On the Function of Warning Coloration: A Black and Yellow Pattern Inhibits Prey-Attack by Naive Domestic Chicks

Author(s): Werner Schuler and Elke Hesse

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On the function of warning coloration: a black and yellow pattern inhibits prey-attack by naive domestic chicks

Werner Schuler and Elke Hesse
II. Zoologisches Institut der Universität, Berliner Strasse 28, D-3400 Göttingen, Federal Republic of Germany

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Summary. Young chicks were offered a choice of warningly coloured black and yellow and non-warningly coloured green (or olive) prey. Unfed chicks were given palatable painted mealworms on their first day. They directed their first peck at both colour types at the same probability; however, they ate the warningly coloured ones at a much lower rate. This is due to an inhibition of attack which becomes effective after pecking. Chicks which were a few days old showed the same behaviour. Since the control prey was in this case painted with an olive mixture containing the same colours as the warningly coloured mealworms, it can be concluded that the inhibition is caused by the black and yellow coloration. With accumulating positive experience of the chicks, the inhibition decreased. For permanent avoidance it must therefore be supplemented by unpleasant experience. Accordingly, chicks handled the unpalatable black and yellow ringed caterpillars of *Tyria jacobaeae* only a few times and always for a short period when offered repeatedly. The inhibition caused by the black and yellow pattern is attributed to a genetically fixed predisposition to avoid warningly coloured black and yellow prey which is the result of evolutionary adaptation.

Introduction

It is generally held that warning colorations, i.e. the conspicuous patterns of noxious prey animals, are signals indicating unpalatability to potential predators. In most cases of warningly coloured insects studied, the avoidance response of the predator is acquired (Morgan 1896; Mostler 1935; Windecker 1939; Schneider 1954; J.V.Z. Brower 1958; L.P. Brower 1969; Evans and Waldbauer 1982; but see Davies and Green 1976). For a long time it was therefore assumed that the only function of warning coloration is to facilitate avoidance learning and recognition. Warning coloration was regarded to be only a "besonders prägnantes Dressurmerkmal", i.e. an especially significant stimulus for learning (Wickler 1968, p. 118). Evidence for innate avoidance responses to warningly coloured snakes was reported at first for predatory fishes (Rubinoff and Kropach 1970) and a mammal (Gehlbach 1972). Later, Smith (1975, 1977) demonstrated innate avoidance responses to coral snake patterns in two neotropical bird species (see also Caldwell and Rubinoff 1983). Therefore it was concluded that "some predators have evolved innate avoidance reactions to particular aposematic signals ..., but more often predators learn to avoid such prey ..." (Harvey and Greenwood 1978).

The statement that the avoidance reaction is acquired does not say how naive birds respond to warningly coloured prey, even though it suggests that they react to it in the same manner as to other novel prey. In contrast to this, experiments carried out recently have shown that inexperienced birds kill, even during the first encounter, warningly coloured noxious insects less frequently than other prey (Wiklund and Järvi 1982). This was attributed to the chemical and mechanical defense of the species tested. However, warning coloration without noxious properties may have a similar effect: Naive birds eat warningly coloured harmless prey items at first less frequently than differently coloured ones (Coppinger 1970; Schuler 1982). Coppinger attributes this to the unusual appearance of warningly coloured prey (novelty hypothesis), whereas Schuler assumes an innate tendency to avoid such prey. The essential point is that Coppinger draws upon a common unspecialized behaviour whereas Schuler assumes a specific adaptation on the predator's side. A decision as to which of these two explanations is correct is impossible on the basis of available data (see Curio 1976, p. 105 for Coppinger's results).

In this investigation we have tried to disprove Coppinger's novelty hypothesis. For the experiments a precocious bird species which starts eating on its own shortly after hatching seemed to be much more appropriate than the altricial species tested until now, because the experience gained by the experimental subjects prior to testing can be controlled in a precocious species much more easily. We chose as our experimental species the domestic chicken, which eats, as does its ancestor, the Red Jungle Fowl (*Gallus gallus*) (Collias and Collias 1967), insects and other invertebrates in addition to seeds and plant material (e.g. McBride et al. 1969; Fölsch and Stahel 1982). Under conditions of feral life, invertebrate prey seems to be especially important for young chicks (for other Phasianidae see e.g. Glutz von Blotzheim et al. 1973) since they have higher protein requirements than adults (Scott et al. 1978).

The domestic chicken is also suitable for the present investigation because one does not have to assume that an adaptation to warningly coloured prey, possibly existing in its wild ancestor, has been lost in the course of domestication, since chicks were exposed – as long as they were kept outdoors – at least to the selection pressure exerted by warningly coloured black and yellow wasps (Vespidae). This is indicated by the observation that adult chicks reject wasps as well as black and yellow banded caterpillars on sight (Windecker 1939, p. 131f; Bergmann 1953, p. 184).

Based on these considerations we decided to use a black and yellow ring pattern, similar to that tested in young starlings (Schuler 1982), as the warning coloration in our tests.

Materials and methods

The experimental birds were unsexed broiler chicks (Lohmann hybrids) which were obtained for each experimental series on the morning of the hatching day from a local hatchery.

The artifical prey used was painted mealworms (larvae of *Tenebrio molitor* L). In one experimental series larvae of the cinnabar moth (*Tyria jacobaeae*, Arctiidae) were offered additionally. The mealworms were killed in boiling water and painted with non-toxic finger colours (yellow: CK 22, C. Kreul, Forchheim; black, and green: Marabu, Art. Nr. 030142). The black and yellow larvae had four equidistant black rings about 2 mm wide on a yellow background. All insects were stored in a deep freezer and thawed some minutes before the tests of the day started.

The uncovered test cage (91 × 63 × 20 cm) was made from grey PVC, except for its Plexiglas front. A partition left an arena 65 × 62 cm whose floor was lined with whitish paper. In every test five larvae of both types were offered. They were placed alternately in two rows of five on the floor of the arena at distances of 4.5 cm. The position of the types was exchanged for each new session. The chicks were tested in pairs since isolated ones are inclined to utter distress calls. Prior to the first test, arbitrarily taken pairs were marked individually with felt-tip pens. Subsequently, the more active chick of each pair was designed to be the focus bird for the observation of behaviour during the tests.

For the tests the chicks examined on the first day of their lives were placed in the arena. The older chicks were put into a starting box from which they could be released by means of a nylon thread. The behaviour of the chicks was observed through a one-way mirror window and documented on tape or by an event recorder (Peiseler-Stoppdrucker). In some tests a video camera and recorder (Sanyo VC 500 and VTC 7100) were also used. The test was stopped after 5 min or when all insects had been eaten. After each test the number of larvae eaten by both chicks together was noted.

Except during testing, the chicks examined on their first day were kept in a cardboard box and warmed by means of a 150 W infra-red bulb (Crompton R 125 reflector ruby). These chicks did not receive food and water until they had gone through their third and last session. The chicks which were first tested on their third day were accustomed in pairs to the test cage and the starting box on their second day. They were housed as a group in a cage similar to the test cage, the bottom of which was lined with whitish paper and strewn with white sand. A 100 W infra-red bulb producing no visible light (Elstein Infrarotstrahler) provided warmth. Chicken starter pellets and water were offered in white one litre feeders with a red base. On the first days pellets were spread on the floor and at the same time given in an earthenware dish. In one experimental series egg food (a mixture of hard boiled, mashed egg and shredded wheat) was given initially. On each experimental day food and water was withdrawn from all chicks simultaneously; it was replaced only after finishing the day's tests. To avoid accustoming the chicks to green objects (trees outside the window, doors painted green), the window and the doors of the room were covered with white paper.

The data were treated statistically following Siegel (1956), Rohlf and Sokal (1969) and McCornack (1965). All *P*-values given are one-tailed, according to our hypothesis that warningly coloured prey is eaten *less frequently* than other prey.

Results

The attack upon a black and yellow prey is inhibited

Chicks which had never been fed before were offered a choice between black and yellow larvae and green larvae three times on their first day. This experiment was carried out two times with ten pairs of chicks each. The two groups differed in activity, as can often be observed in chicks of the same breed from different hatching days (cf. Wallman 1979). However, both treated the larvae in basically the same manner. Calculating the data for each group separately yielded corresponding results and their data were therefore combined. Three chicks were excluded since they ignored the larvae in all three sessions.

In the course of the three sessions the chicks

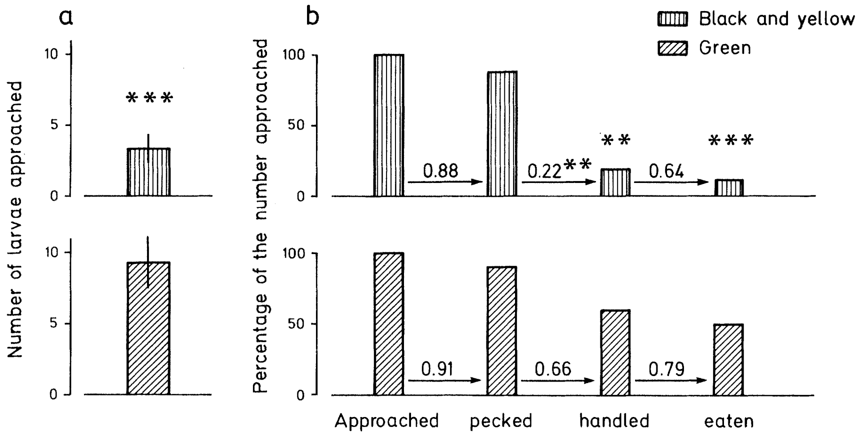

Fig. 1 a, b. Analysis of the behaviour of the chicks towards black and yellow or green prey tested on their first day. **a** Number of larvae approached in three sessions (mean ± SE per focus bird); **b** course of events during all attacks. *Handled:* picked up, carried and/or beaten on the ground. *Arrows*: probability for the transition to the following phase. ** $P<0.01$; *** $P<0.001$ for the difference to the corresponding value with green larvae (Wilcoxon matched-pairs signed-ranks test)

ate more than ten times less black and yellow larvae than green ($n=17$; mean ± SE per focus bird: 0.41 ± 0.31 vs 4.41 ± 1.28; $P<0.001$; Wilcoxon matched-pairs signed-ranks test). To find out how this enormous difference came about the behaviour of the chicks was analysed in detail.

The attack of a chick on an insect takes the following course: The chick approaches the prey with its head forward and fixates it from a short distance (in the following abbreviated as "approached"); pecks at it ("pecked"); picks it up, carries it some distance, treats it by beating it on the ground and by nibbling beak movements ("handled"); and finally swallows it ("eaten"). Initially all these phases are more or less distinct; carrying and treating may take up to one minute or even longer. With accumulating experience in hungry chicks the whole sequence is reduced to approaching, picking up and swallowing. In partially satiated chicks or with novel prey, all phases may still be distinct. The sequence is not completed each time when released – it may be discontinued after each phase by inexperienced as well as by experienced chicks.

Figure 1 shows that the behaviour of the chicks toward black and yellow larvae differed in two respects from their behaviour toward green larvae. First, black and yellow larvae released the sequence in the course of the three sessions less frequently (Fig. 1 a). Second, if released, the sequence was completed less frequently (Fig. 1 b). This second difference depends mainly on the fact that the sequence was carried on after pecking at a lower rate. This means that the attack upon black and yellow larvae was inhibited after pecking.

The responses described so far could be influenced partially by learning from gustatory experience and by feedback from the digestive system. This experience was not yet present in the chick pecking at its first larva. This very first physical contact was released by both colour types in nearly the same number of chicks (in 7 chicks by black and yellow and in 10 by green; NS; binomial test). The inhibition was effective shortly afterwards, because none of the chicks which ate at least one larva consumed a black and yellow one first ($n=11$; $P<0.001$; binomial test).

The inhibition was already effective during the first attack. As can be seen from Fig. 2, this attack was stopped after pecking in all instances of black and yellow larvae whereas with green larvae it was carried on until handling or even eating in a substantial proportion of the cases. This is true for the very first attack by each chick as well as for its first attack on the second colour type pecked (Figs. 2a and b, respectively). These data demonstrate that the inhibition to handle black and yellow larvae cannot come from experience resulting from handling or eating them. Experience with other types of food can also be ruled out because the chicks were not fed before. However, since the inhibition was effective only after pecking, it cannot be excluded that it was produced by an unpleasant taste stimulus. An indication of an inhibition in which such a stimulus war surely not present results from the observation that only half of the chicks which had first chosen green larvae later attacked black and yellow ones, whereas all chicks that had started with black and yellow subsequently attacked green larvae (5 out of 10 chicks vs 7 out of 7; $P=0.04$; Fisher exact probability test).

Exclusion of unpleasant taste as a cause of inhibition

The possibility that the inhibition of attack was caused by an unpleasant taste of the colours used was tested using control larvae coloured with a mixture of yellow and black paint. This mixture, containing black and yellow in the same propor-

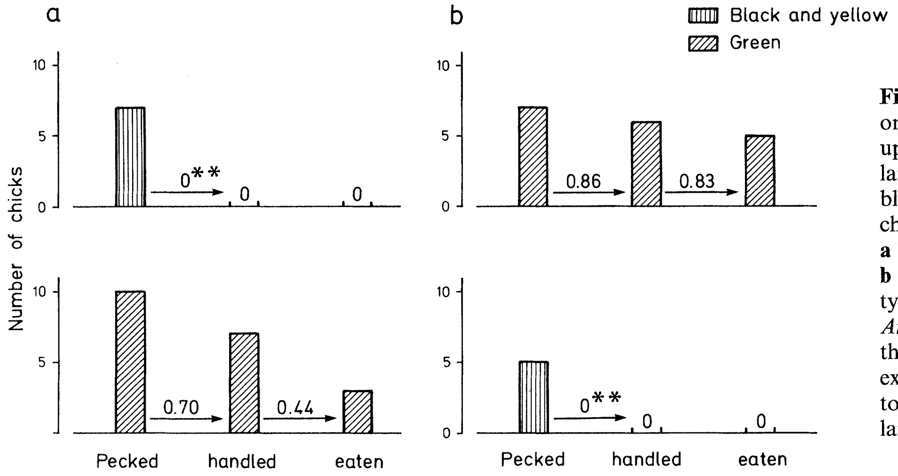

Fig. 2a, b. Behaviour of the chicks tested on their first day during their first attack upon black and yellow larvae and green larvae. *Upper half:* chicks attacking black and yellow larvae first; *lower half:* chicks attacking green larvae first. **a** The first attack of each chick; **b** the first attack on the other colour type by the same chicks. *Arrows*: probability for the transition to the following phase. ** $P < 0.01$; Fisher exact probability test for the difference to the corresponding value with green larvae

tions of weight as the black and yellow painted larvae, appears dark olive-coloured. The chicks were tested in this case once a day with a choice of black and yellow larvae and olive ones from their third to their tenth day of life. Apart from the tests they were given only egg food at first. After completing the third experimental session (on their fifth day), egg food was replaced by chicken starter pellets.

During the first three sessions these chicks behaved in a way very similar to those tested before: When pecking at their first larva they did not choose black and yellow significantly less frequently than the olive control larvae (4 vs 6 focus birds; NS; binomial test); however, the first larva eaten was never black and yellow ($n = 7$; $P < 0.01$; binomial test). The behaviour of the individual chicks showed that those birds which first attacked an olive larva, either continued handling this colour type exclusively until eating the first larva or until the end of the third session, or only occasionally and briefly pecked at black and yellow ones, whereas those chicks which had started with the black and yellow either changed to the olive larvae after the first attack, or they did repeat the attack upon the former, but stopped each time after a short period. Therefore, in this experimental series the first attacks on black and yellow larvae were also inhibited, from which it is evident that the inhibition resulted from the *distribution* of the colours but not from their taste.

The behaviour of the chicks in the further course of the series gives additional evidence that the black and yellow larvae did not taste worse than the controls. Nine pairs of chicks were tested here and one pair was excluded from the computation because they did not eat larvae at all until the end of the series. In the remaining eight pairs the mean percentage of larvae eaten continued to increase in both colour types. In the last session they did not consume significantly less black and yellow than olive larvae (mean ± SE: 3.5 ± 0.81 and 5.00 ± 0, respectively; NS; Wilcoxon matched-pairs signed-ranks test). Their selectivity was therefore essentially lower than during the first session in which they started eating larvae (black and yellow: 0.25 ± 0.25; olive: 4.00 ± 0.50; $P < 0.01$; Wilcoxon-test).

To test whether those chicks that had as pairs finally eaten all the larvae offered would continue to prefer olive larvae, the respective chicks were tested individually on their day 11. Now, six out of ten experimental birds consumed all the larvae, four of them in a random order (for each of them $P > 0.10$; comparison of the ranks of both colour types by means of the Mann-Whitney U-test). Therefore this sensitive measurement indicates also a reduced selectivity on the part of the chicks at the end of the experiment.

The decreasing selectivity in reverse order to the growing experience of the chicks demonstrates again that the black and yellow painted larvae cannot be considered as unpalatable for the chicks since unpalatability can be defined operationally best as *increasing* selectivity depending on accumulating experience (Edmunds 1974).

Stabilisation of the inhibition by an insect's defense

Morgan (1896) and Windecker (1939) reported that naive domestic chicks pecked at the black and yellow ringed larva of the cinnabar moth (*Tyria jacobaeae*) at first and subsequently rejected it. Both authors attributed this behaviour to the unpleasant taste of the caterpillar which contains histamine and poisonous alkaloids (Aplin et al. 1968). After having found that a black and yellow prey without an unpleasant taste can cause similar behaviour, we tested whether naive chicks treated this caterpillar under the conditions of our experiments in any other way than the black and yellow painted mealworms tested so far. For this experiment seven pairs of chicks were daily given a choice of *Tyria* caterpillars and green mealworms of equal length from the third to the tenth day of their lives.

The first peck was not aimed significantly less often at the caterpillars than at the green mealworms (in two and five focus birds, respectively; $P > 0.20$; binomial test). In contrast, none of the five focus birds which ate test insects took a caterpillar first ($P < 0.05$; binomial test). No essential difference could therefore be seen between the behaviour of these chicks and those tested with black and yellow painted mealworms.

In the further course of the experiment none of the seven pairs consumed a single caterpillar, whereas in the corresponding series described above black and yellow painted mealworms were eaten by six out of nine pairs. This difference is significant ($P < 0.02$; Fisher exact probability test). In the course of the eight sessions, the caterpillars were attacked by all seven pairs, although only a few times (3.0 ± 0.8 times per chick) and always for a very short period (total duration of contacts: 2.2 ± 1.0 s per chick).

This result shows that the inhibition of attack is much more stable in the *Tyria* caterpillars than in the painted mealworms. It can be assumed that this results from the taste of the poisons, although other characteristics might be responsible (e.g. the hairs of the caterpillars). Indications of distastefulness could not be observed every time a chick pecked at a caterpillar. However, in some instances they were unmistakable. One chick, which had eaten two green mealworms quickly and picked up the third with a caterpillar lying right next to it, showed head-shaking and bill-wiping for several minutes.

Discussion

These experiments demonstrate that naive chicks are inhibited in their attack of prey by a black and yellow warning coloration: Although they direct their first peck at black and yellow prey items in the same manner as at non-warningly coloured green or olive ones, they eat them at a considerably lower rate. This shows that there is no contradiction between Morgan's (1896) proposition that naive chicks peck at everything with the greatest impartiality and our finding that they eat palatable black and yellow coloured larvae less frequently than differently coloured ones.

Our experiments do not exclude pecking preferences. Really Morgan's classic sentence is not quite correct (Hess 1973), because naive chicks tested in large numbers peck at certain colours (e.g. Hess 1956; Fischer et al. 1975) and forms (Goodwin and Hess 1969) more often than at others. These pecking preferences, however, cannot explain the behaviour of our chicks, since they consumed mainly green larvae, whereas in the pecking preference tests green was the colour least preferred.

The rejection of palatable warningly coloured prey could be demonstrated even in chicks never fed before. Coppinger's (1970) novelty hypothesis, according to which warningly coloured insects are rejected because they look different from the prey to which the bird is accustomed, can for that reason not be valid in this case. Consequently it is legitimate to assume that the inhibition is innate. It must be understood as a genetically fixed predisposition to avoid warningly coloured prey.

An influence by food was not be observed in our experiments. This does not exclude the possibility that older birds, accustomed to a variety of insects prior to testing, respond differently to novel warningly coloured prey (see Evans and Waldbauer 1982). The probability that a naive chick attacks a mealworm can be influenced by its motivational state (Hogan 1965, 1966) and by unspecific experience, e.g. by the possibility to see and peck at its "wormlike" toes (Wallman 1979). Even though these factors cannot explain the origin of the inhibition, it is unknown whether it can be modified by an influence of this type.

The inhibiting effect of the black and yellow pattern decreased with accumulating positive experience. Therefore, as for the starlings (Schuler 1982), one has to postulate that the initial tendency to reject warningly coloured prey must, for permanent avoidance, be supplemented by unpleasant experience. This means that the inhibition must be understood as a genetically fixed predisposition to learn to avoid warningly coloured prey. This hypothesis is supported by the fact that the *Tyria* caterpillars were handled only a few times and always for a short period when offered repeatedly. Although further experiments are necessary to clarify which effect poisons have without a warning coloration, this experiment already corroborates the finding that a predator does not have to kill warningly coloured prey for the process of learning to avoid it (Järvi et al. 1981; Wiklund and Järvi 1982). This is important for the question whether warning colorations protect *via* individual selection.

The predisposition of the chicks to avoid warningly coloured black and yellow prey must be understood as an evolutionary adaptation. The prerequisites for this are fulfilled: First, a selection pressure can be assumed since chicks which approach black and yellow coloured prey hesitantly expose themselves less to the dangers of the defense of black and yellow noxious prey. Second, colour choice tendencies can be altered by selection as shown by Kovach (e.g. 1978, 1983). According to this idea the reaction of other bird species to warningly coloured prey should also be an adapted one: Only patterns that are meaningful for the predator in question should be effective and the type of response should be tuned to the prey's degree of harmfulness. Even though more work is necessary to prove these hypotheses, there are already some relevant results: An adaptation of the stimulus processing mechanism is indicated by the fact that bird species coming from the same geographical range as coral snakes show innate avoidance reactions to coral snake dummies (Smith 1975, 1977), whereas naive birds from other regions do not (Smith 1980). An adaptation of the type of response can be derived from the observations that the typical response to lethally poisonous warningly coloured snakes is flight (Smith 1975, 1977; Caldwell and Rubinoff 1983), whereas warningly coloured insects, which are less dangerous for birds, are sooner or later cautiously attacked. Finally, bird species for which warningly coloured insects are not noxious should not hesitate to eat them which is supported by the fact that young Bee-eaters prefer black and yellow patterns (Koenig 1950).

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