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Prey with hidden colour defences benefit from their similarity to aposematic signals

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Some camouflaged animals hide colour signals and display them only transiently. These hidden colour signals are often conspicuous and are used as a secondary defence to warn or startle predators (deimatic displays) and/or to confuse them (flash displays). The hidden signals used in these displays frequently resemble typical aposematic signals, so it is possible that prey with hidden signals have evolved to employ colour patterns of a form that predators have previously learned to associate with unprofitability. Here, we tested this hypothesis by conducting two experiments that examined the effect of predator avoidance learning on the efficacy of deimatic and flash displays. We found that the survival benefits of both deimatic and flash displays were substantially higher against predators that had previously learned to associate the hidden colours with unprofitability than against naive predators. These findings help explain the phenological patterns we found in 1568 macro-lepidopteran species on three continents: species with hidden signals tend to occur later in the season than species without hidden signals.

1. Introduction

Predation is one of the key drivers shaping the evolution of animal coloration [1,2]. Indeed, concealment from predators (crypsis) is perhaps the most common form of prey defence [3]. However, several other forms of defensive coloration have been recognized, notably warning predators of unprofitability through conspicuous coloration (aposematism) and/or mimetic resemblance of other unprofitable species (mimicry) [3]. Each of these latter colour signals tends to be constantly and passively displayed to predators. However, some cryptic animals have bright colour patches that are normally hidden from view and display them only transiently as secondary defences. Such defences are called deimatic and flash displays [4,5] (figure 1).

The terms deimatic and flash displays have been used broadly and sometimes inter-changeably to describe sudden revealing of bright colour patches in normally cryptic animals [5]. Here, however, we distinguish between these two revealing displays based on their psychological effects on predators [6]. We define revealing displays as deimatic when animals use them to startle and/or threaten predators [7,8]. During deimatic displays, the signallers often stay put until the predator moves away or voluntarily gives up attacking the prey [9–11]. By contrast, we define flash displays as a behaviour that is performed only in motion to confuse or misdirect a predator in the pursuit of prey [12,13]. The display of bright colours while fleeing gives false information about the prey's resting colour to pursuing predators and impairs subsequent searching once the prey have settled down on a new position with its normal cryptic appearance [14]. Alternatively, or in addition, dynamically flashing

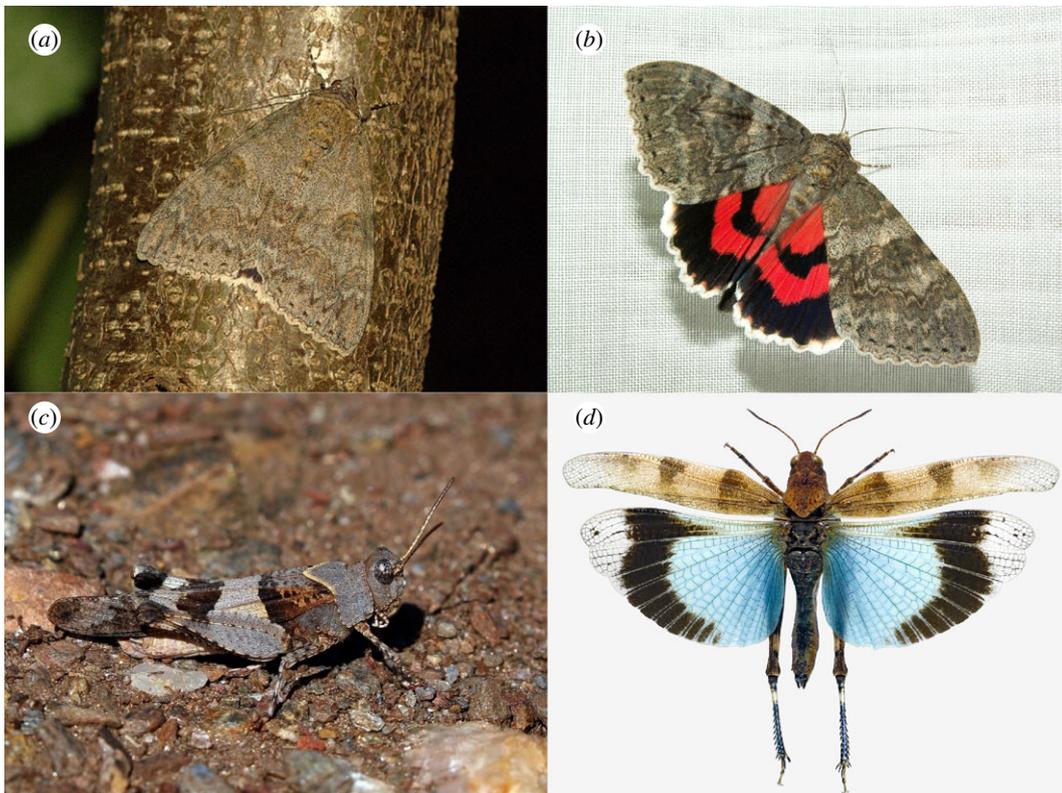


Figure 1. Examples of deimatic and flash displays in nature. The underwing moth, *Catocala nupta*, is normally cryptic (a) but has conspicuous hindwings (b). The hindwings of the blue-winged grasshopper (c), *Oedipoda caerulescens*, are only exposed when flying (d). Image sources: Kurt Kulac, Oputina; Charles J. Sharp, Didier Descouens.

conspicuous and cryptic colours while fleeing interrupts precise targeting of the prey [15].

Hidden colour displays are exhibited by a range of insect orders including Lepidoptera, Mantodea, Orthoptera and Phasmatodea, constituting approximately 20% of the species groups that have been surveyed [16–18]. One overlooked property of these hidden signals is that the bright colours employed resemble aposematic signals used in nature (figure 1). This can potentially enhance its psychological effects on predators and help protect the prey if the display reminds predators about their earlier unpleasant experience with aposematic prey [19–21]. For instance, when predators encounter deimatic displays of prey, they often remain around the prey to further assess it [9,11]. If predators have already learned to avoid aposematic phenotypes, then the chance of them leaving the prey unharmed would be higher. Likewise, the motivation of predators to pursue brightly coloured fleeing prey may be lower if predators consider these signals to be indicative of unpalatability. We therefore predict that the survivorship advantage of both deimatic and flash displays will be higher if predators have already learned to associate these transient signals with unprofitability due to their resemblance to aposematic signals. We tested this hypothesis by performing two experiments that tested the effect of predators' prior experience with aposematic prey on the efficacy of both deimatic and flash displays using birds and humans as predators.

If predators' avoidance learning on aposematic prey affects the survival of prey with deimatic/flash displays, it might generate strong selection on the phenology of species with hidden signals. Thus, natural selection will tend to favour species defences to be deployed in a form and at a time that are effective in deterring the local predator community [22–24]. This is well documented in model–mimic relationships in Batesian

mimicry: mimics derive a survival advantage by delaying their activities until local predators have learned to avoid the models [25]. However, we know next to nothing about the phenology of species with hidden colour signals compared to aposematic species. We hypothesize that the phenological patterns in model–mimic systems will similarly appear in species with deimatic/flash displays: if predators' learned avoidance towards aposematic prey increases the survivorship of prey species with hidden signals, then natural selection may favour delaying the activities of those species until educated predators predominate [26]. We tested this hypothesis by comparing the phenology of 1568 macro-lepidopteran species with different forms of defensive coloration (cryptic, conspicuous and hidden conspicuous) in three different geographical locations: South Korea, the UK and the USA. Our prediction was that the species with hidden conspicuous signals emerge later than the species with other defensive strategies.

2. Methods

All experimental procedures were approved by Institutional committees (approval number: MNU-IACUC-2019-010 for deimatic display experiment, MNUIRB-180919-SB-009-01 for flash display experiment).

(a) Deimatic display experiment

We began by testing whether avian predators' avoidance learning on aposematic prey increases survivorship of the prey with deimatic display. To do this, we bought new-born chicks (*Gallus gallus domesticus*) from a local farm (day 1). We marked them individually using a non-toxic marker on their crown and

randomly assigned the chicks into two groups: experienced and naive groups. We trained experienced group chicks ($n=22$) to associate aposematic colours with distastefulness but did not train naive group chicks ($n=23$). On day 2, we trained all chicks to forage in the arena ($90 \times 60 \times 60$ cm metal cage) by providing several mealworms on the floor. From day 3 to day 7, we conducted learning trials. We deprived of food from all chicks one hour before each trial to motivate foraging.

During each learning trial, we used triangular-shaped moth-like paper and mealworms to make prey items: we placed a mealworm under each paper in a way that half of the mealworm was visible while the other half was hidden underside of the paper. For each trial, we placed 12 such prey items in the arena haphazardly. For the experienced group of chicks, we used six different colours to make prey (two each, 12 in total): red, orange and yellow as aposematic colours, and grey, green and brown as non-aposomatic colours. For aposematic prey, we placed a distasteful mealworm while a normal mealworm was used for non-aposomatic prey. To make distasteful mealworms, we sprayed 2.5% denatonium benzoate (Bitrex) solution on dead mealworms three times. For a normal mealworm, we sprayed diluted water instead. For the naive group of chicks, we used paper with one of the three non-aposomatic colours (grey, green or brown) to make prey items (four each, 12 in total). We used only normal mealworms for the naive group. Each learning trial was continued until the chicks finished tasting all mealworms or up to 2 min. We conducted learning trials two times per day and continued for 5 days.

On day 8, each chick (from both the experienced and naive groups) was presented with a robotic moth that can suddenly display the wing parts (triggered remotely by the experimenter) to display hidden colours beneath them in the arena (electronic supplementary material, figure S1a, video S1). This robotic moth has been successfully used in a previous study to elicit startle responses of avian predators in the field [9]. The moth's shape was the same as those prey used in learning trials. We used grey colour for wing parts and an orange colour for the hidden colour (electronic supplementary material, table S1). The orange colour used here generally resembled the colour used in learning trials but differed slightly: we used a slightly different colour because deimatic colours can resemble aposematic colours in general, and do not necessarily closely mimic any given species. We displayed the wings when each chick approached close to the robotic moth (approx. 10 cm) to eat the mealworm. One experimenter (Y.H.) controlled the display timing consistently. The robotic moth maintained the display for 10 s and closed the wings. Three other palatable prey items were placed around the robotic moth as well to enhance the motivation of chicks to forage, and confirm their interest in eating.

(b) Flash display experiment

Next, we tested whether predators' avoidance learning on aposematic prey increases survivorship of the prey with flash display. We used humans as visual predators and a modified prey searching game from previous studies to test our hypothesis [12,14]. We used a colour-calibrated 15' LCD monitor (calibrated using SpyderX, Datacolor) and recruited 90 human participants from Mokpo National University (Muan, South Korea). We assigned half of the participants to the experienced group and the other half to the naive group (see below). Before playing the game, each participant watched a tutorial video.

Each game consisted of 16 prey searching trials in which the initial 14 were learning trials while the last two were testing trials. Each trial had two phases: escape and search phases. At the beginning of the escape phase, a square prey item (30×30 pixels) was set at a random position on a grass background image (1152×767 pixels; electronic supplementary material, figure S1b).

Any movement of the mouse pointer prompted the prey to flee either to the left or right of the screen, whichever was the longer. The prey disappeared by flying out of the screen within 1–2 s. Prey movement was not continuous but comprised a rapid sequence of discrete random steps towards either side. After fleeing, the participant was asked to click either the 'follow' or the 'not follow' button. Having this option was pivotal to test our prediction because if human predators consider that a fleeing prey is not worth following because they are likely to be unprofitable, then they would not follow it. If the participant followed the prey, then the search phase began straight away, and the horizontally flipped grass image was shown as background (to prevent prey being revealed by contrasting otherwise an identical image) with the same prey present on a new random position. In this phase, the participants had to either find the prey and click it or give up finding it if they believed that there was no prey present. If the participant did not follow the prey, then the trial ended and moved on to the next trial (electronic supplementary material, video S2). A scoreboard displayed the current points accumulated (see below).

In learning trials, the participants experienced 12 prey as well as two 'dud' presentations. A dud presentation occurred when prey was present in the escape phase but was not present at all in the search phase. We used these dud presentations to get the participants used to the fact that there can sometimes be no prey on a search screen after it had escaped (mimicking a situation where a predator searches an area where no prey is present). For the 12 prey, we used red, orange and yellow for conspicuous prey, and light green, dark green and grey for non-conspicuous prey (two for each; see electronic supplementary material, table S1 for the RGB values used). For the naive group, catching any prey in the search phase resulted in scoring one point. However, for the experienced group, catching a conspicuous prey resulted in the volunteer losing one point while catching non-conspicuous prey resulted in the volunteer gaining a point. In this way, the participants in the experienced group learned to avoid conspicuous prey while those in the naive group had no opportunity to learn. Prey presentation order was random. All prey showed the same colour both when in motion (escape phase) and when resting (search phase).

In testing trials, two treatment prey were presented in random order: cryptic prey and flashing prey. Cryptic prey had mean background RGB colour both when resting and in motion. Flashing prey showed the same cryptic colour when resting, but showed a different conspicuous colour in motion. One-third of the participants experienced a red flashing colour, another one-third experienced yellow flashing, and the other one-third experienced orange flashing. We used different colours here to determine whether our results can be generalized to a variety of different flash colours. In theory, flash displays should confuse predators as long as the colours are conspicuous and different from the resting colour [14]. The red, yellow and orange colours used here generally resembled the conspicuous colours used in learning trials but differed slightly (see electronic supplementary material, table S1 for RGB values used).

(c) Phenological relationships of macro-lepidopteran species

We chose to quantify the phenological patterns in abundance of moths because (i) they are well recognized for the presence of hidden colour defences and (ii) visual predators are thought to be the main agents that have driven the evolution of their wing colour patterns [25–28]. We predicted that the species using deimatic/flash displays would occur later than the species using other strategies to defend themselves. Although information about moth behaviour would enable us to confirm the presence of those defences and distinguish between deimatic and flash displays, the behaviours of the majority of moths

were largely unknown and a behavioural survey on this large scale was practically impossible. Instead, we focused on morphological traits, especially the coloration of forewings and hindwings, to make inferences about the presence of deimatic/flash displays. The bright hindwings in cryptic species are mostly associated with the deimatic and flash displays, and other functions (e.g. courtship) have been only rarely reported in nocturnal moths [18,29].

When comparing interspecific phenological relationships, it is essential to control for geographical differences because the occurrence of species is largely influenced by geographical factors such as latitude [30]. Here, we analysed long-term monitoring data that collected at three different geographical locations: Jiri Mt. (South Korea), Hertfordshire (UK), and HJ Andrews Experimental Forest (Oregon, USA). In all locations, the moth survey was conducted within the restricted area, so that within-location latitudinal/longitudinal differences were considered negligible.

The South Korean phenologies were obtained from published data [31]. In the Korean study, 11 families of macro-moth communities were monitored at six sites in Jiri Mt. once every month from May to October for 13 years (2005–2017; see electronic supplementary material, table S2 for analysed families for each location). We obtained UK data from a published book [32]. In this book, the frequency distribution of adult flight period, as well as the maximum number of individuals in peak weeks was available for each moth species in the Hertfordshire region from 1995 to 2006. We analysed eight the most common macro-moth families. The US data comprised 6 years of macro-moth monitoring data (1994–1996, 2005–2007, nine families). US monitoring was done a few times every month from May to October at various sites in HJ Andrews Experimental Forest, Oregon. In all locations, monitoring was conducted using light-traps. We excluded those species that appear only above 1000 m altitude from the analysis because the moth species and its predators may not overlap with other species in the same survey. We also excluded USA October data because there were only 223 individuals recorded due to infrequent monitoring attempts. In total, we analysed phenological data of 37 604 records of 821 South Korean species, 64 556 records of 349 UK species, 62 286 records of 398 US species.

For the classification of defensive strategies, we obtained three specimen images of each species from online (see electronic supplementary material for the sources). Using these photos, we classified each species into one of the three groups: cryptic, conspicuous and contrasting. We defined a species as cryptic throughout when the colour patterns of both of its fore-/hindwings resembled those of natural substrates such as leaves, tree barks, dead leaves or lichens (e.g. green, brown and grey colours). We defined a species as conspicuous throughout when forewings (and also usually hindwings) showed colours that are typically associated with aposematism (e.g. orange, yellow, red, purple, blue and white) often with highly contrasting patterns regardless of the hindwing colours. When a species showed internal contrasting patterns on forewings, we distinguished disruptive contrast (that has evolved for camouflage [33]) and aposematic contrast carefully: contrast for disruption usually consisted of one of the colours that resembled those of natural substrates while aposematic contrast consisted of typical aposematic colours (see forewings of the grasshopper in figure 1*c,d* for an example of disruptive contrast and forewings of the conspicuous moth in figure 4 for aposematic contrast). We considered disruptive contrast as cryptic and aposematic contrast as conspicuous. We defined a species as contrasting when its forewings showed cryptic features while hindwings were conspicuous and therefore highly contrasting against its forewings. When hindwings were contrasting against forewings but neither wing was conspicuous (e.g. brown forewings with grey hindwings), we considered this species as cryptic.

Two people conducted the classification independently (Y.K. and C.K.). The results disagreed for only 3.8% of the total species. For those species, we examined further photos in google images together and reached an agreement. A third person (T.N.S.) additionally classified the disagreed species and 22 species (1.4% of the total) remained disagreed with the revised consensus. For those 22 species, we analysed them in either way and found no differences in patterns regardless of how they were treated.

We recognize that our classification is crude since the judgement of colour type depends on observers' visual systems [34]. Even then, its efficacy cannot be confirmed without accounting for behavioural factors. However, lepidopteran colours such as red, yellow or orange are conspicuous in both human and bird vision, and green, brown or grey are seldom conspicuous. Thus, it is unlikely that cryptic colours in human vision are conspicuous from birds' eye view and vice versa unless ultraviolet (UV; which birds can see but humans cannot) is associated [35]. Since most natural substrates lack UV reflection, UV colours on lepidopteran wings are likely to be conspicuous. Naturally, web images did not have colour information in the animal-visible UV region (300–400 nm). To check whether UV-induced classification error occurred, we photographed 482 species of Korean species in both UV and human-visible spectrum and found that notable UV colours were always present on already conspicuous visible colours mainly on white, but also on yellow, and red. This suggests that our conspicuousness-based classification using web images is less prone to error even when UV was neglected. A human classification has proved to be useful in understanding the function and evolution of animal colour patterns, especially in large-scale comparative studies [13,36]. It has also often correlated well with bird-eye-vision based classifications [37,38].

(d) Statistics

We used R 4.0.2 for all statistical analysis [39]. For deimatic display data, we analysed whether the mealworm survived until the closure of robotic moth wings and compared the frequency of survived prey between the experienced and naive groups using Fisher's exact test. We used one observation per chick. For flash display data, we fitted generalized linear mixed models (assuming binomial error) and used predator group (the experienced and naive), prey type (flashing or cryptic) and the interaction between the two as explanatory variables. We used (1) prey survivorship and (2) whether participants followed the prey or not once it fled as response variables. Human participant ID was set as a random factor. We present the results of the model with the lowest Akaike information criterion value. We additionally compared the survivorship (and whether participants followed the prey or not) between the experienced and naive groups using flashing prey data to more directly analyse the effect of predator experience on the survivorship of flashing prey.

For phenological comparisons, we conducted an Anderson-Darling *k*-sample test to determine whether the phenological distribution of each colour group was drawn from a common unspecified distribution. As we were interested only in documenting community-scale patterns of abundance of different moth phenotypes, not uncovering associations between traits, we did not control for phylogeny. For a graphical comparison, we calculated the total number of individuals of all moths that occurred for each colour group and month. Then we calculated the proportion of a given colour group as a fraction of the total of all groups observed for a given month. We were particularly interested in the comparison between cryptic and contrasting group because these two groups share the same primary defences but mainly differ in the presence of secondary defences in terms of morphology. Thus, if there are any differences in the phenological patterns, they are likely to be related to predation.

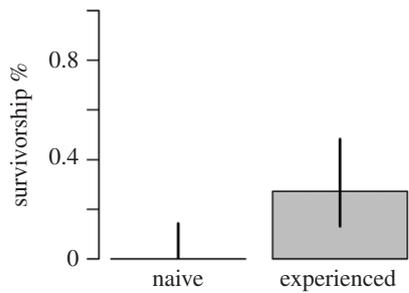


Figure 2. Mean prey survivorship comparisons in deimatic display experiment ($n = 23$ for naive, 22 for experienced group). Vertical lines show 95% Wilson binomial confidence intervals.

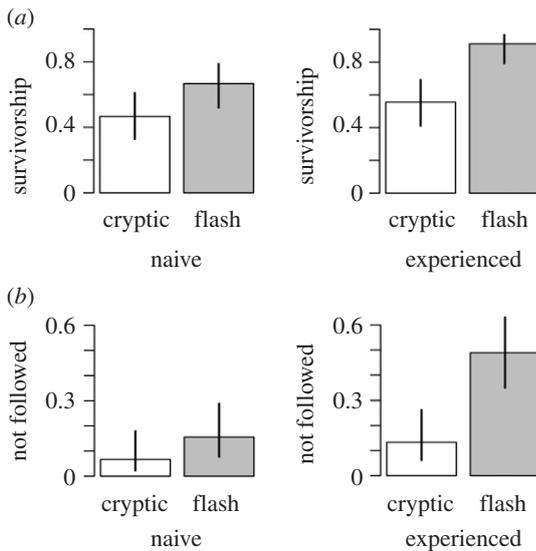


Figure 3. Mean survivorship comparisons (a) and the mean proportion that human participants did not follow the prey (b) in flash display experiment ($n = 90$). Vertical lines show 95% Wilson binomial confidence intervals.

3. Results

(a) Deimatic display experiment

In the experiment with avian predators, prey survivorship was higher against avian predators in the experienced predator group than naive group (26% versus 0%, figure 2; $p = 0.009$).

(b) Flash display experiment

Overall, prey survivorship was 28% higher in flashing prey than non-flashing prey (figure 3; $\chi^2_1 = 14.75$, $p < 0.001$; see electronic supplementary material, tables S3 and S4 for the estimated coefficients), and 17% higher in the experienced group compared to the naive group ($\chi^2_1 = 6.51$, $p = 0.01$). The interaction effect was non-significant ($\chi^2_1 = 2.96$, $p = 0.08$). This survivorship advantage was largely affected by the tendency of volunteers to refrain from following escaped prey more often in the experienced group than naive group (31% versus 11%, $\chi^2_1 = 6.33$, $p = 0.01$). Participants also refrained from following more frequently for flashing prey than non-flashing prey (32% versus 10%, $\chi^2_1 = 8.84$, $p = 0.003$), but the interaction between prey type and participant group was non-significant ($\chi^2_1 = 1.07$, $p = 0.30$).

An additional comparison of the survivorship of flashing prey between the experienced and naive groups revealed that, once the prey fled, the participants in the experienced

group refrained from following flashing prey 30% more frequently than the participants in the naive group (figure 3; $\chi^2_1 = 11.88$, $p < 0.001$). Consequently, the survivorship of flashing prey was 25% higher in the experienced than naive group (figure 3; $\chi^2_1 = 8.49$, $p = 0.004$).

(c) Phenology analysis

Of those 1568 species we studied, 141 species were classified as conspicuous, 1371 species as cryptic and 56 as contrasting (see electronic supplementary material, table S5 for the proportion for each location). The phenological patterns of each colour group differed among each other in all three localities (Anderson–Darling k -sample test; all $p < 0.001$; figure 4). There existed some general trends shared by all locations. First, the relative proportions of cryptic species were consistently higher than other groups but declined to some extent between July and August (mid-late season in all localities) due to an increase in the abundance of both conspicuous and contrasting species. Second, the relative proportions of both conspicuous and contrasting species gradually increased from May to July, with peak flight period usually in or after July. Third, the relative abundances of contrasting species were constantly low between May and June. Although the relative abundances of contrasting species were usually less than 10% throughout all seasons, it went up above 50% in the UK in August largely due to a few highly abundant yellow underwing species (*Noctua* genus). Indeed, a separate analysis revealed that contrasting species generally appear later than both cryptic and aposematic species in all three localities (Anderson–Darling k -sample test, $p < 0.001$ for both comparisons in all three localities).

4. Discussion

Our experimental results demonstrate that predators' prior experience with aposematic prey reinforced the survivorship advantage of both deimatic and flash displays. In our deimatic display experiment with the robotic moth, no mealworms survived at all in naive groups, which could be attributed to the chicks' strong desire to eat mealworms, even after being startled in response to deimatic displays. By contrast, 27% of the birds in the experienced group rejected eating the mealworms, which shows that birds' prior unpleasant prior experience with aposematic prey affected their choice, despite similar levels of motivation. In our flash display experiment, the main reason why flashing prey had higher survivorship in the experienced group was that the participants simply did not follow the prey once they saw prey with the conspicuous colour fleeing. The fact that previously encountered conspicuous prey were unprofitable, so not worth following, clearly affected their decisions. Altogether, our results suggest strategic decisions made by educated predators increase the probability of survival for prey with deimatic/flash displays.

Our results show that prey with deimatic/flash display can gain an initial survivorship advantage through predators' learning to aposematic prey. However, note that in principle predator learning can have both beneficial and harmful effects on prey species depending on what is learned. In particular, it has been well documented that avian predators habituate to deimatic display through multiple encounters with the same prey [40]. This is evidenced in predator

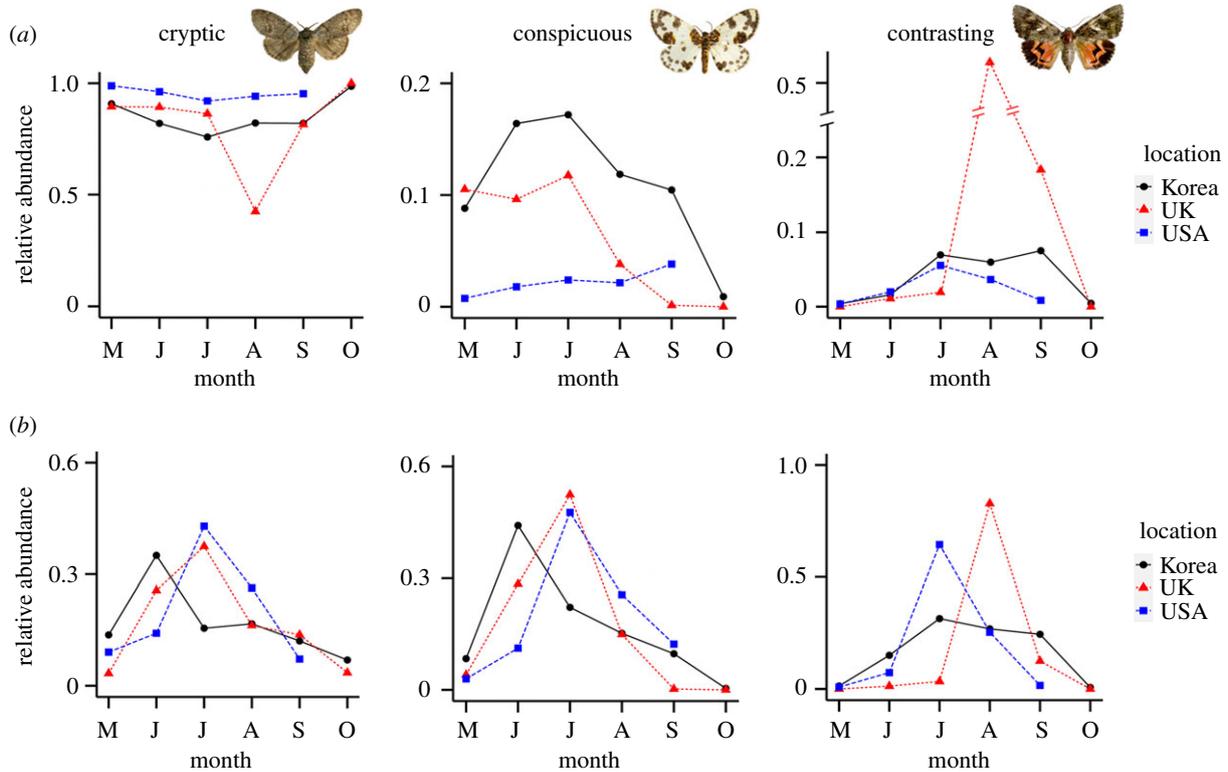


Figure 4. Phenological relationships among different colour groups. Each dot represents the relative proportion of each colour group for each month. Panels (a) and (b) show the same data, but the sum of all colour groups is one for a given month in (a) while the sum of a given colour group over the entire season is one in (b). We used the term ‘contrasting’ when if a species has cryptic forewings and conspicuous (thus contrasting) hindwings. Photos show the example species for each group: *Calliteara lunulata* (cryptic), *Abraxas niphonibia* (conspicuous), *Catocala dula* (contrasting). Image sources: Yongsu Kim. (Online version in colour.)

populations: birds that live sympatrically with the mountain katydid, *Acripeza reticulata*, which uses deimatic display when threatened, were more likely to consume this insect than birds that live allopatrically [10]. This type of habituation may well be prey specific and deimatic displays must be repeatedly encountered, therefore more likely to occur when predators encounter the same prey species multiple times. Intriguingly, Sargent [29] argued that hindwing diversity of sympatric *Catocala* moth species was maintained by selection to ameliorate the effects of habituation. On the other hand, if a prey is well-defended, multiple encounters with the same prey can increase the survival of prey with this phenotype by facilitating predators’ avoidance learning [41]. Thus, the effects of predator learning are context-dependent. Considering i) prey with deimatic/flash display are less likely to encounter predators due to cryptic appearance, leaving less chance for predators to habituate those signals (but see [10]), and ii) intermittent reminders with aposematic prey may potentially reduce the extent of habituation [21], the net benefits of predators’ learning on the survivorship of prey with deimatic/flash display are more likely to be positive, at least in the short term.

The nature of selection by bird communities, the main predators of moths, is affected by multiple factors including the degree to which the birds move and their timing of reproduction which collectively affect the experience accumulated in a community. In particular, the emergence of naive fledglings has long been thought to have an important effect on insect signals [42]. Although detailed data on the abundance of fledglings for each month at each location were not available, the primary breeding seasons of British passerine birds begins in April and May, and those in Oregon and South Korea are similar (in some cases slightly earlier) based on the

breeding season comparisons of *Parus* genus [43–45]. Thus, we expect that naive birds to be particularly abundant in May, with the relative proportion of experienced birds increasing from May as the season continues. Indeed, in field experiments by Mappes *et al.* [42], the survivorship of aposematic prey steadily increased from May to October in Finland, where the breeding seasons of most birds are later than the UK [45]. This implies that the propensity of wild birds to attack aposematic prey will decrease as the season progresses due to gradual avoidance learning in birds. Under these circumstances, one might expect natural selection to favour the phenological shift of deimatic/flushing species to appear late in the season.

Although phenological relationships in nature are often complex, it is clear that mimetic species will derive greater survivorship benefits from mimicry when they occur later than model species through predators’ avoidance learning on models [25,26,46]. Regarding deimatic/flash displays, specific model–mimic systems have not been reported to date, but their hidden signals generally resemble common aposematic signals. In this circumstance, predators’ avoidance learning can be derived not only through encounters with aposematic adult Lepidoptera, but also more generally from any aposematic organism such as caterpillars or beetles that occur early in the season. Thus, both the comparison between aposematic and contrasting species and the comparison between cryptic and contrasting species are important. Cryptic species and contrasting species share similar primary defence strategy (camouflage), but differ in their hindwing colours (secondary defences). Therefore, if there are any consistent phenological differences between these two groups, they may be at least partially accounted for by their differences in hindwing colours.

Contrasting species indeed appear later in season than both cryptic and aposematic species in our analysis. Our results are therefore consistent with the classical model–mimic phenological view: contrasting species occur late in the seasons when educated predators are more common.

Our phenological comparisons are correlative, and while the broad scale abundance patterns are consistent with predictions we cannot infer causality. The predator community is known as one of the main drivers that may affect the phenology of adult insects, but naturally other factors may influence the flight season of contrasting species such as availability of food sources and body size [47]. Since contrasting species are typically larger than cryptic species [17], they may simply need more time to develop into adults due to their large size. Indeed, in our data, while wingspan did not correlate with peak flight period of each species in both the USA and UK populations (Kendall's rank correlation test, $p > 0.10$), it did correlate significantly in the South Korean moth species ($\tau = 0.13$, $p < 0.001$). Every moth species has its own story since the phenology of a species is likely to be affected by multiple ecological and evolutionary factors. Nevertheless, considering (i) predation pressure is one of the main evolutionary drivers that has shaped contrasting hindwings in moths, (ii) deimatic/flash signals are more effective after a period of aversion learning and (iii) our large-scale comparisons found similar results in three different continents, the phenological patterns we found are likely to have arisen at least in part because predators show a greater tendency to avoid prey with revealing signals that remind them of earlier unpleasant experiences.

Studies of the colour forms of Lepidoptera, from mimicry to industrial melanism, have provided key insights into evolutionary processes [48]. However, signals that are hidden from view have been largely ignored even though they are widespread across diverse animal taxa [49]. Only recently have we begun to understand the evolution and the mechanisms by which those signals protect the prey [10,12,13]. Our study highlights that the prey with hidden colour signals can benefit from their general resemblance to aposematic signals in a similar way that has been widely recognized in Batesian mimicry.

Ethics. All experimental procedures were approved by Institutional committees (approval number: MNU-IACUC-2019-010 for deimatic display experiment, MNUIRB-180919-SB-009-01 for flash display experiment).

Data accessibility. The datasets used for all analyses in the current study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.w3r2280nr> [50].

Authors' contributions. C.K. conceived and designed the overall study. S.R. conducted flash display experiment developed by T.N.S., Y.H. conducted deimatic display experiment. S.R., Y.K., J.A., S.C., J.C.M. gathered phenological data. C.K. and Y.K. performed the statistical analysis. Y.K., C.K. and T.N.S. wrote and revised the paper.

Competing interests. The authors declare no conflict of interest.

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