Anim. Behav., 1990, **39**, 466–473

Responses of domestic chicks to artificially coloured insect prey: effects of previous experience and background colour

T. J. ROPER
School of Biology, University of Sussex, Brighton BN1 9QG, U.K.

Abstract. Domestic chicks, *Gallus gallus domesticus*, which had no previous experience of insect prey were given a choice between red- and brown-painted mealworms (*Tenebrio molitor* larvae) on differently coloured backgrounds and after different types of prior exposure to similar colours in their home cages. When prey were presented on a white background, naive chicks preferred brown to red mealworms. This preference was not affected by prefeeding the chicks on red rather than brown chick crumbs but was reversed by rearing the chicks in red cages. When chicks had been given no deliberate exposure to either red or brown in their home cages they preferred brown to red prey on both brown and red backgrounds; but chicks previously exposed to both colours in their home cages preferred red prey on a brown background and brown prey on a red background. The results suggest that the relative aversion of chicks to red prey is specific to that colour, rather than reflecting a general aversion to novel colours or to colours that contrast with the background.

The term 'aposematism' (or 'warning coloration') refers to the observation that many prey that are unprofitable (for example, because they taste bad, are poisonous or are hard to catch) are also conspicuously coloured (Jones 1932; Cott 1940; Edmunds 1974). Most theories concerning the adaptive value of aposematism revolve around two interrelated hypotheses, namely: (1) that predators are able to learn to associate the appearance of a prey species with the fact that it is unprofitable, and (2) that such learning proceeds more effectively if the prey is conspicuous than if it is cryptic (Harvey & Greenwood 1978). The first of these hypotheses is supported by a wealth of evidence from a wide variety of predator and prey species (see review by Guilford, in press); the second has been less often tested, but such evidence as is available suggests that it is correct (Gittleman & Harvey 1980; Roper & Wistow 1986; Roper & Redston 1987).

Although it seems likely that aposematism is adaptive primarily because predators can learn to associate the appearance of a prey item with its unprofitability (Harvey & Paxton 1981), several studies suggest that at least some predators are reluctant to sample conspicuously coloured natural or artificial prey that they have not previously encountered (e.g. Smith 1975, 1977; Schuler 1982; Caldwell & Rubinoff 1983; Schuler & Hesse 1985). One of the most recent and most rigorously controlled of such studies is that of Schuler & Hesse, who used painted mealworms as experimental 'prey' for naive (i.e. completely unfed) domestic chicks. Given a choice between black-and-yellow striped and plain olive-green mealworms, chicks pecked equally at both prey types but ate considerably fewer of the striped ones.

The present study uses a similar technique to ask what features of a prey object trigger unlearned avoidance. One possibility is that prey are avoided to the extent to which they are novel (e.g. Coppinger 1969, 1970); another is that prey are avoided if they contrast with the background against which they are presented (e.g. Cott 1940; Gittleman & Harvey 1980); a third is that prey are avoided if their colour patterns involve contrasting colour boundaries (Guilford, in press); and a fourth is that particular colours or patterns act as specific releasers for avoidance in particular predator species, regardless of the visual context in which they are presented (e.g. Sillén-Tullberg 1985a). I attempted to assess the relative importance of some of these factors by presenting domestic chicks, *Gallus gallus domesticus*, with mealworms of different colours, on backgrounds that either matched or contrasted with them, after different degrees and types of prior exposure to the same colours.

GENERAL METHODS

Subjects and Housing Conditions

The subjects were male domestic chicks of the Warren strain, obtained from a commercial supplier and aged about 18 h at time of arrival (designated day 1). They were housed in pairs during days 1 and 2, and individually from day 3 on. Cages, measuring 23 × 23 × 30 cm, were constructed of grey-painted aluminium with white paper towelling covering the floors. Each cage was continuously warmed and illuminated from above by a 25-W bulb, and food (chick starter crumbs) and water were continuously available except for a 1-h food-deprivation period prior to each training or test session.

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Apparatus

The chicks were tested in a grey-painted aluminium arena, measuring 60 × 40 × 30 cm, illuminated from above by a 60-W bulb and resting on a floor covered with white paper towelling.

The experimental prey were mealworms (larvae of *Tenebrio molitor* L.), which were killed by brief immersion in boiling water and then cooled, dried and deep-frozen until required. To prepare them for experimental use they were reduced to a uniform length of 1 cm by removing segments from the tail end of the body, and then painted using artists' acrylic colours. Red mealworms were painted with a uniform coat of Naphthol Crimson 328 (Windsor & Newton Ltd) and brown ones with a mixture of Yellow Ochre 353 and Raw Sienna 344. The latter mixture produced a shade matching as closely as possible, to the human eye, the colour of unpainted mealworms.

Procedure

The chicks were given three 4-min training sessions to habituate them to the test arena: one on day 3 and two on day 4, separated by an interval of a few hours. In each session the chicks were allowed to peck at and consume chick crumbs scattered over the floor of the arena.

Test sessions, 3 min long, were conducted at a rate of one per day, beginning on day 4 or 5. In each session a chick was placed in the arena in the centre of a circle of six mealworms, three red and three brown, arranged alternately. An observer recorded on a dictaphone the colour of mealworm at which the chick directed its first peck, the colour of mealworm first eaten, and the total number of mealworms of each colour eaten during the session.

EXPERIMENT 1

The main purpose of the investigation was to see how early experience and background colour would affect the response of chicks to brightly coloured prey (see experiments 2 and 3). However, manipulation of these variables would be difficult using striped prey of the type found by Schuler & Hesse (1985) to be aversive to chicks. Experiment 1, therefore, was conducted to discover whether chicks would display an unlearned aversion towards uniformly coloured prey. Red was chosen as the experimental colour since it is often regarded as a warning colour in terrestrial arthropods (Rothschild 1984, 1985; see also Sillén-Tullberg 1985a, b).

Methods

Thirty-six chicks were given a choice between three red and three brown mealworms in the test arena, using the procedure already described. The background consisted of white paper towelling.

Results

The results (Fig. 1) showed a significant preference for brown mealworms with respect to all three measures of behaviour. The first worm pecked in the test session was more frequently brown than red (binomial test, $P=0·05$), the first worm eaten was more frequently brown (binomial test, $P=0·05$), and individual chicks ate more brown than red worms (Wilcoxon test, $T=22·5$, $N=19$, $P<0·01$). Thus chicks showed a relative aversion to red prey.

EXPERIMENT 2

The purpose of this experiment was to manipulate the early experience of chicks in order to determine whether prior exposure to red or brown would affect their relative aversion to red mealworms. In experiment 2a food colour was manipulated by giving one group of chicks red-dyed food in the home environment while the other received normal undyed brown food. In experiment 2b environment colour was varied by rearing the chicks in red or brown cages. Testing involved giving the chicks a choice between red and brown mealworms on a white background, as in experiment 1.

Methods

Each experiment involved 80 chicks, assigned to two equal groups, and was run in two replicates balanced for order of testing. In experiment 2a chicks were housed prior to testing in standard grey cages with white floors, but group 1 was fed from

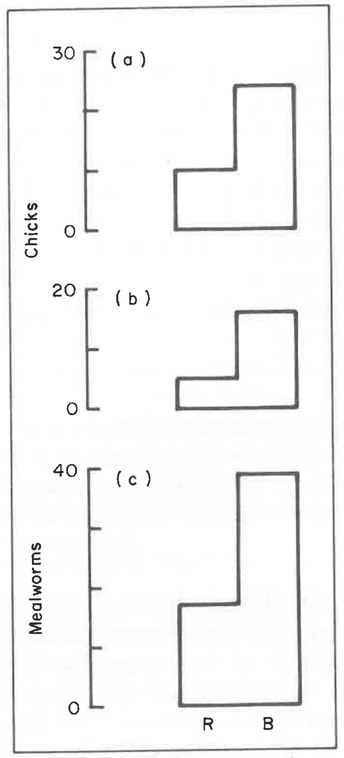

Figure 1. Results of experiment 1. (a) Number of chicks whose first peck was directed towards a red (R) or brown (B) mealworm. (b) Number of chicks that first ate a red or brown mealworm. (c) Total number of red or brown mealworms eaten by all chicks during the session.

arrival on red food while group 2 was fed on normal (i.e. brown) food. Red food was produced by mixing 1 litre of chick crumbs (sieved to remove dust and broken crumbs) with 15 ml of red food colouring diluted in 135 ml of water, spreading the crumbs out to dry at room temperature, and then sieving them again.

In experiment 2b the cages were altered to provide a red environment for group 1 chicks and a brown environment for group 2. This was done by covering the floor and walls of the cages with thin red card or with brown wrapping paper chosen to match as closely as possible, to the human eye, the colours of the experimental prey. To eliminate food colour as a confounding variable, all chicks were fed on blue-dyed chick crumbs.

Results

Considering first experiment 2a, the results (Fig. 2a–c) showed no significant between-groups difference in any of the three measures of behaviour, indicating that the two groups of chicks responded similarly to red versus brown prey. Thus, chi-squared tests revealed no significant between-groups difference in the number of chicks first pecking red versus brown mealworms ($\chi^2=1{\cdot}13$, $df=1$, $P>0{\cdot}2$) and no significant difference in the number of chicks first eating red versus brown prey ($\chi^2=1{\cdot}36$, $df=1$, $P>0{\cdot}2$). Similarly, analysis of variance on the individual scores for number of mealworms eaten showed no significant groups × colours interaction ($F_{1,51}=3{\cdot}26$, $P=0{\cdot}07$). Combining the scores across all 80 chicks in both groups, a strong overall preference for brown over red mealworms was evident in all three measures of behaviour (binomial tests, $P<0{\cdot}001$ for the first two measures; analysis of variance, $F_{1,51}=58{\cdot}02$, $P<0{\cdot}001$, for the third measure).

Considering now experiment 2b, the results (Fig. 2d–f) showed that red-reared chicks preferred red prey while brown-reared chicks preferred brown prey. Thus, there was a significant between-groups difference in the number of chicks first pecking red versus brown prey ($\chi^2=13{\cdot}01$, $df=1$, $P<0{\cdot}001$) and in the number of chicks first eating red versus brown prey ($\chi^2=12{\cdot}36$, $df=1$, $P<0{\cdot}001$). Similarly, analysis of variance on the scores for number of worms eaten revealed a significant groups × colours interaction ($F_{1,50}=4{\cdot}60$, $P<0{\cdot}05$).

Taken together, the results show that manipulation of food colour had no effect on the chicks' relative preference for brown mealworms, while manipulation of cage colour reversed the preference.

EXPERIMENT 3

Experiment 3 investigated the ability of background colour to affect chicks' aversion to red prey. It is often assumed that the 'conspicuousness' of a prey item is primarily, or even solely, a function of the degree of contrast between the prey and its background (e.g. Cott 1940). Furthermore, there is evidence that contrast between prey and background is sufficient to affect measures of predatory behaviour such as latency of attack, rate of attack, and speed and durability of avoidance learning when the prey tastes unpleasant (Gittleman & Harvey 1980; Roper & Wistow 1986; Roper & Redston 1987). On the other hand, Sillén-Tullberg (1985a) reported that zebra finches, *Taeniopygia guttata*, attacked red insect larvae, *Lygaeus equestris*, less vigorously than grey ones regardless of whether the prey were presented on red or grey backgrounds. Furthermore, in experiments 1 and 2a chicks preferred brown to red mealworms on a white background, against which both colours of prey were highly conspicuous. It is thus possible that coloration per se, rather than contrast, is responsible for the relative aversion to red.

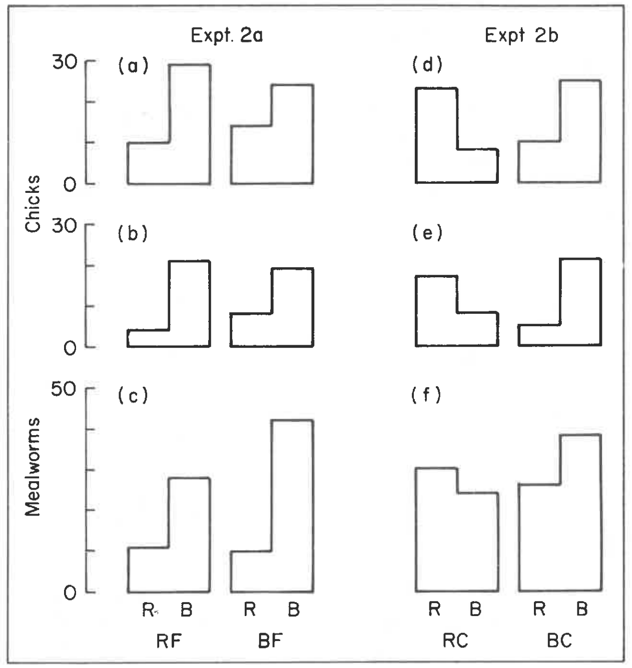

Figure 2. Results of experiment 2a (a–c) and 2b (d–f). (a) and (d) Number of chicks whose first peck was directed towards a red (R) or brown (B) mealworm. (b) and (e) Number of chicks first eating a red or brown mealworm. (c) and (f) Total number of mealworms of each colour eaten. RF: prefed on red food; BF: brown food. RC: reared in red cage; BC: brown cage.

In experiment 3 chicks were given a choice between red and brown prey on red or brown backgrounds. In experiment 3a the chicks had no prior exposure to red or brown in their home cages; in experiment 3b they were reared, prior to testing, in cages coloured half red and half brown.

Methods

Each experiment involved 48 chicks assigned to two equal groups. In experiment 3a the birds were housed prior to testing in standard grey cages with white floors, while in experiment 3b two walls and half of the floor of each pen were covered with red card and the other two walls and half of the floor with brown paper. To eliminate food colour as a confounding variable, all chicks in both experiments were fed on blue-dyed chick crumbs.

During training trials the floor of the test arena was the same colour as the floor of the chicks' home cages: i.e. white in experiment 3a and half red/half brown in experiment 3b. Blue chick crumbs were present in the arena for all chicks during training. All chicks were given two test trials, on days 5 and 6, respectively, in which the floor of the arena was covered either with red card or with brown paper. In each experiment group 1 chicks experienced the red floor on day 5 and the brown floor on day 6; for group 2 chicks the order of floor colour was reversed. All chicks were given the standard choice of three red and three brown mealworms.

In experiment 3a some chicks failed to peck at or eat any mealworms during testing on one or other background, presumably because feeding was inhibited by the novel background colour. These

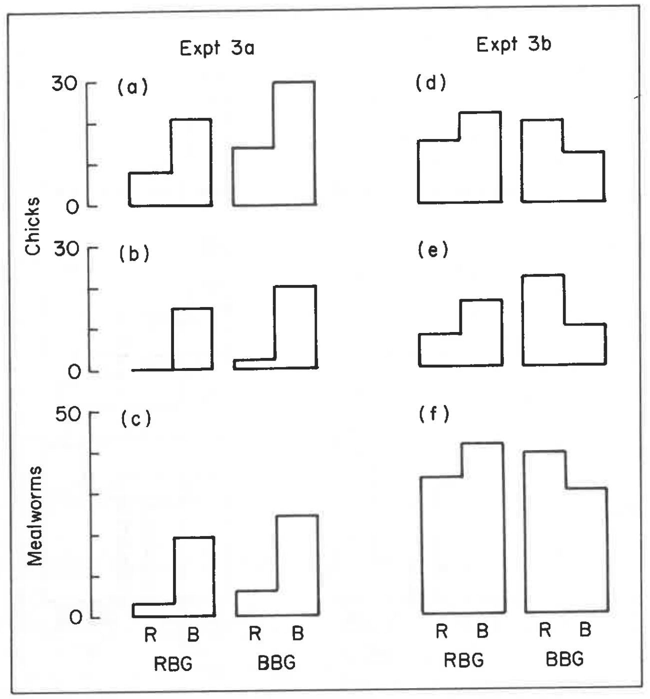

Figure 3. Results of experiment 3a (a–c) and 3b (d–f). (a) and (d) Number of chicks whose first peck was directed towards a red (R) or brown (B) mealworm. (b) and (e) Number of chicks first eating a red or brown mealworm. (c) and (f) Total number of red or brown mealworms eaten. RBG: tested on red background; BBG: brown background.

birds were given a second trial on the relevant background colour on the afternoon of the same day.

Results

Since there were no significant differences between groups owing to order of testing in either experiment (chi-squared tests, $P>0{\cdot}3$) the scores were combined over all 48 chicks for each background colour in each experiment. The results of experiment 3a (Fig. 3a–c) showed a relative aversion to red mealworms on both red and brown backgrounds, with no significant difference between backgrounds either in the number of chicks first pecking at worms of each colour ($\chi^2=0{\cdot}15$, $df=1$, $P>0{\cdot}8$) or in the number of worms first eaten (analysis of variance, backgrounds × colours interaction, $F_{1,57}=1{\cdot}73$, $P=0{\cdot}19$). Scores for number of chicks first eating mealworms of each colour were too small to permit statistical testing, but showed the same trend. Combining the scores over both backgrounds, all three measures of behaviour showed a highly significant preference for brown mealworms. (For number of chicks first pecking at or eating mealworms, binomial tests, $P<0{\cdot}001$ in both cases; for number of worms eaten, analysis of variance, $F_{1,57}=94{\cdot}6$, $P<0{\cdot}001$.)

In experiment 3b, by contrast, chicks tended to prefer brown mealworms when tested on a red background and red ones on a brown background (Fig. 3d–f). Statistical analysis showed a significant between-backgrounds difference in the number of chicks first pecking mealworms of each colour ($\chi^2=3{\cdot}39$, $df=1$, $P<0{\cdot}05$) and in the number of chicks first eating mealworms of each colour ($\chi^2=6{\cdot}92$, $df=1$, $P<0{\cdot}01$). Data on the total number of worms eaten followed the same trend but the between-backgrounds difference was not significant (analysis of variance, backgrounds × colours interaction, $F_{1,81}=2{\cdot}04$, $P=0{\cdot}16$).

To summarize, chicks preferred brown over red mealworms regardless of background colour when the colours in question were novel, and this suggests that red coloration per se is aversive. When the colours were familiar, however, chicks preferred prey that contrasted with the background colour.

GENERAL DISCUSSION

Experiment 1 showed that chicks with no previous experience of insect prey preferred brown-painted to red-painted mealworms when these were presented on a white background. This relative preference was not altered by prefeeding chicks on red crumbs (experiment 2a) but was reversed by rearing them in red cages for the first few days of life (experiment 2b). When the colour of the test background was manipulated, chicks not deliberately exposed to either red or brown in their home cages preferred brown prey on both background colours (experiment 3a); but chicks habituated to both colours in their home cages preferred whichever colour of prey contrasted with the background colour (experiment 3b).

Before discussing the significance of these results within the context of aposematic coloration it would be as well to consider two possible methodological objections. First, in experiment 1 chicks were fed in their home cages on brown chick crumbs, and this, by a process of generalization, could be responsible for their preference for brown mealworms. However, the same preference for brown worms was found in chicks prefed on red (experiment 2a) or blue (experiment 3a) food, so it seems that such generalization does not occur. This may be connected with the fact that chicks respond differently to the two types of food: they peck at and swallow crumbs with little hesitation, whereas their handling of mealworms involves a complex sequence of actions including pecking repeatedly at the prey, picking it up, mandibulating it, carrying it around, beating it on the floor, and often eventually rejecting it (Hogan 1965, 1966). Thus from the chick's point of view, crumbs and mealworms may be sufficiently different types of prey for generalization between them on the basis of colour to be inappropriate. Failure to generalize between different prey classes could also account for the fact that many fruits and berries that are red are attractive to avian predators, despite the fact that red is commonly regarded as a warning colour in terrestrial arthropods (e.g. Rothschild 1985).

A second possible objection to my experiments is that the relative aversion to red could result from a difference in the taste or smell of the two types of paint, red being more aversive. However, there was no obvious sign (e.g. from head-shaking or beak-wiping) that either colour of mealworm was aversive when approached or ingested. Furthermore, in two groups of chicks reared in red cages (in experiments 2 and 3) there was a relative preference for red worms, suggesting that preference is indeed based on the visual characteristics of the prey.

Given this conclusion, what do the results tell us about the precise stimulus features that contribute to an unlearned aversion? A well-established idea is that novelty is aversive, and many studies have shown that avian predators respond tentatively to novel insect prey (see reviews by Coppinger 1969, 1970; Barrows et al. 1980). The same applies to chicks confronted for the first time with mealworms, whatever their colour (Hogan 1965; personal observations). The present study, however, concerns the question of what determines differential responding to prey that are equally novel (in the sense that chicks have had no previous experience of them) but that differ in one particular feature (in this case, colour). As Greig-Smith (1987) has pointed out, the concept of 'novelty' is too crude to do justice to such cases. Rather than postulating that red mealworms might in some general sense be more 'novel' to chicks than brown ones, we need to ask more specific questions about the effects of particular kinds of experience. Experiment 2b, showing that chicks exposed to red or brown in their home cages prefer mealworms of the same colour, shows that previous experience can affect choice of colour, and suggests that novelty of coloration, other things being equal, is indeed aversive.

A different approach is to focus on the colours themselves and their relation to background colour. Many studies have shown relative aversions, in naive predators, to prey of this or that colour or pattern (e.g. Smith 1975, 1977; Järvi et al. 1981; Schuler 1982; Wiklund & Järvi 1982; Caldwell & Rubinoff 1983; Schuler & Hesse 1985; Sillén-Tullberg 1985a, b; Wiklund & Sillén-Tullberg 1985; Madsen 1987). In all these studies the prey were either real or were naturalistically painted, and in most of them striped prey were found to be aversive relative to plain-coloured prey. This, together with the fact that striped aposematic prey are common in nature, has led to the suggestion that striping is in itself conspicuous because it results in internal colour-contrast boundaries (Guilford, in press). The present results do not directly address the question of whether striping contributes to aposematism (see Roper & Cook, in press), but they do show that it is not a necessary condition for unlearned avoidance (see also Sillén-Tullberg 1985a, b).

Two remaining hypotheses are that aversiveness is determined by the degree of contrast between the prey item and its background (e.g. Cott 1940) and that particular predator species are averse to particular colours or patterns, regardless of background (e.g. Smith 1975; Caldwell & Rubinoff 1983). As regards the first hypothesis, there is evidence that predators learn more effectively to avoid noxious prey if it contrasts with its background (Gittleman & Harvey 1980; Roper & Wistow 1986; Roper & Redston 1987); but in the present study and others (e.g. Schuler 1982; Schuler & Hesse 1985; Madsen 1987) the different types of prey were so easily visible to predators that it seems implausible to invoke contrast as a source of the unlearned aversions. Furthermore, contrasting prey actually seem to be more attractive to naive predators in at least some circumstances (Gittleman & Harvey 1980; Roper & Wistow 1986; Roper & Redston 1987; and the results of experiment 3b).

We are left, then, with the idea that specific sign-stimuli are aversive in themselves, regardless of background colour; and this fits with my observation that naive chicks found red prey more aversive than brown on both red and brown backgrounds (experiment 3a). On the other hand, habituation to red in the home cage can clearly overcome such an effect (experiment 3b). Thus while a preference for brown over red is unlearned, in the sense that it occurs in chicks that have never before experienced prey of the relevant type, it is nevertheless open to modification by certain sorts of previous exposure to the colours in question.

ACKNOWLEDGMENTS

Some of the data reported here were collected during the course of undergraduate projects by P. Chapple, S. Clarke and C. Hart. I thank them for their enthusiastic help.

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(Received 16 September 1988; initial acceptance 2 November 1988; final acceptance 29 December 1988; MS. number: 3286)