindwing coloration of *L. delicatula* may reinforce the learning processes in naive young birds present in the habitat around the time when the adult insects emerge (June/July). Since none of the birds in October is likely to be naive, this ‘reinforcement of learning’ effect of hindwing coloration, which could have occurred earlier, may not be detected at this time any longer. *Lycorma delicatula* may cause digestive problems in birds, and we have seen wild birds rejecting *L. delicatula* after initial pecking. Therefore, we believe that the display of *L. delicatula* does not simply function to promote startle reaction in the predator, but also to signal unpalatability. If this were the case, then the two hypothetical reasons above (i and ii) could not have fully explained why *L. delicatula* have red hindwing patches. However, even in those cases when wing display does startle the predators (the first and the second possibilities explained above), it may cease to be effective if the predators quickly habituate to startle displays (Ruxton *et al.*, 2004). It is known that sometimes only naive predators are startled by the display (Vaughan, 1983; Schlenoff, 1985). Because even the young birds in the wild were no longer naive at the time of our experiments, we cannot exclude possible presence of habituation to the pure startle effect of the display (regardless of any association with unpalatability) by most predators present at our study site.

Although there was no sex difference in the probability of being recaptured, a higher proportion of males than females suffered wing damage regardless of the presence or absence of the red patch. The wing display in *L. delicatula* is activated in response to tactile, rather than visual, stimuli associated with

pecking or grabbing an insect by a predator (C.-K. Kang, H. M. Moon, S.-I. Lee & P. G. Jablonski, in preparation). Additionally, the shape of the missing wing surface often matched avian beak shape (C.-K. Kang, pers. obs.). Therefore, wing damage indicates bird attempt(s) at predatory attacks that did not lead to consumption of an insect. One can predict that wing damage occurs mostly in individuals who have a low tendency to jump in response to the predatory attacks, and therefore are subsequently pecked more times and handled more (at least by those predators who are not immediately deterred by the wing display) before the predator abandons them (due to aposematism). Because females have higher tendency to escape by jump than males in response to repeated pecking (Fig. 4), they are less likely to be handled by the predators, which may contribute to less wing damage in females than in males. Additionally, because females have larger yellow patches on their abdomen, which are visible to the predator during handling of the displaying prey, they may trigger predators’ avoidance sooner than males do owing to stronger intensity of this possibly aposematic signal (Johnston & Burne, 2008; Aronsson & Gamberale-Stille, 2009). This would also contribute to less wing damage. Although nothing is known about the sex difference in the content of the defensive chemical (Xue & Yuan, 1996) in the body of *L. delicatula*, we cannot exclude the possibility that females may be chemically better defended than males. If predators, while handling the prey, taste-detected such a chemical defence (Skelhorn & Rowe, 2006a,b, 2007, 2010) earlier in females than in males, then less wing damage would have been observed in females than in males. Some or all of these effects may be sufficiently strong to counterbalance the hypothetical higher initial attack rates on females owing to female’s larger body size and more noticeable marking.

The two alternative antipredator strategies of *L. delicatula* (staying put with startle and jumping away without startle) cause different types of costs. Staying put with startle is energetically cheap but bears a risk of predation because insect survival depends on predator’s experience and status (e.g. hunger). Jumping away without performing the startle display is beneficial when not followed by the predator, but includes energetic costs such as direct cost of muscle use or indirect cost of loss of feeding time by the prey (Ydenberg & Dill, 1986). At the time of our experiments, females *L. delicatula* were getting ready to oviposit. If a female dies before oviposition she does not leave offspring (her fitness is zero). This may explain why females jumped away more often than the males did. Males, on the other hand, have probably already mated many times, depositing their sperm in the bodies of the females. Therefore, we hypothesise, that males can risk being attacked and harmed as a consequence of staying put rather than jumping away.

In summary, the probability of being recaptured did not depend on the presence or absence of the hindwing red patch in an aposematic insect *L. delicatula*, at least during the time of our experiments. Although this indicates that conspicuous hindwing coloration did not noticeably affect the predation risk, we hypothesised that this could be due to the learning and generalisation by the predators to avoid *L. delicatula*. Further

studies are desirable earlier in the season when many predators are naive and inexperienced. We hypothesise that the yellow stripe patterns on the abdomen could also be an aposematic signal that may contribute to less handling of females by the predators during non-lethal attacks.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

10.1111/j.1365-2311.2011.01319.x

Video S1. Deimatic display of *Lycorma delicatula* in response to tactile stimulus.

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