

Reactions of hand-reared and wild-caught predators toward warningly colored, gregarious, and conspicuous prey

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Recently there has been debate over the importance of innate avoidance of aposematic prey by predators, particularly birds. There is evidence that the predators have innate or unlearned, thus, inherited avoidance against certain colors, but whether there is any innate avoidance against gregariousness or conspicuousness is unclear. Previously predator behavior toward these characters of aposematic prey have been tested in separate experiments. We designed an experiment to separate inheritance toward color, gregariousness, and conspicuousness. We simultaneously offered the predators warningly colored and nonwarningly colored prey items, both aggregated and solitary, on white (conspicuous) or brown (cryptic) backgrounds. The predators we used were naive (hand raised), wild-caught yearling and adult great tits (*Parus major* L.). The results confirm previous results regarding the innate avoidance of color. Naive predators seemed to have a genetically or culturally transmitted avoidance of yellow and black prey compared to brown prey. Surprisingly, yearling wild-caught great tits were more selective than adults, which did not show as strong avoidance of yellow and black prey. More importantly, birds did not find gregarious prey more aversive than single prey, which indicates that grouping alone does not serve as an innate avoidance signal. Conspicuousness itself was not aversive to the predators. Our results suggest that the avoidance against a particular color pattern probably has an inherited basis, whereas gregarious and conspicuous characters of prey presumably aid the avoidance learning. *Key words:* aggregation, aposematism, color preference, conspicuousness, gregariousness, inherited avoidance, warning colors. [*Behav Ecol* 10:317–322 (1999)]

Warning coloration, the conspicuous colorful patterns of prey individuals associated with, for example, noxiousness, is understood to be an advertisement of unprofitability of the prey to potential predators (Cott, 1940; Edmunds, 1974; Poulton, 1890). Generally it is considered that predators are persuaded to encounter the aposematic individuals and that they learn by experience to avoid these and other individuals with similar phenotypes, thus facilitating recognition and avoidance learning (Cott, 1940; Mallet and Singer, 1987; Wickler, 1968). The main function of warning colors is therefore assumed to help predators to easily recognize the unprofitable species and hence to learn more rapidly and to remember longer to avoid these species (Guilford, 1986, 1990a).

However, there is also evidence for innate (Rowe and Guilford, 1996; Schuler and Hesse, 1985; Smith, 1975, 1977) or unlearned (Roper and Cook, 1989) avoidance by predators of some features of aposematic prey. It can be advantageous for a naive predator to avoid aposematic species in the first encounter because some of these species are highly poisonous (e.g., coral snakes). There are indications that predators have a genetic basis that causes them to avoid colors associated with warning function (Caldwell and Rubinoff, 1983; Smith, 1975, 1977; but see Brodie and Janzen, 1995). For instance, some naive predators may have unlearned avoidance behavior against black/yellow/red and preference toward green/brown/blue-colored prey (Fischer et al., 1975; Kovach, 1987; Mastrota and Mench, 1994, 1995; Roper and Cook, 1989; Rowe and Guilford, 1996; Schuler and Hesse 1985; Schuler and Roper, 1992). Alternatively, avoidance in the first encoun-

ter can also be explained by neophobia toward novel food (Coppinger, 1970, Marples et al., 1998, but see Barrows et al., 1980), the oddity effect (e.g., Landeau and Terborgh, 1986), generalized avoidance (Brodie and Janzen, 1995), or as preference for familiar food—for instance, search image (Tinbergen, 1960). However, the latter possibilities may not apply to naive predators, who encounter their first prey items in the wild; rather such differences would imply an inherited basis to prefer some and to avoid other prey types.

The innate tendency to behave differently toward different colors may also express itself by more rapid learning. Marples and Brakefield (1995) were able to select two lineages of quails which differed in their speed of response in accepting new food in their diet. They concluded that the genetic variation among predators was mainly associated with foraging on unfamiliar prey items rather than with a more general fearfulness or insensitivity. Thus it seems that learning also plays an important role in the avoidance of aposematic individuals.

The significance of unlearned behavior of predators to other typical features in aposematic insects (e.g., gregariousness or conspicuousness) has not received much attention. There is some ambiguity as to whether gregariousness would serve as an unlearned signal similar to the way colors do to naive predators (Gamberale and Tullberg, 1996a) or whether gregariousness merely enhances avoidance learning by predators (Alatalo and Mappes, 1996; Gagliardo and Guilford, 1993).

In addition to their colorfulness, aposematic insects are usually conspicuous (i.e., very different from the background). It is difficult to distinguish the function of the conspicuousness from the color per se. Birds do learn more rapidly to avoid conspicuous signals (Gittleman and Harvey 1980; Roper and Redston, 1987), but coloration seems to be a more important signal than conspicuousness (Roper, 1990; Sillen-Tullberg, 1985). However, grouping might also increase the conspicuousness and thus influence the learning of a predator by a

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stronger signal through a more intense total stimulus (Gamberale and Tullberg, 1996b, 1998).

Most studies investigating the innate avoidance of predators toward features of aposematic prey have been made using precocial species. This is largely due to the difficulty of separating any innate avoidance from possible influences on altricial birds during the rearing period prior to the experiment. Furthermore, altricial predators might be subject to a level of cultural learning because parental behavior might influence the food preference of juveniles (Avery, 1996; see also Rabinowitch, 1968). Therefore, these juveniles might never be totally naive when encountering the first prey item in the wild on their own. Nevertheless, to the aposematic prey individual, it does not make any difference whether predator behavior originates from cultural learning or genetically inherited initial or innate avoidance because in both cases the protection will be gained without initial predator training (i.e., sampling). However, if all the predator generations have to learn to avoid aposematic prey species through experience, this makes a great difference to each aposematic individual (see Alatalo and Mappes, 1996).

We conducted a series of experiments to investigate the reactions of naive and experienced predators toward the color, gregariousness, and conspicuousness of prey individuals. We were interested in how birds with different histories were behaving toward features of aposematic prey. We also tried to test whether there is inherited avoidance toward these characteristics of aposematic prey.

MATERIALS AND METHODS

Experiments were conducted in the Konnevesi Research Station, central Finland, in summer and autumn 1996. The experiment was conducted in two stages because we were unable to test breeding wild birds simultaneously with the naive birds.

Naive predators

In order to test the possibility that naive predators inherited prey preferences, we hand raised great tits (*Parus major* L.). We had permission from the local environmental office (Keski-Suomen ympäristökeskus) to capture and hand raise wild birds from nests (permission LS-02/96). We collected 14- to 17-day-old chicks from nest-boxes around Konnevesi, taking 1–6 birds from each nest depending on the size of the brood. At least half of the original chicks were left in each box to prevent desertion by parents. Most ($n = 30$) of our experimental birds were collected from the first clutches (between June 16 and July 7), and a few birds ($n = 9$) were collected from the second clutches (between July 24 and August 8). We hand raised a total of 39 chicks for the experiment. Naive birds were sexed later in the autumn.

Birds were first kept in nest-boxes and then housed individually in a plywood cages ($60 \times 60 \times 100$ cm³) with a photoperiod of 18 h light:6 h dark. Chicks were fed hourly from 0800 h to 2400 h and twice (0400 h and 0600 h) during the night with a mixture of dog food, minced meat, pig's heart, boiled egg yolk, vitamin syrup, and additional calcium. Birds were fed by forceps until they could feed themselves. Birds were tested on average when they were 35 days of age. They were housed over the critical winter period and were released back into the wild the following spring.

Experienced predators

In the autumn (16 September–19 October 1996), 24 wild-caught yearlings and 24 adult great tits were captured with a mist net and kept individually ($60 \times 60 \times 100$ cm³) for a few

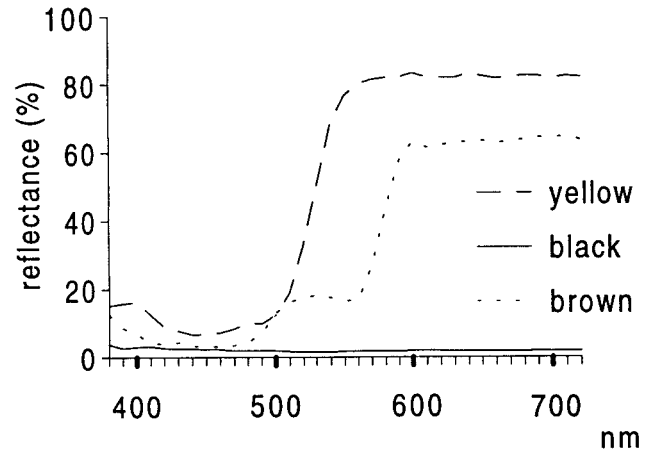


Figure 1

The mean reflectance spectra from three measurements expressed as relative to a calibrated 98% (LabSphere™) reflectance standard of each color in the experiment. Reflectances from the colors were measured using a E. G. & G. Gamma Scientific GS 3100 Spectroradiometer (receptor 700–8D, 250–1700 nm; coupler 700–3K, 250–880; monochromator NM 5DH 190–820 nm, detector D-46CQ 200–930 nm) with illuminating with the same light bulbs (Airam 3W/14V) as used in the experiment. Illumination and measuring optics were held at 45° angle from the measured surface. Spectra were recorded in 2-nm steps from 360 nm to 700 nm.

days to be ringed and released after the experiment (under permit LS-23/96 to catch wild birds). Birds were kept in continuous light to ensure that they were feeding in captivity. Birds were provided with sunflower seeds for food and fresh water ad libitum.

Prey

We used last instar mealworm larvae (*Tenebrio molitor*) as experimental prey, which were new to the predators. The birds, hand raised or wild, had no previous experience with the prey because it is not naturally available in our area. Mealworms were first boiled for a few seconds to soften them and then painted with nontoxic Decorlack (Marabuwerke GmbH & Co.) colors. Measurements with an E.G. & G Gamma Scientific GS 3100 Spectroradiometer of reflected light indicated that the colors in our experiment were yellow, black, and brown (Figure 1). Mealworms had eight alternate yellow and black stripes (four of each color), and control mealworms had eight brown stripes.

Experimental cages

We offered the mealworms in controlled conditions in the experimental cages, which were $30 \times 24 \times 40$ cm³ in size. Cages were placed on a plywood board, and there was an opening of 9×9 cm² in the plywood, under which four small trays could be placed. The trays were arranged in two rows and two columns (2 + 2). The birds were isolated from the observer by a plywood screen in front of the cage. Observations were made through a hole in the screen. Wild-caught birds were allowed to habituate to their experimental cages over night before the experiment. Hand-reared juveniles were much calmer and therefore were allowed to habituate to the cages for just an hour before the experiment. Birds have tetrachromatic vision, so the cages were illuminated with non-UV-emitting bulbs (Oy Airam Electric, 3W/14V E10, 230V) to minimize light effects. Water was available continuously, but food was available only during the habituation time.

Trials 1 and 2

Before the experiment, we divided birds into two groups. In the first trial one group was offered mealworms on the brown (i.e., cryptic) background, while the other group was offered mealworms on the white (i.e., conspicuous) background. In the second trial, the same procedure was repeated but with background color reversed. We conducted two trials to see whether the conspicuousness or the color of the background have any effects. The two trials were made for the same birds to minimize any random effects and thus increase the test power. Two trials also enabled a test of possible learning effects.

To accomplish the same motivation level, naive birds were food deprived for 1 h, and wild-caught birds were deprived for 2 h prior to the experiment. At first birds were simultaneously offered four different groupings of prey: a solitary brown mealworm (single control; sc), a group of five brown larva (group control, gc), a single yellow and black mealworm (syb), and group of five larvae painted yellow and black (gyb). These four groups of mealworms were arranged in four small trays (each 3 cm diam), which were presented to the predator at the same time. There are only 24 possible orders of how the 4 groups of prey items (2 + 2 trays) can be arranged. All these permutations were used randomly once for each background and remaining trials (19 for white, 20 for brown) randomly.

When the trays were presented to the predators, birds were allowed to take one prey item. This prey type was given a score value of 1. After the bird had taken and eaten the prey, we removed the trays. If the bird took one mealworm from either of the aggregations, the whole group was removed. After the removal of the preferred prey type, the remaining three prey types were offered to the bird. The prey type the predator chose next was given a score value of 2. Again the trays were removed, and the two remaining ones were presented to the predator. The prey type the bird took as third choice was given a score value of 3 and the remaining fourth type was given a value of 4. Thus, the bird was not allowed to eat the fourth mealworm. The aim of the procedure was to score the preference for prey types by the bird, scoring the prey type from one to four.

On the following day, the procedure was repeated for each bird but with the other background color for the second trial. The order of the four small trays of the mealworms was not the same as in the first trial. Five birds refused to eat any mealworms during the second trial. The average ranking order for these birds is therefore the ranking order from the first trial.

Contrast trial

To test the importance of conspicuousness in a simultaneous experiment, birds were offered single brown and yellow-black mealworms on both brown and white background on the third experimental day (four mealworms total). The mealworms were arranged similarly in 4 small trays as in previous trials, and all the 24 permutations were used 3 times and the remaining 5 randomly. We recorded the times when the birds took these prey items as well as the order. There were seven birds on which the last trial could not be performed.

Data analysis

Statistical tests were made using SPSS program (SPSS, 1992). Because simultaneously offering prey types makes the preference scores dependent on each other, we used a repeated-measures ANOVA which takes into account the dependent

structure of the data. Repeated-measures ANOVA was used to examine whether there were any interactions among conspicuousness, gregariousness, and colors. We used the preference scores for different prey types as four levels of a dependent factor in the model. Age of predators and background color were used as independent variables. All p values are two tailed.

We used the statistical parameters of a two-way ANOVA to test the preference along the two factors (color and conspicuousness) and their interaction. However, because the preference scores present a dependent data structure, the estimated F values cannot be compared with F tables to derive the corresponding p values. Therefore, we used a randomization method to attain the p values (see Potvin and Roff, 1993). We simulated 1000 random data sets 25 times with respect to preference ranks with the given sample sizes. Consequently, we could estimate the probabilities of obtaining equally high or higher F values by chance, and we can present the significance values with 95% confidence intervals using the 25 estimates.

RESULTS

There was no three-way interaction between prey type, age, and background color (cryptic or conspicuous) in the first or the second trial (repeated measure: $F_{6,160} = 0.38$, $p = .891$, $F_{6,150} = 0.70$, $p = .650$, respectively). Furthermore, there were no interactions between the preference score and the background color ($F_{3,81} = 0.52$, $p = .672$, $F_{3,76} = 0.27$, $p = .849$). The differences in the preference scores between the first and the second trials (with different backgrounds) did not differ (repeated measure $F_{3,78} = 0.29$, $p = .835$), and therefore we used the mean preference score of the two trials. In the mean preference scores, there was a significant interaction between age and the preference score of prey type (repeated measure $F_{6,166} = 3.04$, $p = .008$). Thus, different age groups differed in their behavior toward the prey, and all the following analyses are made separately to each age group.

Yearlings were more selective than naive birds (repeated-measure ANOVA, interaction between prey type and age, $F_{3,59} = 5.53$, after Bonferroni correction, $p = .006$; see Figure 2), and there was a tendency that they were also more selective than adults (repeated-measure ANOVA, interaction between prey type and age, $F_{3,44} = 3.36$, after Bonferroni correction, $p = .081$). Naive birds did not differ from the adults (repeated-measure ANOVA, interaction between prey type and age, $F_{3,59} = 1.21$, after Bonferroni correction, $p = .948$).

Naive predators

The average preference scores for four types of prey were significantly different (repeated measure, $F_{3,36} = 5.32$, $p = .004$). There was an interaction between color and grouping ($n = 39$, $F = 7.46$, 95% CI, $.018 < p < .022$) because single brown mealworms were preferred, while there was no similar preference within groups (Figure 2). The color had a significant effect ($F = 14.85$, 95% CI, $.0005 < p < .001$), whereas the grouping did not have a main effect ($F = 1.05$, 95% CI, $.369 < p < .381$). This indicates that the behavior toward coloration has an inherited component, but there is no evidence that this applies for grouping.

In the contrast trial, there was no interaction between prey color and background color ($n = 34$, $F = 0.29$, 95% CI, $.637 < p < .649$). When comparing mean scores of brown against the mean scores of yellow-black mealworms, the predators were still avoiding the yellow-black mealworms in the last trial ($F = 51.24$, 95% CI, $.000 < p < .001$). Moreover, there was no effect between the conspicuousness of the prey in either brown or yellow-black signal ($F = 1.57$, 95% CI, $.270 < p < .381$).

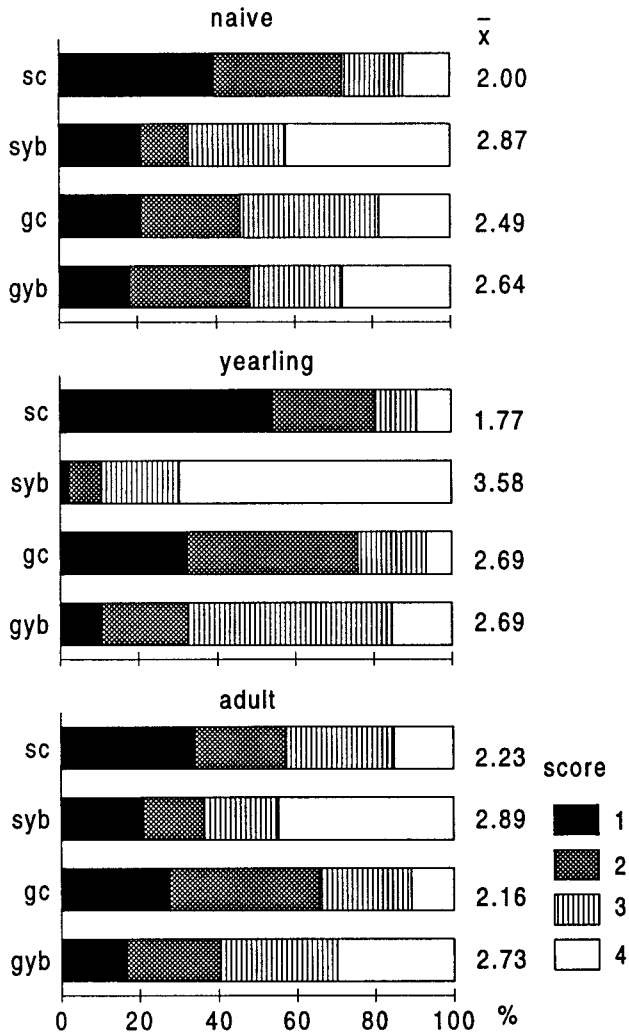


Figure 2
The percentage distribution of preference scores from two trials of four different prey types (sc = single control, syb = single yellow-black, gc = group of controls, and gyb = group of yellow-blacks) in three different age groups. The mean preference scores from two trials are also given.

.282; Figure 3). This indicates that the predators were not avoiding more conspicuous prey, but they were using colors as cues for prey choice. Therefore it seems that there is no inherited avoidance toward more conspicuous prey.

Yearlings

In the mean scores there were highly significant differences; single yellow-black mealworms were never taken first in the first trial (repeated measure, $F_{3,21} = 30.11, p < .001$). There was an interaction between color and grouping ($n = 24, F = 14.18, 95\% \text{ CI}, .001 < p < .002$); yearlings avoided single yellow-and-black mealworms but did not find grouped yellow and black prey as aversive (Figure 2). The main effects from both color and grouping were significant ($F = 78.05, 95\% \text{ CI}, .000 < p < .0001, F = 6.06, 95\% \text{ CI}, .034 < p < .039$, respectively). Thus, the birds preferred brown mealworms and avoided yellow-and-black individuals effectively. However, birds were not avoiding groups per se (Figure 2).

In the contrast trial there was no interaction between color of the prey or the background color ($n = 21, F = 0.07, 95\%$

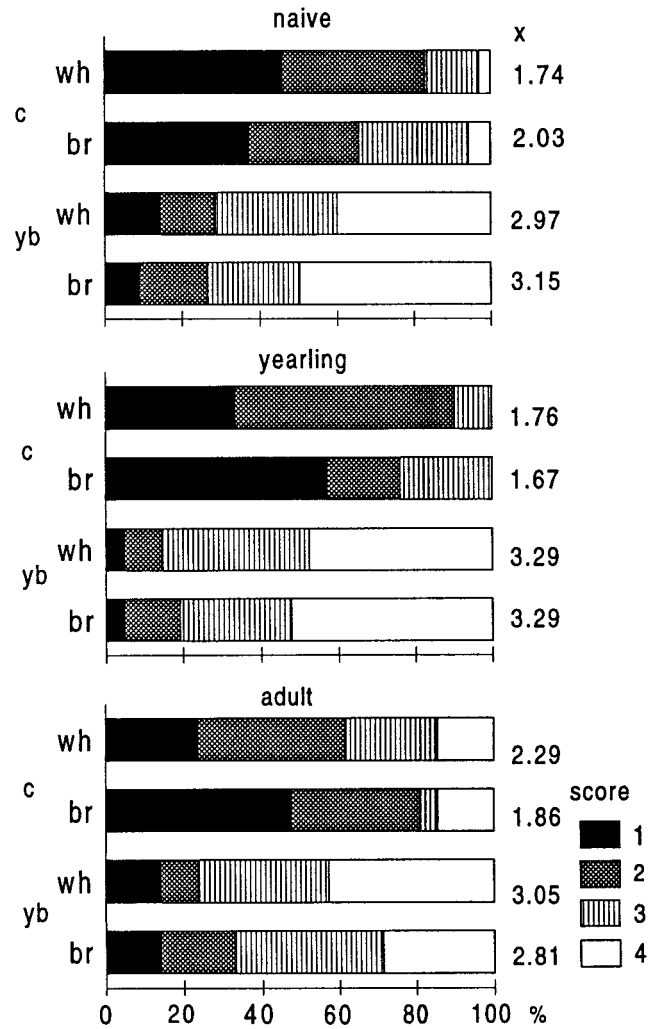


Figure 3
The percentage distribution of preference scores in the contrast trial in three age groups. The mean score from control and yellow-black mealworms from both white (wh) and brown (br) backgrounds in three age categories are also given.

CI, $.826 < p < .836$). The yearlings continued avoiding the yellow-black mealworms ($F = 78.20, 95\% \text{ CI}, .000 < p < .000$; Figure 3). There was, however, no difference between conspicuous or cryptic background ($F = 0.07, 95\% \text{ CI}, .825 < p < .836$). This indicates that color is a more effective signal than conspicuousness of the prey, even in experienced young predators.

Adult birds

In contrast to yearlings from the wild, there were not equally clear differences in the mean scores among adults (repeated-measures ANOVA: $F_{3,21} = 3.03, p = .052$). There was no interaction between color and gregariousness ($n = 24, F = 0.06, 95\% \text{ CI}, .845 < p < .854$). There was a significant effect toward color signal ($F = 13.97, 95\% \text{ CI}, .001 < p < .002$), but the predators did not avoid or prefer the groups ($F = 0.49, 95\% \text{ CI}, .533 < p < .544$; Figure 2).

In the contrast trial, no interaction was found between prey color or the background color ($n = 21, F = 0.18, 95\% \text{ CI}, .700 < p < .712$). Adults did take significantly more brown mealworms than yellow-and-black mealworms ($F = 14.18, 95\%$

CI, $.002 < p < .003$), but they did not prefer more conspicuous prey ($F = 2.14$, 95% CI, $.206 < p < .217$; Figure 3).

DISCUSSION

This experiment demonstrates that juvenile birds have inherited, initially or culturally transmitted avoidance and preferences that are later enhanced by experience. This avoidance was mainly toward color, but not toward conspicuousness or gregariousness.

Tests of inherited avoidance against grouping have had contradictory results. In experiments with chickens, Gamberale and Tullberg (1996a) found that naive chicks avoided grouped aposematic prey in contrast to single prey, but it is unclear to what degree this would reflect learning or initial avoidance. On the other hand, the benefit from grouping can be achieved by more rapid learning, as documented in experiments with naive chicks (Gagliardo and Guilford, 1993) and great tits (Alatalo and Mappes, 1996), or by increasing the signal repellence (Gamberale and Tullberg, 1998). The benefit of grouping might also be gained by predators leaving the place where they have found aposematic individuals. This experiment suggests, like Gamberale and Tullberg's (1998), that grouping does not function as an initial signal to naive predators. If grouping was acting as an inherited signal per se, both brown and yellow-black groups should be avoided more by predators than single prey items, regardless of their color. Experienced birds did not avoid grouped prey either. Moreover, in a previous experiments, wild great tits did not hesitate to attack grouped prey, and even preferred them at the first encounter (Mappes and Alatalo, 1997). However, we cannot entirely rule out the effect of overshadowing in our experiment. Because many cues are offered simultaneously, the predators might use the most intense stimulus, in this case the color.

Throughout the experiment, predators did not select prey types according to the two different backgrounds. This suggests that conspicuousness is not initially a signal, and differences in the preference scores are due more to the colors themselves (see Brodie, 1993; Roper, 1990; Sillen-Tullberg, 1985). The advantage of being conspicuous is more likely related to the avoidance learning, which has strong experimental support (Gittleman and Harvey, 1980; Roper and Redston, 1987; Roper and Wistow, 1986). Conspicuousness might also reduce recognition errors by experienced predators (Guilford, 1986).

There was an inherited component (either active avoidance or preference) in the behavior toward color signals in our experiment. Innate (i.e., without prior experience) avoidance against yellow-and-black color pattern or innate preference for alternative colors have previously been demonstrated for precocial species (Roper and Cook, 1989; Schuler and Hesse, 1985). There are only few studies with altricial species because they might have cultural transmission of food preference (see Avery, 1996), and therefore the results might be difficult to interpret. However, in the wild there might be similar cultural transmission in precocial species because juveniles follow and copy their parents for a few days after hatching (Nice, 1962). One might argue that our birds were not naive in the sense of having had no experience. However, we did not teach the naive birds to avoid certain colors, and the preference for brown might then be achieved through the feeding process. Nevertheless, for a prey individual avoidance of certain colors by predators is beneficial irrespective of its inheritance.

Wild-caught birds, yearlings, and adults differed in their behavior toward the aposematically colored mealworms. The reason yearlings avoided the yellow-and-black mealworms the most might be due to a fairly recent experience with apose-

matic models in the wild. Schuler (1982) showed that juvenile starlings (*Sturnus vulgaris*) were also more selective than adult birds. Moreover, adults might be more knowledgeable than yearlings and generalize the shape of all mealworms to palatable prey. Adults might also be more bold and try different prey types, while juveniles prefer safer options. These results also support the importance of additional learned avoidance toward yellow and black colors because yearlings were more selective than hand-raised birds in avoiding the signaling prey individuals.

Guilford (1990b) pointed out that the importance of the inherited avoidance is understandable if the prey items are deadly poisonous, but if the inherited avoidance is merely a difference in preference and can be altered due to cultural transmission, it is harder to understand. However, the initial preference or avoidance might form a fertile ground for learning by enhancing the learning rate. It is also important to bear in mind that aposematism supposes that there is a negative feedback (Edmunds, 1974). Therefore, if predators inherit avoidance of certain colors, this phenomenon is gradually lost without the negative reinforcement (Brower, 1989).

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