

Original Article

Mimicking multiple models: polyphenetic masqueraders gain additional benefits from crypsis

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Many prey organisms avoid predation by mimicking inanimate objects: a phenomenon known as masquerade. It is expected that masquerade will show a frequency-dependent advantage such that masquerading species benefit more from their appearance when they are rare in comparison with their models. In such circumstances, selection may favor the coexistence of different phenotypes (polyphenism or polymorphism). The American peppered moth caterpillar *Biston betularia cognataria* appears to show polyphenetic masquerade: caterpillars found on birch trees look like birch twigs; those on willow trees look like willow twigs. Here, we show in laboratory experiments that the caterpillar does benefit from masquerade and that polyphenism is key to this benefit: avian predators misclassified birch-fed larvae as birch twigs and willow-fed larvae as willow twigs. In a second experiment where the benefits of masquerade were excluded, we show that larvae are less likely to be attacked when located on the host species whose twigs they resemble than when found on an alternative species whose twigs they do not resemble; thus, the polyphenism provides antipredatory benefits through crypsis as well as through masquerade. This is the first time that a species has been demonstrated to have the capacity to benefit both from masquerade and from crypsis, and the first time, polyphenism has been demonstrated to benefit masquerade. *Key words:* *Biston betularia*, camouflage, detection, frequency dependence, peppered moth, predation. [*Behav Ecol* 22:60–65 (2011)]

Many prey organisms avoid predation by mimicking inanimate objects such as twigs, leaves, stones, and bird droppings: a phenomenon known as masquerade (Endler 1981; Allen and Cooper 1985; Skelhorn, Rowland, and Ruxton 2010). In a recent experiment, we demonstrated that predators misclassify masquerading prey as the inedible models that they appear to resemble (i.e., prey benefit from masquerade) rather than simply fail to detect them (which would be classed as crypsis). By manipulating the predators' previous experience of the putative model (a twig), but keeping their exposure to the masquerader (a caterpillar) the same, we were able to show that birds that had previous experience with twigs were slower to attack twig-mimicking caterpillars than either birds that had no experience with twigs or birds that had experience only with twigs whose appearance had been changed so that they no longer resembled the caterpillars (Skelhorn, Rowland, et al. 2010).

Because masquerading prey gain protection from predation by being mistaken for the object/species that they resemble (Skelhorn, Rowland, et al. 2010), it is expected that masquerade will show a frequency-dependent advantage such that masquerading species benefit more from their appearance when they are rare in comparison with their models (Skelhorn, Rowland, and Ruxton 2010). This is akin to the frequency-dependent benefits experienced by Batesian mimics of defended prey types (Ruxton et al. 2004). In both cases, the predator must try and differentiate between models

(the defended prey for mimicry or inedible objects for masquerade) and the mimic or masquerader. Time investment in careful examination of an individual becomes less economically attractive to the predator if it is more likely to be faced with a model. Conversely, as masqueraders become more common relative to their models, we can expect predators to be more willing to invest in careful inspection and so the benefits of masquerade to be weakened.

When the benefit of masquerade is frequency dependent, then selection may favor the coexistence of different phenotypes driven either by variation in environment (polyphenism) or genetic variation (polymorphism). Essentially, this within-population variation in appearance could reduce the costs associated with masquerading species becoming abundant relative to their models, if the population of masquerading individuals is spread over a number of different models. Examples of both polymorphisms and polyphenisms can be found in masquerading species. For example, the caterpillar *Nemoria arizonaria* mimics oak twigs when fed on oak leaves or oak catkins when fed on oak catkins (Greene 1989). Although it is unlikely that these caterpillars can change from one morph to another when their diet is changed, there are species in which visual appearance is plastic. The appearance of the American peppered moth caterpillar *Biston betularia cognataria* is influenced by the color of light in the feeding environment and changes in light color correspond with changes in appearance (Noor et al. 2008), thus allowing individuals to adapt to the background on which they find themselves. As a result, caterpillars found on birch trees *Betula nigra* bear a striking resemblance to birch twigs, and caterpillars found on weeping willow trees *Salix babylonica* bear a striking resemblance to willow twigs. Furthermore, moving caterpillars from one host plant to another results in individuals changing their visual appearance.

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Although it is widely believed that these polymorphisms/polyphenisms in masquerading species are adaptations to reduce the risk of predation (e.g., Noor et al. 2008 and references therein), there is no evidence to support this. Furthermore, whether any benefits associated with polymorphisms/polyphenisms are due to masquerade or crypsis is unclear. Although our previous experiment was designed to eliminate effects of crypsis (Skelhorn, Rowland, et al. 2010), masquerading prey might be expected to gain additional anti-predatory benefits from crypsis (being difficult to detect) when viewed in a natural situation. Consequently, different morphs could be misclassified as different twig species, and thus the benefits associated with polymorphisms/polyphenisms would be due to masquerade; and/or morphs could be more difficult to detect when found on their own host plant, and thus the benefits associated with polymorphisms/polyphenisms would be due to crypsis.

Here, we used an experimental system of domestic chicks foraging on polyphenic larvae of the American peppered moth *B. b. cognataria* to investigate how masquerading prey benefit from polyphenisms. Our first experiment asked whether different morphs are misclassified as different models and our second experiment asked whether masquerading prey can gain additional benefits from crypsis, and if so, whether morphs were more cryptic when found on their own host plant.

MATERIALS AND METHODS

Subjects and housing

One hundred female domestic chicks of the “brown shaver” strain (*Gallus gallus domesticus*) were purchased from a commercial hatchery on the day they hatched (68 were used in experiment 1, and 32 in experiment 2). They were housed in cages measuring 120 × 50 × 50 cm and were subject to a 14:10 h light:dark cycle using uncovered fluorescent lights with full daylight spectrum. The temperature of the laboratory was maintained at 25–28 °C using a room heater. Water was provided ad lib, as were chick starter crumbs except during training and experimenting when food deprivation was necessary. Chicks also received mealworms *Tenebrio molitor* twice a day in their home cages. All deprivation periods were in accordance with Home Office regulations and guidelines. At the end of the experiment, chicks were donated to free-range smallholdings.

Prey species

We used fourth instar larvae of the Peppered Moth *B. b. cognataria* as prey in our experiment. This species looks remarkably like the twigs of its host plants and is commonly believed to benefit from masquerade (Porter 1997). It is widespread across the northern hemisphere and feeds on a wide variety of deciduous trees (Porter 1997). The larvae demonstrate polyphenism: they look remarkably like birch twigs when fed on birch *Betula nigra* and remarkably like willow twigs when fed on weeping willow *S. babylonica* (see Figure 1 in Noor et al. 2008). The larvae used in the experiment where captive-bred specimens purchased from the online Lepidoptera suppliers “World Wide Butterflies” (www.wwb.co.uk/). They were reared in groups of 5 individuals, in clear plastic containers housed in a room lit by natural daylight between July and August of 2009. Half of the larvae were fed on freshly cut birch and half were fed on freshly cut weeping willow. This resulted in 2 visually distinct morphs; those fed on birch were brown and those fed on willow were green (We will refer to these as birch-fed and willow-fed larvae).

Training

On day 1 posthatch, chicks were left to acclimatize to the laboratory for 1 h, and the 48 experimental chicks were then trained to eat chick starter crumbs from the white laminated cardboard floor of an experimental arena. Two identical arenas were used, each consisting of a cage identical to the housing cages, with a section measuring 20 × 50 × 50 cm partitioned off using wire mesh to create a separate “buddy arena.” In all training and experimental trials, 2 chicks were placed in the buddy arena to reduce any potential distress from placing experimental chicks alone in the arena. These buddy chicks were changed every 3 trials. They were housed separately from experimental chicks and were not given access to insect prey at any point during the experiment.

During training, chicks were given 6 trials at regular intervals throughout the day. In all trials, chick crumbs were scattered over the floor of the experimental arena, and chicks were then placed in the arena for an interval of 2 min. In the first 2 trials, chicks were placed in the area in groups of 3; in the following 2 trials, chicks were placed in the arena in groups of 2; and in the final 2 trials, chicks were placed in the area individually. By the end of trial 6, all chicks were eating crumbs in the arena.

EXPERIMENT 1: DO BIRDS MISCLASSIFY DIFFERENT LARVAL MORPHS AS DIFFERENT MODELS?

Methods

Experience manipulation trials

Sixty-eight chicks were used in this experiment: 48 served as experimental chicks and 20 served as buddy chicks. On day 2, the 48 trained experimental chicks were divided into 8 groups, each containing 6 individuals. Birds in all groups received four 2-min trials, in which they were placed in the experimental arena individually (as in training, 2 chicks from the stock of 20 were placed in the buddy arena in each trial). However, the items placed in the experimental arena during these trials differed among groups. Two groups encountered a birch branch complete with leaves. The branches measured approximately 20 cm in length and containing between 8 and 12 twigs. Two groups encountered a manipulated birch branch that had been bound in purple cotton thread to change its visual appearance without influencing its odor. Two groups encountered a willow branch complete with leaves, and the final 2 groups encountered a manipulated willow branch that had been bound in purple cotton. The branch was placed in center of arena, and the latency to peck the branch and the number of times the chick pecked the branch in each trial were recorded. Chicks were trained in a random order. Importantly, the 4 different types of stimulus were equally as interesting to the chicks and received similar investigation from them (Figure 1).

Testing

On day 3, birds received a single testing trial. A single test stimulus was placed in the experimental arena, 15 cm from buddy arena and 25 cm from arena wall. Birds were food deprived for 30 min (in an empty cage the same size as their home cage) and where then placed in the experimental arena. They were positioned 15 cm away from the test stimuli and 30 cm away from the buddy arena and were orientated so that they were facing the stimulus. The test stimulus differed among groups: one group trained with birch branches, one trained with manipulated birch branches, one with willow branches, and one with manipulated willow branches, received a single birch-fed larva and birds in the remaining groups received a single willow-fed larva. Caterpillars were allowed to settle on

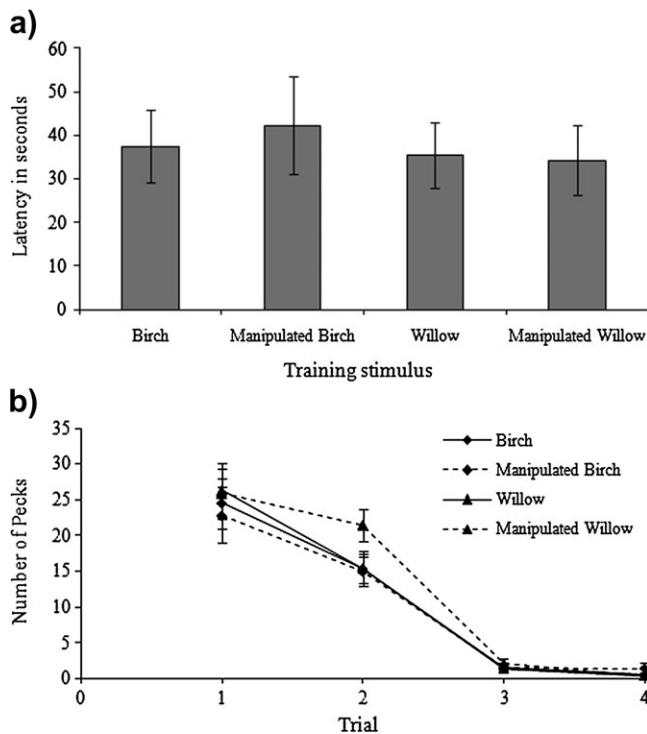


Figure 1

Experiment 1: (a) The mean time in seconds (\pm standard error of the mean) taken to peck the training stimulus in the first experience manipulation trial. (b) The mean number (\pm standard error of the mean) of times that birds pecked the training stimulus in each of the 4 experience manipulation trials.

branches in natural positions. The branches were then refrigerated before use, which prevented them from moving (when not refrigerated, caterpillars appeared to move around less on their own host plant than on the other branch type). The latency to peck the stimulus was recorded.

Statistical analysis

We used Kruskal–Wallis tests to test the following a priori predictions:

1. Birds trained on unmanipulated birch branches would take significantly longer to attack the birch-fed larva than birds trained on manipulated birch branches, unmanipulated willow branches, or manipulated willow branches, and birds trained on unmanipulated willow branches would take significantly longer to attack the willow-fed larva than birds trained on manipulated willow branches, unmanipulated birch branches, or manipulated birch branches. That is, the larva will only be mistaken for a twig if birds have experience with unmanipulated branch of the species the larva was fed on (and therefore resembles).
2. Birds given unmanipulated birch branches in training and a birch-fed larva in testing and birds given unmanipulated willow branches in training and a willow-fed larva in testing would not differ significantly in the time taken to attack the larva in testing. That is, each larval morph will benefit equally from masquerade.

Results

Importantly, birds given branches and birds given manipulated branches did not differ significantly in either their latency to peck the first twig (Kruskal–Wallis test: $\chi^2 = 0.082$, $P = 0.994$,

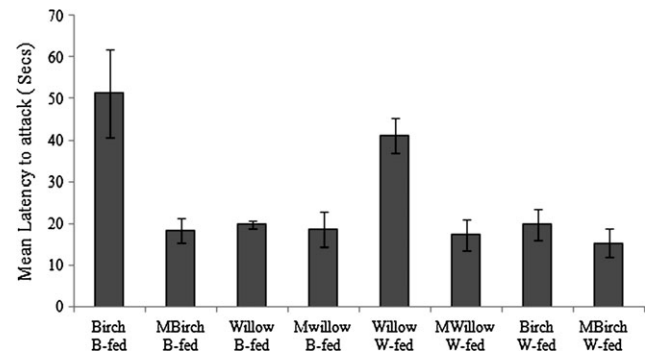


Figure 2

Experiment 1. The latency in seconds (mean \pm standard error) to attack the caterpillar for each experimental group ($N = 6$ for each group). Groups are indexed first by the type of branch used in training (birch or willow, suffixed by an M if they were manipulated with thread) and then by the type of caterpillar presented during the test: birch-fed (B-fed) or willow-fed (W-fed).

degrees of freedom [$df = 3$] or in the total number of times they pecked the branches across the 4 experience manipulation trials (Kruskal–Wallis test: $\chi^2 = 3.532$, $P = 0.317$, $df = 3$); see Figure 1. This demonstrates that neither binding branches in colored thread nor the species of branch used influenced birds' willingness to peck them or their motivation to peck them.

The time taken to attack the larva differed significantly among the experimental groups (Kruskal–Wallis test: $\chi^2 = 25.64$, $P = 0.001$, $df = 7$; see Figure 2). In order to test our first prediction, we compared the data collected from birds trained on unmanipulated birch branches with the combined data collected from birds trained on manipulated birch branches, unmanipulated willow branches, and manipulated willow branches, and we compared the data collected from birds trained on unmanipulated willow branches with the combined data collected from birds trained on manipulated willow branches, unmanipulated birch branches, and manipulated birch branches. As predicted, birds trained on unmanipulated birch branches took significantly longer to attack the birch-fed larva than birds trained on manipulated birch branches, unmanipulated willow branches, or manipulated willow branches (Kruskal–Wallis test: $\chi^2 = 12.27$, $P < 0.001$, $df = 1$), and birds trained on unmanipulated willow branches took significantly longer to attack the willow-fed larva than birds trained on manipulated willow branches, unmanipulated birch branches, or manipulated birch branches (Kruskal–Wallis test: $\chi^2 = 12.03$, $P = 0.001$, $df = 1$). This demonstrates that birds mistake larvae for twigs when they have experience with unmanipulated branches of the species that the larva was fed on (and therefore resembles).

Birds given unmanipulated birch branches in training and a birch-fed larva in testing and birds given unmanipulated willow branches in training and a willow-fed larva in testing did not differ significantly in the time taken to attack the larva in testing (Kruskal–Wallis test: $\chi^2 = 0.026$, $P = 0.873$, $df = 1$). This indicates that the benefit of masquerade is similar for each morph.

Discussion

Birds that experienced unmanipulated branches from the larval food species took longer to attack larva than birds that had experienced manipulated branches from the larval food species and those that had experienced either manipulated or unmanipulated branches from the alternative host species that the larva had not fed on. This shows that birds misclassified

birch-fed larvae as birch twigs and willow-fed larvae as willow twigs. Misclassification was caused by the visual resemblance between the twigs and the larvae because manipulated branches resembled unmanipulated branches in all aspects except in visual appearance. Our experiment therefore demonstrates that both larval morphs benefit from masquerade; however, each morph mimics a different model. Furthermore, the benefit of masquerade was similar for each morph because birds given unmanipulated birch branches in training and a birch-fed larva in testing took a similar amount of time to attack the larva as birds given unmanipulated willow branches in training and a willow-fed larva in testing.

Our results suggest that when predation on masquerading prey is frequency dependent, then polyphenism could potentially reduce the costs associated with masqueraders becoming abundant relative to their models. This is because if more than one model is mimicked, there are more models in the environment (Skelhorn, Rowland, and Ruxton 2010).

EXPERIMENT 2: DO MASQUERADING LARVAE GAIN ADDITIONAL PROTECTION FROM CRYPTIS?

Although masquerading prey clearly benefit from predators misclassifying them as the models that they resemble, they may also gain additional benefits from crypsis (i.e., avoiding detection). If masquerading prey do gain additional benefits from crypsis, we would expect predators to be less likely to attack larvae when they are found on their own host plant than when found on other plant species. We tested this hypothesis by comparing the relative mortality of birch-fed and willow-fed larvae when presented on birch branches and on willow branches. To ensure that any difference in mortality was due to differential crypsis, and not birds being more likely to misclassify larvae as twigs when found on their own host species, we used naive birds that had no experience of models (i.e., birch and willow branches).

Methods

Testing

Thirty-two chicks were used in this experiment: 20 were trained to eat crumbs in the experimental arena (exactly as in experiment 1) and 12 served as buddy chicks. On day 2, the 20 trained chicks were divided into 2 groups, each containing 10 individuals. Birds in both groups received a single test trial, in which they were placed in the experimental arena individually (as in training, 2 chicks from the stock of 12 were placed in the buddy arena in each trial). In the experimental arena, each chick encountered a branch (20 cm in length), containing 8 twigs complete with leaves and 2 caterpillars: 1 willow-fed larva and 1 birch-fed larva. However, the type of branch differed between groups; one group received a willow branch and one group received a birch branch. The branches containing caterpillars were refrigerated before use, which prevented the caterpillars moving. Birds were left in the arena until they attacked one of the caterpillars, and the morph attacked was recorded.

Statistical analysis

We used a Fisher's test to test the predictions that birds given birch branches and birds given willow branches would differ in their choice of caterpillars, and we used Binomial tests to test the predictions that birds given willow branches would show a significant preference for birch-fed larvae, whereas birds given birch branches would show a significant preference for willow-fed larvae. That is, larvae will be more difficult to detect when found on their own host plant than when found on an alternative plant species.



Figure 3

Experiment 2. The number of birds in each group that attacked the birch-fed larva (black) and the willow-fed larva (unfilled).

Results

As predicted, the experimental groups differed significantly in the type of caterpillars that they attacked (Fisher's test, $P < 0.001$, $n = 20$; see Figure 3). Birds given willow branches showed a significant tendency to attack the birch-fed larva (binomial test, $P = 0.002$, $n = 10$), whereas birds given birch branches showed a significant tendency to attack willow-fed larva (binomial test, $P = 0.022$, $n = 10$). Furthermore, 8 of the 10 birds given a willow branch attacked the birch-fed larva before pecking the branch, and 7 of the 10 birds given a birch branch attacked the willow-fed larva before pecking the branch.

Discussion

Our findings clearly show that larvae are less likely to be attacked when located on the host species whose twigs they resemble than when found on an alternative species whose twigs they do not resemble. We can be sure that this benefit was due to larvae being more cryptic on their own host species than on alternative host species rather than birds being more likely to misclassify the larvae as twigs when found on their own host species because the birds used in this experiment had no experience of the model prior to the test trial. Furthermore, in most cases, birds attacked the larva before pecking the branch, so it is highly unlikely that birds learned that twigs were nonrewarding during the trial. Masquerading prey can therefore gain additional benefits from crypsis when found on their own host species.

Although masquerade is clearly an effective defense against predators with experience of the inanimate model, it will be of little use against naive predators with no, or little, experience of the model. Crypsis therefore may be particularly important in defending masquerading prey against naive predators. Furthermore, the findings of this experiment may help to explain why some species of masqueraders are often found in close spatial proximity to their models. We recently demonstrated that predators were less likely to misclassify masquerading prey as their models when models and masqueraders were viewed simultaneously than when they were viewed in isolation from their models (Skelhorn and Ruxton, 2010). This makes it difficult to understand why masquerading prey would choose microhabitats in which their models are common (Skelhorn, Rowland, and Ruxton 2010). However, the findings we present here suggest that this behavior may still be adaptive if the benefits associated with crypsis outweigh the costs associated with reduced misclassification.

GENERAL DISCUSSION

Our experiments clearly demonstrate that the polyphenetic larvae of the Peppered moth (*B. b. cognataria*) masquerade as 1 of 2 distinct models: predators misclassified birch-fed larvae as birch twigs and willow-fed larvae as willow twigs. We also provide the first evidence that masquerading prey can gain additional benefits from crypsis and that each morph is more difficult to detect when found on its own host species than when found on an alternative food species. Our results suggest that the polyphenism will allow caterpillars to exploit a wider range of food plants while retaining the antipredatory benefits of both masquerade and crypsis. Furthermore, mimicking 2 different models will increase the relative frequencies of models to masqueraders, which may increase the benefit of masquerade if predation on masquerading prey is frequency dependent. We expect the benefits of masquerade to be frequency dependent from consideration of the economics of foraging. Twig-mimicking caterpillars are not identical to twigs (Skelhorn, Rowland, et al. 2010; Skelhorn and Ruxton, 2010), but close inspection of an object that might be either a twig or a caterpillar likely requires time investment. The average return to the forager on this investment increases with the likelihood of the inspected object being a caterpillar; that is, with the ratio of caterpillars to twigs. Polymorphisms/polyphenisms are an effective way to counteract this effect because by having the ability to masquerade as more than one type of twig, the caterpillar population effectively increases the size of the relevant local twig density against which foragers must compare them (Skelhorn, Rowland, and Ruxton 2010).

There is some limited evidence from natural populations that predation on masquerading prey is frequency dependent. Predation by birds is known to have severe effects on stick insect populations that are moderately abundant locally (Bedford 1978). During periodic population explosions, avian predators migrate to outbreak areas, releasing stick insect populations in abandoned areas from predation pressure and causing their numbers to explode in the following year. However, predation by birds was found to have no measurable effect on stick insect numbers during periodic population explosions, demonstrating that frequency-dependent predation is not the only factor influencing the population dynamics of masquerading prey (Bedford 1978).

The frequency-dependent benefit of masquerade may not be the only selection pressure for polymorphisms/polyphenisms in masquerading prey. If the availability of models (twigs of a given tree species in the case explored here) is spatio-temporally variable, then polymorphism or polyphenism should increase the ease of finding suitable microhabitats in which masquerade will be successful. In our case, if the relative frequencies of willow and birch change over the spatial scale of adult moth dispersal, then polyphenism allows females to disperse without being restricted by difficulty in finding a suitable host tree for their offspring. Similarly, if the female is time limited when searching for a host tree, this polyphenism increases her choice of available trees.

A particular advantage of polyphenism is that it allows change in appearance within the lifetime of an organism triggered by change in environment; this may be particularly beneficial for twig-mimicking caterpillars. It is not difficult to imagine how wind and rain can sometimes knock such caterpillars from the host tree. Their slow speed of movement and likely high vulnerability while on the ground should select for them to crawl to the nearest tree. If their masquerade were inflexible, then this change of host would likely destroy the benefit of masquerade, if the new host has different-

looking twigs from the original. Polyphenism provides a way to overcome this cost, with the caterpillar changing appearance to increase the effectiveness of masquerade on its new host.

Polymorphisms/polyphenisms in masquerading prey may also be driven, at least in part, by crypsis. In particular, polymorphism in cryptic prey is often explained in terms of a search image effect (for an overview, see Bond 2007). Essentially, this is the observation that improved ability to detect cryptic prey of a certain appearance with repeated experience of detecting that prey type comes at the cost of decreased ability to detect cryptic prey of other types. Thus the polyphenism described in our study species should reduce overall detection rates on the caterpillars (relative to a monomorphic population) by preventing predators forming a single accurate search image. Furthermore, when prey use 2 different host species, predators cannot restrict their searches to a single host species, and consequently, the mean time taken to detect a prey item is likely to increase.

We found that both the morphs of *B. b. cognataria* were equally good mimics of the twigs of their respective host plants. However, it is unclear whether we would expect this as a generality in polyphenic or polymorphic masquerading prey. Variation between morphs in the quality of masquerade might occur through differences between models (twigs of the different tree species in our case) in how long they have been exploited by the masquerading species, how commonly they are exploited (relative to other models), as well as features such as characteristic levels of illumination, predator community, and predation pressure. For example, masquerade might need to be less exact for one morph of a twig-mimicking caterpillar if that morph is associated with a tree with a particularly dense canopy that reduces the typical light levels under which predators see the caterpillars.

Although predation is commonly assumed to be the underlying driver in many polymorphisms/polyphenisms in appearance across a range of taxa, empirical demonstrations of this are scarce (see Losey et al. 1997; Wennersten and Forsman 2009). It may be that the close association between microhabitat (host species) and appearance type in polyphenic caterpillars such as that studied here might make them an ideal model species for study of polymorphism/polyphenism generally, allowing unusual levels of control in experimental manipulation simply by moving caterpillars between hosts or variation in the local densities of different host plants. This may be particularly valuable because understanding the evolution and maintenance of polymorphism are likely to be germane to our understanding of speciation and the maintenance of biodiversity (Gray and McKinnon 2007). Masquerade may turn out to be a very useful tool for evolutionary ecologists.

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