From deception to frankness: Benefits of ontogenetic shift in the anti-predator strategy of alder moth *Acronicta alni* larvae

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Abstract Animals can avoid predation by masquerading as objects that are not food to their predators. Alder moth *Acronicta alni* larvae go through an impressive ontogenetic change from masquerade to highly conspicuous appearance: early larval stages resemble bird droppings but in the last instar the larval coloration changes into striking yellow-and-black stripes. We hypothesized that such a change may be driven by differential predation favoring dissimilar anti-predator strategies in different life stages. We show with a series of laboratory assays that larvae are distasteful to birds regardless of their developmental stage, suggesting that ontogenetic color change is not driven by the differential chemical defense. Birds showed higher variance in hesitation toward conspicuous prey; some individuals hesitated long time before attacking whereas all birds attacked instantly masqueraded prey. We also found that the activity level of the larvae increased with age, which fits to the fact that larvae need to move from foliage to pupation sites. In the field by using artificial larvae resembling the two life-history stages we found predation risk to vary during the season: In early summer larger yellow-and-black larvae were attacked most, whereas later in the summer small 'bird-dropping-larvae' suffered the highest predation. We conclude that the ontogenetic switch from masquerading to aposematism is adaptive most likely because actively moving prey cannot mimic immotile objects and thus, aposematism during the active and vulnerable period when larvae are searching for pupation sites becomes beneficial [*Current Zoology* 60 (1): 114–122, 2014].

Keywords Aposematic, Masquerade, Predation, Defense, Warning signaling

Animals have evolved a range of strategies to avoid predation, and one of the most fascinating strategies is to masquerade. Masquerading animals are hard to recognize, because they resemble an inanimate object of no interest to the observer (predator or prey), such as a leaf, stone or a twig (Endler, 1981; Ruxton et al., 2004; Skelhorn et al., 2010a). For example, weedy sea dragons *Phyllopteryx eques* exhibit amazing resemblance to seaweeds that are not food to their predators. When floating slowly in the water, leafy appendages of the weedy sea dragon make it difficult to distinguish the animal from see weeds (Ruxton et al., 2004).

The efficacy of masquerading can be challenged if there is a need for active movement that is likely to reveal the deception (Skelhorn et al., 2010b; Cooper and Sherbrooke, 2012). For example, *Uropyia meticulodina* moths seemingly masquerade as curled, dead leaves with astonishing accuracy, but the deception appears to fail when the moths move and spread their wings for flight (MDFIDF, 2009). Masquerading may also be in conflict with the life-history of the animal: a need to

increase food consumption in some life stages may require more intense and active foraging behavior (Booth, 1990). Therefore, if an animal is forced to move because of its life-history requirements, an optimal solution could be to adopt another anti-predator strategy at this time. For example, if a masquerading animal is chemically defended, development to aposematism, whereby prey advertises its secondary defenses (e.g. chemicals) to potential predators with a warning signal (e.g. coloration) (Poulton, 1890) may be advantageous. Such ontogenetic switches in anti-predator strategies are seldom recorded and poorly understood (but see Grant, 2007).

Alder moth *Acronicta alni* larvae go through an impressive color change making the species a feasible target for the study of ontogenetic color chance. In early life stages the larvae seemingly resemble bird droppings, but when molting into the last instar their appearance changes into remarkably bright yellow and black stripes (Carter and Hargreaves, 1986) which at face value seem like a classic warning signal (Fig. 1). The adaptive func-
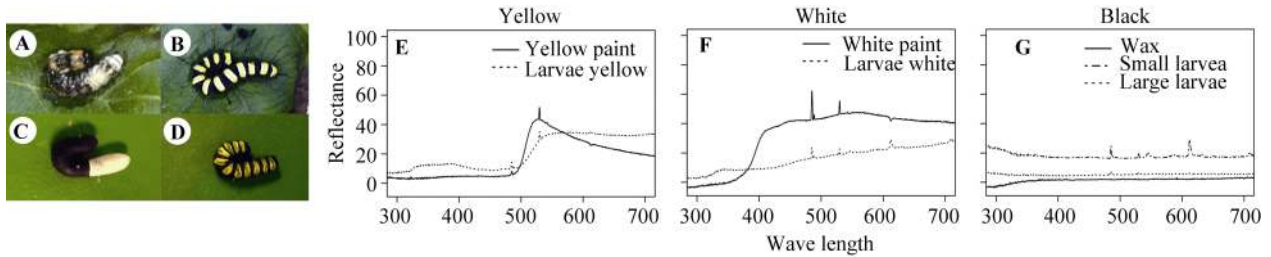
Fig. 1 Early masquerading (A) and late aposematic instar of the alder moth larvae (B) and corresponding artificial larvae (C, D) used in the field predation experiment
Reflectance curves for yellow stripes of late aposematic larvae and yellow paint used for artificial larvae (E), white part of early masquerading larvae and white paint (F) and black (G) parts of early and late instar larvae and black plasticine used for artificial larvae.

tion of such a color change is not yet understood, but the striking switch in appearance hints at the possibility that the first larval stages of alder moths utilize masquerade whereas the last larval stage use aposematism. Natural development of alder moth larvae requires feeding on leaves, mainly on alder (*Alnus sp.*) and birch (*Betula sp.*). The larvae typically pupate in late summer and overwinter inside decaying wood on the ground. The adult stage appears to exhibit cryptic coloration (Waring et al., 2009).

We propose that the ontogenetic color change during the larval stage may be driven by life-history constrains, and we consider three possible scenarios for its evolution. The first scenario is that early larval stages of the moth are not chemically defended (e.g. due to slow accumulation of defense chemicals) and their best option would be to avoid predators by masquerading as bird-droppings. Later instars however, may be able to accumulate sufficient amounts of secondary compounds from the host plant (Bowers, 1992; Dyer and Floyd, 1993) allowing aposematism to be used as a defensive strategy. The second scenario is that masquerading is a more effective anti-predator strategy compared to aposematism when the larvae are on their host plant. For pupation, however, the larvae have to move to find a suitable substrate. Additionally, as the larvae grow, food consumption increases meaning migration to the next leaf of host plant occurs more often, increasing larvae motility. This increased activity during the last instar may hamper the efficacy of the masquerade favoring warning signaling instead. The third scenario is that although the larvae are chemically defended, aposematism is not the best strategy throughout larval life because the size of the caterpillar and thereby the size of the warning signal can affect its efficacy (Gamberale and Tullberg, 1996; Forsman and Merilaita, 1999; Lindström et al., 1999; Mänd et al., 2007, Lindstedt et al., 2008). Small larvae may not be able to display sufficiently substantial signals to gain protection from pre-

dators making the masquerade a better strategy in the early instars.

To resolve which is the likeliest scenario, we assessed whether 1) different larval forms (masquerading and conspicuous) of the alder moth are chemically defended and differ in their palatability to predators, 2) birds fail to recognize the early instar larvae as food items and treat them differently to conspicuous larvae, 3) activity level of the larvae changes during their growth, and 4) whether coloration and size of the larvae affects their predation risk in the field. If larvae are chemically defended, birds should reject them as prey after initial sampling. Additionally, if birds find the early larval stages more acceptable than the last instar (when the possible effect of their appearance is excluded), it would suggest that differences in chemical defense drive the ontogenetic change. Alternatively, if both larval stages are unpalatable but the larvae activity level increases closer to pupation, predation is more likely to drive the ontogenetic switch. If birds hesitate to attack equally to both early and last instar larvae, it would indicate that they do not recognize the early larval stages as food and masquerading is therefore as effective in deterring predators as conspicuous coloration. Furthermore, if the absolute size of the warning signal limits its efficacy as an anti-predator strategy, we can expect birds to attack large warning-colored prey less willingly than small ones in the field.

1 Materials and Methods

1.1 Palatability test

To test whether the two forms of alder moth larvae (bird-dropping-like and yellow-black-striped, henceforth 'masquerading' and 'conspicuous', respectively), are unpalatable and differ in their level of chemical defense, we offered the birds four baits simultaneously, two made from each of the larvae (Fig. 1) and two control baits that we knew to be palatable and distasteful. We compared wild blue tits' *Cyanistes caeruleus* con-

sumption of each prey type and their behavioral reactions to the baits. To exclude the effects of coloration of the larvae in the palatability test, all larvae were smashed and dyed brown with food dye before mixing with water (one third of the volume of the final paste). Alder moth larvae used in the experiment were collected from Central Finland on 1st of July 2011 as egg clutches from the field and reared in room temperature on their natural diet *ad libitum* (*Alnus sp.*). The larvae were then stored in -20°C and thawed to make the baits before the experiment started. The control baits were made of frozen and thawed mealworm *Tenebrio molitor* larvae: a drop of 10 % quinine solution was added on top of the negative (i.e. unpalatable) controls to make them taste bitter to the birds, whereas a drop of water was added on top of the other baits. The larval paste was served to the birds in 2 ml Eppendorf tubes placed in small wells on a Styrofoam platform. The platform (7 × 7 cm) was attached on the floor of the 60 cm × 50 cm × 70 cm sized aviaries where the birds were housed. Before the trials the birds were trained to forage from the wells, and to ensure foraging motivation they were food-deprived for two hours before the experimental trials.

Six blue tits were trapped for the experiment from feeding sites at the Konnevesi research station in Central Finland (lat 63.61°, lon 26.35°). All birds were kept in captivity for a maximum of three days and were then released at the site where they were caught. For a detailed description of methods for catching and maintenance of the birds see Nokelainen et al. (2012).

Blue tits were only used in one trial. The birds were offered the paste of one larva from each group (i.e. conspicuous, masquerading, unpalatable mealworm and palatable mealworm) simultaneously. The trial duration was ten minutes starting from the moment the bird first experienced any of the four larval pastes. We recorded the total mass (mg) of what was consumed from each paste at the end of the trial and converted that into the proportion of total consumption. We also recorded the birds' behavioral responses after they sampled any larval paste: beak wiping and head shaking are known to indicate an unpleasant experience (e.g. Lyytinen et al., 1999). Proportions of pastes consumed were compared with Friedman's test because of deviation of the normal error distribution.

1.2   Acceptability of early and late instar larvae as prey

To test whether birds fail to recognize masquerading alder moth larvae as food items and whether they treat them differently to the conspicuous larvae we offered frozen and thawed caterpillars of both colorations to wild-caught great tits *Parus major* that were trapped and maintained similarly to the blue tits above (see also Nokelainen et al., 2012 for details). The larvae were offered to 18 great tits on green plates (d = 9 cm) in an experimental aviary (50 × 50 × 80 cm). The birds were randomly divided into two treatment groups where they encountered either a single aposematic or masquerading caterpillar. The birds were food-deprived for two hours prior to the trials to ensure their foraging motivation, and they were also habituated to the experimental aviary before starting the experimental trial. To confirm the birds' foraging motivation we offered them one mealworm larva before and after the alder moth larva. All the larvae were presented to the birds through a small hatch on the side of the experimental cage. We recorded how long a bird hesitated before attacking the larva after detection, and whether the bird consumed the larva and showed any behavioral response that indicated unpleasant experience (e.g. beak-wiping or head-shaking) (Lyytinen et al., 1999). Hesitation time (i.e. the time bird takes to attack after detecting the prey) was limited up to maximum of two minutes. If the bird refused to consume the caterpillar within two minutes after attacking and tasting, it was considered rejected.

The hesitation time was analyzed using Kruskal-Wallis rank sum test because the data were heteroscedastic and not normally distributed. As the mealworm larvae were used only to ensure that birds were motivated to forage, they were not included in the analysis. Frequencies of beak-wiping behavior after attacking the two types of alder moth larvae were tested with Chi squared test.

1.3   Activity level of alder moth larvae

To investigate whether the activity of alder moth larvae changes during their growth we individually followed the behavior of 25 caterpillars during their growth period. Larvae for the activity measurements were reared from eggs that were collected from a wild egg clutch from Central Finland in 2012. They were reared in petri dishes on natural food (*Alnus sp.*) that was offered *ab libitum*. The activity of 25 larvae in the last two instars were recorded every three days (25th, 28th and 31st of July), once a day. Measurements were taken before the larvae started to molt into the last instar and ending just before pupation. All the larvae did pupate between 31st of July and 2nd of August. Observations were conducted without disturbing larvae and were recorded as active (if moving) or non-active (if

stationary), and also as masquerading or conspicuous. As activity was recorded as a binary response (active or not) we used a generalized mixed effect model with binomial distribution to analyze the data. Activity was included as the response variable explained by date (of observation occasion from first to third) and coloration of the larva (masquerading or conspicuous). To take into account that activity was a repeated measure response (three readings per individual), larval ID was included as random factor.

1.4 Attack risk in the wild

To test whether the alder moth larvae of different colorations are attacked differently in the field, we exposed artificial caterpillars to natural predators. The artificial larvae were made of black, non-toxic plasticine (Caran D' Ache Modela 0259.009). We painted them with yellow and white acryl paint (Amsterdam Acrylic 268, 282) to resemble either the masquerading or the conspicuous stages (Fig. 1). As we were willing to avoid any possible effect of detectability, we made masquerading artificial larvae slightly more contrasting that they naturally are and selected the white paint with sufficiently similar values of the maximum reflectance compared to the yellow paint. (Fig. 1). As the caterpillar size and therefore signal size can affect the efficacy of a warning signal (Gamberale and Tullberg, 1996; Forsman and Merilaita, 1999; Lindström et al., 1999; Mänd et al., 2007; Lindstedt et al., 2008) we used a two by two full factorial set up with large (length 48 mm) and small (length 25 mm) caterpillars with both colorations (Fig. 1). Alder moth larvae can reach at least 25 mm in length before molting into the last conspicuous instar and up to 35 mm before pupation (personal observation; Carter and Hargreaves, 1986). Following previous methods (Hegna et al., 2013; Nokelainen et al., 2014) we controlled the visibility of the artificial larvae by presenting them on standard backgrounds that were crafted from cardboard (i.e. coaster plate, diameter = 10 cm) and painted green (Helmi, M384).

The artificial larvae were exposed to predators in a field experiment that took place between 25th May and 31st of July 2012 in two locations (Reisjärvi/Lestijärvi and Laukaa) in Central and Western Finland. Four of the transects were started on week 21 (25th May), five on week 25, one on week 26, two on week 28, two on week 29 and two on week 30 (31st of July). On each location we set up 8 transects (16 in total) that included ten specimens of each prey type in ten-meter intervals (640 in total). Minimum distance between transects was 1km. The standard backgrounds (see above) with the

prey were mounted on 30–50 cm tall stakes that were placed on visible spots at the shrub level enabling visually hunting avian predators to find them easily. The transects stood for five days and we checked the prey items daily replacing attacked or damaged larvae to keep the proportional hazards constant. Due to heavy rain checking was delayed for one day and the duration of the transect was extended from five to six days (nine transects were extended). Specimens with characteristic U- or V-shaped beak marks were recorded as 'attacked' because we were only interested in attacks by visually hunting predators, i.e. birds. We defined untouched individuals as 'survived'. Some of the larvae were removed from their position but were found nearby with beak marks, these were counted as attacked. The number of larvae that were removed did not differ between the treatments ($\chi^2 = 0.373$, $df = 3$, $P = 0.946$). Replacement larvae that were attacked consecutively (18 in total) were treated as independent attacks (result in total 658 prey items) because they were most likely attacked by different individual birds due the lack of reward gained by the initial attack (artificial preys were made from plasticine and paper). Results remained the same if only the first attacks were taken into account.

We used Chi square test to analyze whether attacks were distributed equally among the prey types. For a more elaborate examination of the data we used a generalized linear model with binomial distribution: fate of the artificial larvae (attacked or not) corrected by the time they were exposed to predation (duration before attack) was included as a response. Coloration (conspicuous or masquerading) and size of the artificial larvae (large or small) was included as factors and time point of season (starting week of each transect) as a continuous covariate. All, possible two and three way interactions of the exploratory variables were included in the model.

2 Results

2.1 Palatability test

Proportions of the consumed larval paste differed between the larval types (Friedman's $\chi^2 = 1.400$, $df = 3$, $P = 0.003$): blue tits consumed more paste of palatable mealworm larva than any other type (Table 1). However, we did not detect any differences between the consumption of the alder moth larval types (Table 1; Fig. 2), which suggest that both larval stages of the alder moth are unpalatable to birds. Five out of six birds shook their heads after tasting the unpalatable mealworm control, and two out of six reacted similarly after tasting the

paste made from conspicuous alder moth larvae, but we did not detect head-shaking behavior after the birds tasted good control paste or paste made of masquerading alder moth larvae.

Table 1 Wilcoxon signed rank test with Bonferroni adjusted significance levels for pairwise comparisons of proportions of larval pastes consumed by blue tits in the palatability test

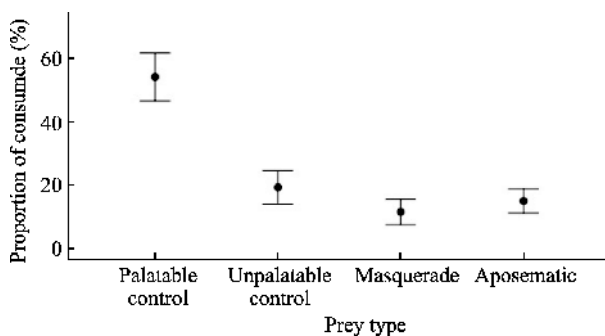| Comparison		Positive ranks	Sig.
palatable control	unpalatable control	21	0.031
	masquerading larvae	21	0.031
	aposematic larvae	21	0.031
unpalatable control	masquerading larvae	21	0.031
	aposematic larvae	13	0.688
masquerading larvae	aposematic larvae	7	0.563

Fig. 2 Proportions (mean±*SE*) of prey pastes that blue tits consumed in the palatability test

The effect of coloration was excluded by destroying larval form to homogenous paste of similar color.

2.2 Acceptability of early and late instar larvae as prey

Larval coloration (conspicuous vs. masquerading) had no effect on the hesitation time of great tits (Kruskal-Wallis $\chi^2 = 0.1314$, $df = 1$, $P = 0.717$) indicating that the birds found the masquerading caterpillars equally unattractive as the conspicuous larvae. However, the variance of hesitation times was larger for conspicuous larvae (Levene $t = 4.6878$, $P = 0.0458$, Fig. 3) suggesting that some individual birds (one juvenile and two adults) hesitated longer to attack conspicuous larvae. All nine birds readily attacked the masquerading caterpillar presented to them and only three birds (out of nine) hesitated for 10 or more seconds (10 to 19 sec.) before attacking the conspicuous larvae. All the prey items offered to the birds were attacked. Frequency of beak-wiping behavior did not differ between the groups that were presented with different larval types ($\chi^2 = 0.900$, $df = 1$, $P = 0.637$). Three of the nine birds that were

presented with aposematic caterpillars wiped their beaks after attacking or eating the specimen, whereas four of nine birds wiped their beaks after eating a masquerading larva. All birds tasted larvae but three birds discarded a conspicuous larva after attacking and one bird discarded a masquerading larva (non-significant difference; $\chi^2 = 1.286$, $df = 1$, $P = 0.576$). All birds consumed the offered mealworm within the time limit after the test caterpillar confirming that the birds did not reject the test prey because they were not hungry.

2.3 Activity level of alder moth larvae

Conspicuous larvae were more active than masquerading larvae. However, since coloration and age are correlated (ontogenetic switch happens only in one direction) and only age of larvae was significantly associated with activity of larvae suggesting that the increase in activity was due to aging rather than the switch in coloration (Table 2). However, it is important to notice that the shift in activity level of larvae seem to happen after they molt in the last conspicuous instar (Fig. 4).

2.4 Attack risk in the wild

From the 658 artificial prey items used, 79 (12%) were attacked. The four prey types were attacked equally often ($\chi^2 = 6.116$, $df = 3$, $P = 0.106$), however, with further examination we found a three-way interaction among larval size, coloration and season (Table 3).
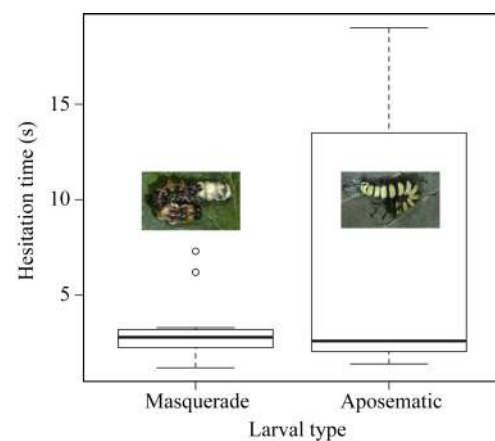

Fig. 3 Median hesitation times before great tits attacked masquerading and aposematic alder moth larvae

Table 2 Generalized mixed model to explain larval activity of alder moths during their development

Source	Estimate	Z	P
Intercept	-7.1204	-4.016	<0.0001
Age	3.3899	3.454	0.0006
Larval coloration	-2.6264	-1.356	0.1751

Activity (moving or not) was included as a response variable and larval ID as a random factor. Age represents observation occasion from first to third.
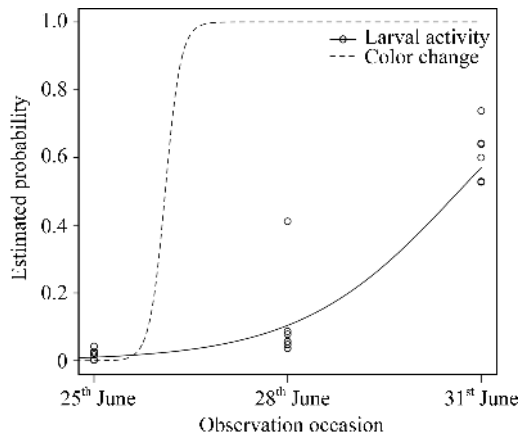
Fig. 4 Probability to detect alder moth larvae as active increased after their color change from masquerade to conspicuous during molting to last instar
Observation occasions 1, 2 and 3 reflect 25th, 28th and 31st of June respectively.

Table 3 Binomial GLM explaining predation risk / hour on differently colored artificial alder moth larvae (attacked or not/hour exposed to predation in the field ~time point of season*larval size*larval coloration)

Source	estimate	Z	P
intercept	-21.1347	-4.302	<0.0001
coloration	15.4720	2.992	0.0028
size	16.0953	3.063	0.0022
season	0.4978	2.918	0.0036
coloration*size	-13.8004	-2.411	0.0159
coloration*season	-0.5382	-2.959	0.0031
size*season	-0.5767	3.099	0.0019
coloration*size*season	0.4834	2.336	0.0195

Factor levels included in the intercept are masquerade coloration and small size.

Early in the season the risk of predation was at its highest for large conspicuous larvae and lowest for small masquerading larvae, but this attack pattern was reversed towards the end of July indicating that ontogenetic change in alder moth larvae is indeed beneficial. Lastly, large masquerading larvae survived relatively well throughout the season (Fig. 5) questioning whether the ontogenetic change of color brings any benefits to the alder moth larvae as an anti-predator strategy.

3 Discussion

Our results indicate that the impressive ontogenetic color change from masquerade to aposematism in the alder moth larvae is beneficial probably because the activity of larvae increases shortly before pupation and actively moving prey cannot mimic immotile object.
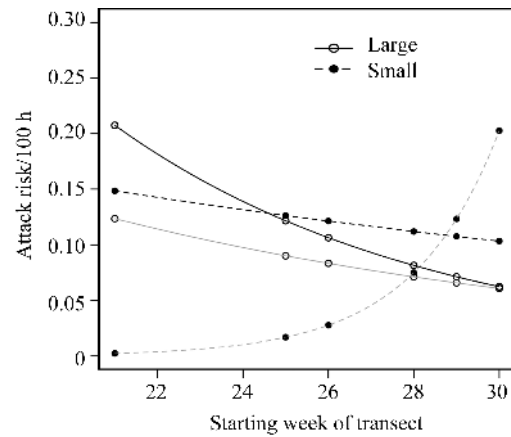

Fig. 5 Attack risk (attacks / 100 hours) of aposematic (black lines) and masquerading (grey lines) artificial caterpillars of small and large categories varied during the season
Field transects were set between 25th May (week 21) and 31st of July (week 30).

This seems the most probable scenario because in the field the last instar larvae need to move from the foliage to ground ready for pupation. Towards the end of the season, the predation on small masquerade larvae increased suggesting that predation pressure may favor an aposematic strategy at this time of the year.

We found that the alder moth larvae are distasteful to birds regardless of their developmental state. Herbivorous insects often sequester chemicals from their diet and use them for their own defense (e.g. Edmunds, 1974; Speed and Ruxton, 2007). It has been suggested that small larvae are not able to reach a level of chemical defense that would be sufficient to deter predators (Bowers, 1992; Dyer and Floyd, 1993). However, this does not seem to be the case with alder moth larvae, because blue tits did not find the last instar larvae more distasteful than earlier instars. Although we used frozen and thawed larvae in our experiments, which can affect the structure of some compounds (Rey, 1975), birds treated the larval paste as distasteful as the unpalatable control. Therefore, lack of secondary defensive compounds in young caterpillars cannot explain the ontogenetic color change of alder moth larvae.

In contrast to our expectations, great tits were surprisingly willing to attack both masquerading (i.e. bird-dropping-like) and aposematic larvae in the laboratory. All nine birds readily attacked the masquerading caterpillar presented to them and only three birds (out of nine) hesitated (up to 19 sec.) before attacking the conspicuous larvae suggesting that part of bird population seem to be unwilling to attack aposematic prey. It is likely that these birds, with extended hesitation times, when

confronted with the caterpillars in the field would be unlikely to attack. Future studies should aim to increase sample size and study, in more detail, what kind of individuals hesitate to attack aposematic prey. Importantly, our results indicate that birds can recognize 'masquerading' alder moth larvae as prey items, at least when they are taken out of their natural habitat and context. It is, however, possible that because the birds were motivated to search for food and trained to expect it on the tray, our assay underestimated the efficacy of both anti-predator strategies. Furthermore, acceptability of the prey can depend on how hungry the predator is (Barnett et al., 2007; Sandre et al., 2010). As we controlled the foraging motivation of the birds by restricting their access to food for two hours before the experimental trials, it is possible that they were too hungry and ready to attack and even consume distasteful prey without considerable hesitation (see also Sandre et al., 2010). On the other hand previous studies have used a two hours deprivation times, which currently is standard for great tits (e.g. Mänd et al., 2007; Ihalainen et al., 2008; Ihalainen et al., 2012). Great tits are bold and explorative (Exenerová et al., 2007), and it is possible that aposematic larvae do not appear overtly scary for them, but the increased variation in hesitation times towards aposematic larvae indicates some level of wariness. Unfortunately, we did not have sufficient amount of caterpillars to test whether birds would have stopped attacking the larvae in later encounters (i.e. generalization test), which would be expected because both larval forms were clearly unpalatable to them.

We found a clear increase in the activity of the alder moth larvae as they aged. This suggests that 'older' conspicuous larvae are more active compared to masqueraded young ones, thus selection has likely acted for change in the anti-predator strategy on the onset of the time in life-history that requires increased activity. This result is in concordance with findings by Grant (2007) who found that ontogenetic change of anti-predator strategy can be facilitated by increased opportunity costs of crypsis and behavioral conspicuousness. Masquerade as an anti-predator strategy is based on mimicking inanimate objects that are not attractive to potential predators (Endler, 1981; Ruxton et al., 2004; Skelhorn et al., 2010a). It has been suggested that the efficacy of masquerade is decreased in environments where the model objects are not present (Skelhorn and Ruxton, 2011), which could restrict habitat use of masquerading animals. However, it is unlikely that the lack of 'models' would be a limiting factor during summer time in

boreal forests. It is expected that movement reveals the deception of an animal that mimics a non-moving object similarly to how it may expose a cryptic animal to predation (Stevens et al., 2011).

Our predation experiment revealed that the likelihood of attack varied for larvae of different size and color throughout the season. This provides some support for the hypothesis that the ontogenetic change of alder moth larvae can indeed be beneficial, and that the phenomenon can be caused by changes in the structure of the predator community (Endler and Mappes, 2004; Valkonen et al., 2012; Nokelainen et al., 2014; Mappes et al. unpublished). Large aposematic larvae suffered high predation early in the season, while small masquerading larvae had a better chance of survival. In late July, attack rate was highest on small masquerading larvae whereas large aposematic larvae seemed to survive best. Intuitively, one could expect that experienced adult birds early in the season are more hesitant to attack aposematic larvae because they already know that warning-signaling prey are not profitable. However, it is possible that costs of increased detectability outweigh the benefits of conspicuous signaling if predators are hungry enough (Barnett et al., 2007; Remmel and Tammaru, 2009; Sandre et al., 2010; Barnett et al., 2012) for instance due to shortage of alternative prey. Alternatively, although not exclusively, birds might forget learned associations between signal and defense during long winter periods in northern areas thereby being required re-learn the association between warning signal and distastefulness annually. It is also important to note that fledgling birds are recruited into predator communities at approximately the same time as the predation pressure on small-bird-dropping masquerade larvae exceeded predation on other larval types. For young birds, the importance of learning to find profitable prey may out weigh the importance of learning to avoid unprofitable prey. Interestingly, large aposematic larvae were in danger early in the season when they do not naturally occur. This hints that conspicuousness is indeed a dangerous strategy when local predators have possibly forgot or have not learnt to avoid the signal, which may partly explain why selection has favored masquerade strategy in alder moths.

Attack risk for small aposematic larvae was rather similar during the season in comparison to large masquerade larvae (Fig. 5). Therefore, we did not find any evidence that small body size would constrain warning signal efficiency in alder moths. Interestingly, survival of large masquerading larvae was similar to that of large

aposematic ones late in the season bringing into question how the color change could be beneficial. However, it is important to bear in mind that we used non-motile artificial larvae in our experiment and thus could not test the possible interaction between coloration and movement.

Our study is the first attempt to investigate adaptiveness of ontogenetic color change in alder moths. We found that for alder moth caterpillars avoiding detection may be more beneficial in early life stages despite their chemical defense whereas aposematism becomes more beneficial when larvae need to move and cannot avoid detection. These first examinations of this fascinating phenomenon lays the ground for future work to test the interaction between behavior and coloration as well as life-history costs related to the ontogenetic color change in relation to potentially shifting structure of predator communities.

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