Behavioral Ecology
doi:10.1093/beheco/arm027
Advance Access publication 29 April 2007

State-dependent decision making: educated predators strategically trade off the costs and benefits of consuming aposematic prey

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Aposematic prey advertise their defences, such as toxins or stings, to visually hunting predators using conspicuous warning coloration. Both the conspicuousness and the chemical content of prey determine the speed of avoidance learning by naive predators, and it has long been assumed that predator education is the main selective pressure in the evolution of aposematism. However, recent theoretical models have considered how educated predators could also exert significant selection pressures on aposematic prey by increasing their attack rates on defended prey in times of food shortage. Currently, there are no clear experimental data to support these models. In this study, we show that European starlings (*Sturnus vulgaris*) increase their attack rates on chemically defended insect larvae when their body masses and fat stores are experimentally reduced. In addition, the increase in attack rate is not simply due to indiscriminate attacks made when energy reserves are low but is based on knowledge about the prey's defences. Taken together, these results suggest that educated adult predators will strategically trade off the energetic benefits of prey against their toxic costs according to their energetic needs. This result challenges classic theoretical models of the evolution of aposematism based purely on predator learning and forgetting rates and demonstrates the need to consider energy-toxin trade-offs in foraging decisions on defended prey. We discuss the implication of these results for the evolution of chemical defences and warning signals. *Key words:* aposematism, discrimination, energetic state, predation, quinine, receiver psychology. *[Behav Ecol 18:645–651 (2007)]*

Aposematic prey signal their chemical defences to predators using conspicuous warning coloration (Cott 1940; Edmunds 1974). The benefits of being conspicuously colored are thought to arise through predator education because naive predators learn to avoid conspicuous defended prey more quickly than cryptic defended prey (Gittleman and Harvey 1980; Guilford 1990). Increasing the speed of aversion learning reduces the numbers of individual prey attacked and eaten during the learning process, providing potential selective benefits to the warning coloration. Aversion learning of conspicuous aposematic prey by avian predators is also faster when prey have higher levels of chemical defences (Skelhorn and Rowe 2006a). Therefore, the role of learning has been dominant in theories surrounding the evolution of aposematism (e.g. Rothschild et al. 1984; Guilford and Dawkins 1993; Speed 1993a; Speed and Turner 1999; Servedio 2000) and has received by far the most attention empirically (e.g. Roper and Redston 1987; Alatalo and Mappes 1996; Roper and Marples 1997; Lindström et al. 1999; Rowe 2002; Skelhorn and Rowe 2005).

However, naive predators are not the only selective pressure acting on prey defence strategies. There are clear experimental data showing that educated predators do not always completely avoid aposematic prey, and their asymptotic avoidance rate can be above zero (Skelhorn and Rowe 2005, 2006b). Given that the education process is likely to be short relative to the entire life span of a predator, educated predators will continue to exert strong selection on aposematic prey, and conspicuous warning signals may also be selected to increase prey recognition by experienced predators (Guilford 1985). Learning theory predicts that the asymptotic attack rate of educated predators will be determined both by the salience of the color pattern and the chemical defences of the prey (Rescorla and Wagner 1972; Skelhorn and Rowe 2006b). However, in a natural foraging situation, the asymptotic attack rate might also result from a trade-off between the energetic benefits obtained from the energetic content of the prey and the potential unpalatability or processing costs of the toxins. For example, when palatable prey are relatively scarce, the benefits of obtaining energy from defended prey increases, and predators could raise their attack rates on aposematic prey despite the costs involved with ingesting toxins (Kokko et al. 2003; Lindström et al. 2004). The energetic requirements of a predator are therefore likely to be important in determining the selection pressures exerted by educated predators on warningly colored prey.

Two recent stochastic dynamic programing models attempting to capture the impact of predatory behavior on evolutionary outcomes have assumed that attack rates on defended prey will increase as the energy reserves of a predator decrease (Sherratt 2003; Sherratt et al. 2004). However, currently there are no data showing that manipulations of a predator's energetic reserves affect its foraging decisions in relation to defended prey. Observational studies suggest that predators increase their frequency of attack on unpalatable prey when undefended prey are rare (e.g. Cook et al. 1969), and some studies have found that food deprivation periods can increase a predator's motivation to attack defended prey (in birds [Chai 1986], lizards [Sexton et al. 1966], copepods [Williamson 1980], and insects [Gelparin 1968; Hileman et al. 1995]). However, these studies fail to show whether this behavior results from strategic decision making caused by

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Received 28 June 2006; revised 20 February 2007; accepted 27 February 2007.

reductions in energetic reserves or through reduced motivation or cognitive capacity to identify defended prey. Moreover, they have failed to directly measure energetic state and so direct state-based consumption of chemically defended prey has yet to be demonstrated. Our experiment specifically investigates the effects of a predator's energetic reserves on its consumption of chemically defended prey and the cognitive processes underlying this behavior in order to better understand the selective forces exerted by educated predators on defended prey.

METHODS

Study species and housing

Subjects were 6 European starlings (*Sturnus vulgaris*) caught under licence from English Nature (licence nos 19991381 and 20001512). All the birds were male in order to reduce variance in behavior arising from sex differences in mass and mass regulation strategies. Prior to the experiment, birds were housed in a larger, mixed-sex group in an indoor aviary. All the birds had previously been used in operant foraging experiments; however, they had not experienced unpalatable prey in the laboratory nor the stimuli or experimental protocol used in the current experiment. For the duration of the experiment, the birds were housed individually in wire mesh cages (450 × 750 × 450 mm, h × w × d) arranged in a single room such that they had visual and acoustic contact with each other. Cages were equipped with 2 dowel perches and 2 water bottles; birds had ad libitum access to water throughout the experiment. The birds were maintained under a 14:10 h light/dark cycle produced by daylight spectrum bulbs. At the end of the experiment, birds were returned to the aviary for future use.

Mass manipulations

The experiment relied on comparing foraging choices of subjects at free-feeding mass (free-fed) and at a reduced mass (restricted). Throughout the experiment, birds were caught each morning when their intestines were empty (ca 0800 h Greenwich Mean Time) and weighed (to the nearest 0.1 g [Ohaus Scout SC6010]). In order to provide an additional measure of condition, birds' furcular fat scores were visually assessed using a scale based on Gosler (1996). To establish the birds' free-feeding masses at the start of the experiment, they received 40 g of pheasant breeder pellets a day, which was more than any bird had previously consumed in a 24-h period. Once their masses had stabilized, we calculated each individual's mean mass over 5 days as its baseline free-feeding mass. From this we calculated a corresponding mass for each subject, which was 95% of its free-feeding mass. This was the reduced mass at which birds would be maintained during the restricted phases of the experiment. To lower the birds' masses to their reduced masses during the experiment (see below), we decreased their daily food intake, initially giving them 14 g, and then slowly reducing the daily ration according to each individual's mass loss. It took birds between 6 and 17 days to reach their reduced masses. Once a subject had reached its reduced mass, it was maintained at this mass for 4 days (Figure 1), before again being given 40 g of food per day in order to return it to its free-feeding mass. The birds' masses were then reduced again to rule out any order effects (see Figure 1).

Prey

The prey were live mealworm larvae (*Tenebrio molitor*) measuring approximately 20 mm in length, a preferred food of starlings. Birds were initially trained to eat single mealworms presented on a 38-mm diameter clear plastic Petri dish placed on the bottom of the cage. During the experimental trials, we used undefended and chemically defended mealworms. Before the start of each experimental trial, the undefended mealworms were injected with 0.02 ml water intraorally, whereas the defended mealworms were injected with 0.02 ml of 2% quinine sulfate suspension intraorally. To allow birds to distinguish between the 2 prey types, we placed colored disks of paper (42 mm in diameter) under the Petri dishes to signal the level of chemical defence. We used 3 color pairings (pink and blue, orange and purple, or yellow and green) to signal the 2 prey types, and by reversing the color-prey type association for half the birds, we ensured that each bird had a unique color discrimination task.

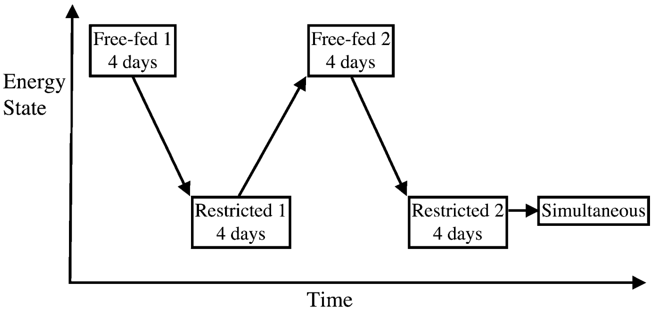

Figure 1
A schematic view of the experimental design. The experiment was split into 4 phases during which we manipulated the energetic state of individuals: in the first and third phases, birds had ad libitum food access, and in the second and fourth phases, birds were kept on restricted diets. Each phase consisted of 4 days during which the birds were offered 16 prey each day (8 undefended and 8 chemically defended prey), and the numbers of prey eaten were recorded. In a final phase of the experiment, birds were given 3 simultaneous choice trials to test which cues they were using to inform their foraging decisions.

Training

Birds were trained at their free-fed conditions but were food deprived for 2 h before the start of each daily trial. During training, each cage was moved to a new position in the room that was behind a white curtain that visually isolated the bird from both the experimenter and the other birds. The bottom of the curtain was level with the bottom of the cage so that the Petri dishes could be inserted and removed, via a central cage door, without disturbing the bird. In order to observe the bird, we used a video camera connected to a television monitor that was placed where the focal subject could not see it.

As soon as the birds readily consumed the mealworms from the dishes, each bird was given daily trial of 16 sequentially presented mealworms. On each presentation, a mealworm in a dish was placed on the cage floor just inside the cage door. If a bird ate the mealworm, the dish was removed immediately (to remove any visual cue which would occur when prey are consumed in the wild), but if a bird failed to eat the mealworm, the dish containing the uneaten mealworm was removed after 1 min. There was a 3-min interval between each successive presentation in order to get the birds used to the frequency of food delivery during experimental trials. Once a bird had consumed 5 consecutive mealworms in a day, we introduced a disk of white cardboard underneath the dish. Once a bird had consumed 5 consecutive mealworms with white cardboard discs underneath, we began the experiment.

Experimental procedure

Birds started the experiment subject to free-feeding conditions. After a 2-h deprivation period, they were each given a daily session of 16 presentations as described above. Birds were given a series of 8 undefended prey (signaled by a colored disc of paper under the dish) and 8 defended prey (signaled by a differently colored paper disc). The sequence of prey was randomized within each block of 4 presentations so that there were 2 undefended and 2 defended prey for every 4 presentations, which ensured that prey were equally distributed within the daily session. As during training, birds had 1 min to decide whether or not to eat a mealworm, and presentations were made every 3 min. We recorded if the mealworm was attacked and consumed and the attack latency. We also recorded other behavior such as bill wiping and head shaking to monitor any effects that the quinine had on the birds. All birds continued to eat the mealworms throughout the experiment.

We gave the birds daily sessions of 16 presentations until they had acquired the discrimination and ate more undefended mealworms than defended mealworms, which took between 6 and 14 days to achieve. We defined acquisition as being when a bird's previous 3-days' choices significantly departed from random using a chi-squared test (χ^2 range = 3.84–16.04, all $P < 0.05$). Once a bird had acquired the discrimination between the 2 prey types, we continued to collect data for 4 more days to provide our initial free-fed measure of discriminatory performance (Figure 1). We then began to reduce the bird's mass for the restricted treatment. Once the bird reached its reduced mass, we collected data for another 4 days, before returning it to its free-fed state. We collected 4 more days of data with the bird at free-fed state before returning it for the final time to their restricted state and collecting 4 more days' data. This alternation of masses enabled us to rule out any order effects on an individual's decisions. We continued to collect data during the periods of mass change in order to look for correlations between mass and prey choice.

Simultaneous choice trials

At the end of the final restricted phase of the experiment, we gave the birds a short series of simultaneous choice trials. Because defended prey consumption increased at lower masses, we needed to test whether this change resulted from a strategic decision by the birds to eat defended prey or was simply a reduction in discriminatory ability. We also needed to establish whether birds had learned the color signals or were using other visual cues to differentiate between undefended and defended mealworms. The trials followed the same basic procedure outlined above, except that instead of presenting a single mealworm in each trial, 2 prey types were presented simultaneously, and the birds had to choose between them. Birds had a single trial of 16 presentations of pairs of prey on each of 3 consecutive days. On the first day, birds were given a choice between the 2 prey types that they had experienced in the experimental phase (color-quinine treatment). This treatment enabled us to test whether birds could discriminate between the defended and undefended prey at low body mass. If birds attacked these prey colors at random, we could conclude that birds no longer used their learned color information at low body mass. On the second day, birds were given a choice between mealworms presented on their colored backgrounds, but now all mealworms were injected with water (color-only treatment). This treatment allowed us to test whether birds were using the learned color signals to distinguish between the defended and undefended prey, rather than any cue associated with the mealworms themselves. On the final day, we gave birds a choice between defended and undefended mealworms without the color cues present (quinine-only treatment). This allowed us to test whether birds could distinguish between undefended and defended mealworms in the absence of color cues or whether they relied entirely on their learned color cues.

RESULTS

The effects of food restriction on body mass of starlings

Our manipulations of body mass and energy reserves were successful. Birds also had lower furcular fat scores in the restricted phases compared with the free-fed phases (free-fed median = 3; restricted median = 1; Wilcoxon signed-rank test: $Z = -2.23$, $N = 6$, $P = 0.026$, Figure 2a). The average masses of the birds were significantly lower in the restricted phases than the free-fed phases of the experiment (free-fed mean ± standard error [SE] = 76.3 ± 0.96 g; restricted mean ± SE = 71.4 ± 0.89 g; paired *t*-test: $t = 24.2$, $P < 0.001$, degrees of freedom [df] = 5, Figure 2b). We performed linear regressions on the daily masses and furcular fat scores for each bird and found that they were highly correlated (for all birds, all $r^2 > 0.78$ and all $P < 0.001$). Therefore, it is likely that the mass loss was due in large part to fat loss.

The effects of body state on foraging decisions

By the end of the training period, birds learned to discriminate between the undefended and defended mealworms (mean total number of mealworms consumed during the final 3 days of training ± SE: undefended = 21 ± 0.68, defended = 7.5 ± 1.34; all $\chi^2 > 3.84$, all $P < 0.05$). During the experimental phases, birds continued to consume a high proportion of the undefended mealworms that were presented to them (see Figure 2c). Given the similarities in behavior between the 2 free-fed and 2 restricted phases, we pooled the data from the 2 replicates for the following analyses. In both the free-fed and restricted phases of the experiment, birds consumed almost all the 64 undefended prey offered, eating slightly more of the undefended prey in the restricted phases than in the free-fed phases (free-fed mean ± SE = 60.8 ± 0.91 mealworms, restricted mean ± SE = 64.0 ± 0.0 mealworms, paired *t*-test: $t = 3.48$, $P = 0.018$, df = 5). This difference occurred due to slightly lower scores in the first free-fed phase, which may be indicative of the birds not having fully learned the task in this first phase of the experiment. However, the difference in the numbers of defended mealworms eaten between restricted and free-fed phases was far more striking (Figure 2c). Birds ate significantly fewer defended mealworms in the free-fed phases than the restricted phases (free-fed mean ± SE = 23.0 ± 4.94 mealworms, restricted mean ± SE = 62.3 ± 0.84 mealworms, paired *t*-test: $t = 9.36$, $P < 0.001$, df = 5). To analyze whether the birds ate relatively more defended mealworms during the restricted phases than during the free-fed phases, we divided the number of defended mealworms eaten by the number of undefended mealworms eaten, and arcsine square-root transformed the resulting ratio to restore normality. We found that the ratio of defended prey consumed was significantly lower in the free-fed treatment than in the restricted treatment (paired *t*-test: $t = 20.5$, $P < 0.001$, df = 5, Figure 3).

During the free-fed phases of the experiment, the mean number of defended prey consumed by birds increased on successive days during free-fed phase 1 and decreased on successive days during free-fed phase 2 (Figure 2c). To test whether these changes were related to daily masses, we plotted the number of defended prey consumed against the standardized mass for each bird during each free-fed phase and drew linear regression lines through the points. The standardized mass was the daily mass divided by the free-feeding mass calculated for each bird. In free-fed phase 1, 4 of the 6 birds consumed fewer defended prey when they were heavier (signs test: $P = 0.34$, Figure 4a), whereas in free-fed phase 2, all 6 birds ate fewer defended prey when they were heavier (signs test: $P = 0.016$, Figure 4b). Therefore, the changes in the number of

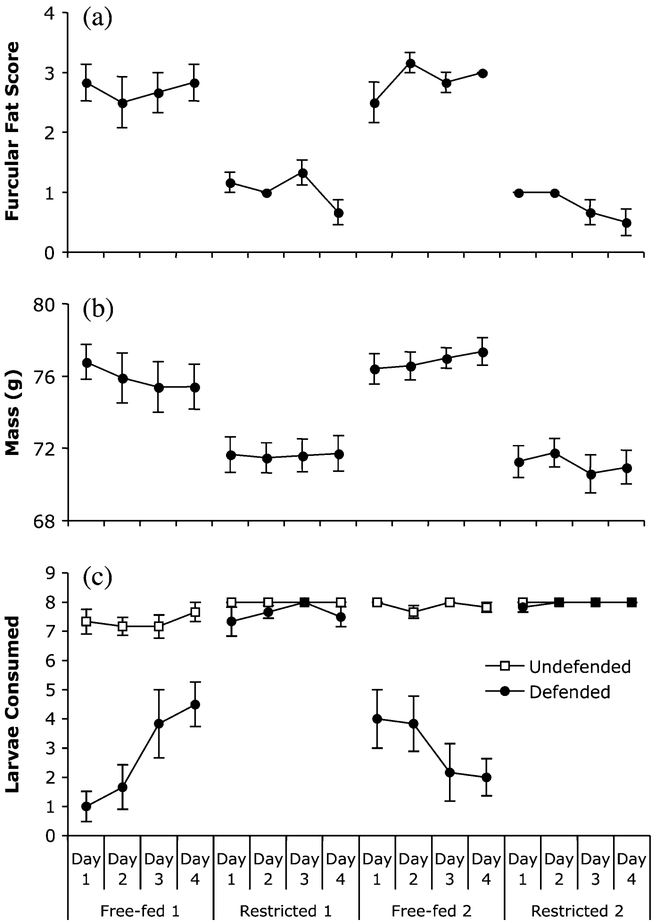

Figure 2
The means (±SE) of (a) furcular fat scores, (b) mass, and (c) numbers of defended and undefended prey consumed on each day throughout the first 4 phases of the experiment.

chemically defended larvae consumed in the free-fed phases could have resulted from daily changes in the birds' masses.

Simultaneous choice trials

In order to investigate the mechanisms of decision making, we conducted a series of 3 sets of simultaneous choice trials. In the first treatment, birds were given a choice between the 2 prey types that they had previously experienced in the experimental phase (color-quinine treatment). Birds could discriminate between the 2 prey types, consuming significantly greater numbers of the undefended prey than the defended prey (paired *t*-test: $t = 7.79$, df $= 5$, $P = 0.001$, Figure 5). In the second treatment, when all mealworms were injected with water (color-only treatment), birds still preferred to attack prey with the undefended color, confirming that they could use color cues in the absence of any potential differences between quinine-injected and water-injected mealworms ($t = 3.83$, df $= 5$, $P = 0.012$; Figure 5). On the third day, when given a choice between quinine-injected and water-injected mealworms in the absence of color cues (the quinine-only treatment), birds were unable to discriminate between defended and undefended prey on the basis of their appearance or taste ($t = 0.19$, df $= 5$, $P = 0.86$; Figure 5). Taken together, the results from the simultaneous choice trials show that birds are still able to discriminate between defended and undefended mealworms when they have fewer reserves and that they do this using learned color cues.

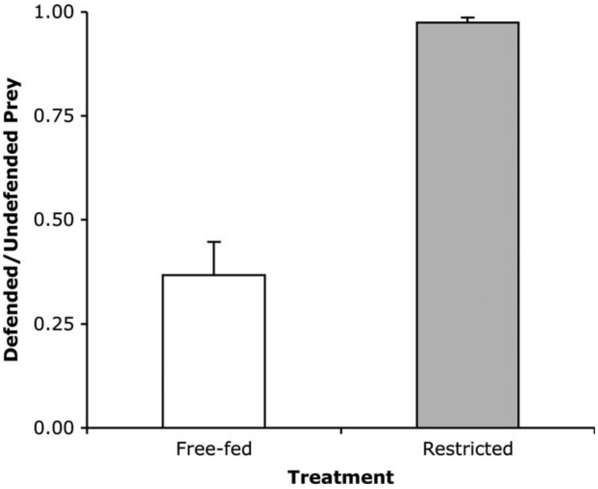

Figure 3
The mean (+SE) ratio of defended prey to undefended prey eaten in each treatment.

DISCUSSION

Our results clearly demonstrate that energy reserves affect the decisions made by educated predators foraging on defended prey. When food was restricted, and birds' fat reserves and masses were reduced, they ate more of the defended prey compared with when they were free-fed. Small, uncontrolled daily fluctuations in individual masses during the 2 free-fed phases also explained much of the variation in the numbers of defended prey attacked on each day. These results are consistent with previous observations and studies on a variety of predators (Swynnerton 1915; Sexton et al. 1966; Gelparin 1968; Chai 1986; Hileman et al. 1995; Gillette et al. 2000) and support the assumptions of recent stochastic dynamic programing models of state-based consumption of defended prey (Sherratt 2003; Kokko et al. 2003; Sherratt et al. 2004).

An alternative explanation for our data is that birds were becoming less discriminating when they had low masses and fat reserves, perhaps through a reduction in their motivation to discriminate or an impairment in their cognitive ability to do so. However, the simultaneous choice trials at the end of the experiment showed that birds were able to discriminate between the defended and undefended prey on the basis of their color signals when they were food restricted. This confirmed that the birds retained the association between the color cues and the defence level of each prey type and could use this information to avoid defended mealworms when prey were presented simultaneously. Therefore, birds can have information about the costly chemical content of prey but trade off that information against the energetic benefits of consuming the prey. The costs to predators of ingesting defence chemicals can occur through increased handling, malaise, or additional costs of processing toxins (e.g., Mostler 1935; Fink and Brower 1981; Gilardi et al. 1999). Our experiment did not quantify the cost of quinine to starlings, but given that it is potentially toxic to birds at very high doses (Alcock 1970), it seems likely that the chemical was having some postingestive effects. We do not currently know how animals detect ingested chemicals or how this information is integrated with information about energetic reserves to inform decision making, which is a complex problem in a varied diet (Yearsley et al. 2006).

One potential criticism of our study is that our manipulations of energetic state in starlings were not realistic and may not lead to selection on defended prey in the wild. However,

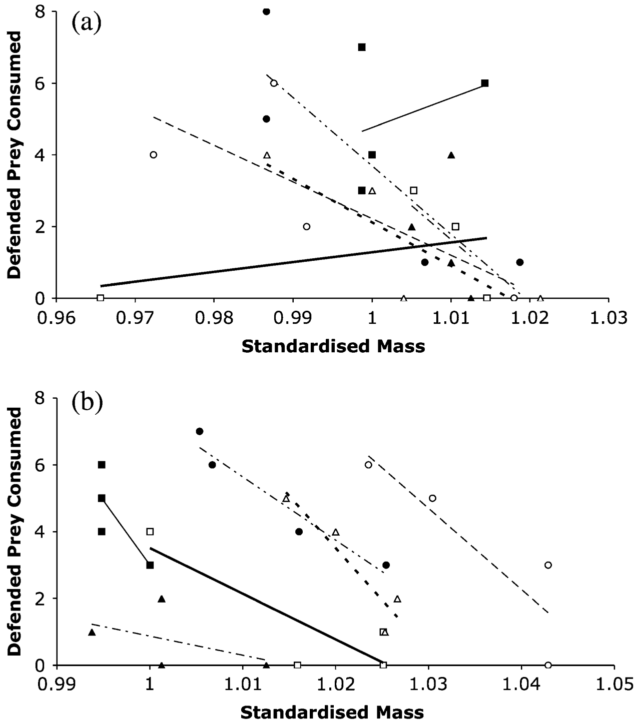

Figure 4
Regressions of the number of defended prey consumed on standardized mass for each bird in (a) the first free-fed phase and (b) the second free-fed phase. Each data point represents the scores and masses for a single day within each 4-day period. The 4 data points for each bird are shown by different symbols, and each line is the regression for a single subject.

a starling's mass can fluctuate by up to 15 g throughout the year (Feare 1984), and migrating birds can also lose a large proportion of their body mass and can arrive at their destination in very poor energetic state (Berthold 2001). Although some of this mass change may be due to other morphological changes rather than simply just changes in fat deposits (Feare 1984), body mass has been shown to be a reliable indicator of fat levels in birds and a good indicator of an individual's energetic state (Blem 1990; Witter et al. 1995). Therefore, a manipulation where birds lost about 5% of their mass is ecologically realistic, and our results are applicable to a natural foraging situation.

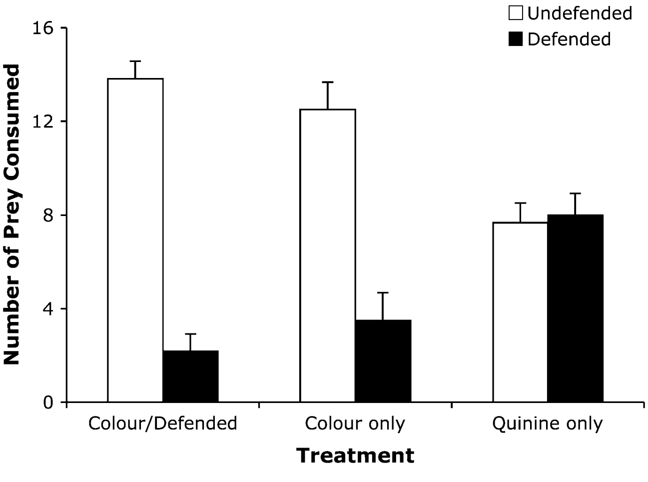

Figure 5
The daily mean number (+SE) of defended and undefended prey consumed during the 3 simultaneous choice treatments. Birds could only discriminate between defended and undefended prey when color cues were available.

Our results highlight the need to consider in more detail the cognitive processes of educated predators in the evolution of aposematism. Studies of predator avoidance learning have been crucial for our understanding of the initial evolution of aposematism, but our results demonstrate that educated predators are a significant selection pressure on aposematic prey. Recent studies show that educated predators continue to attack defended prey with stable asymptotic attack rates, even after learning has occurred (e.g., Skelhorn and Rowe 2005, 2006b). Previous experiments show that the exact level of avoidance depends both on whether the birds can taste the defences and also potentially on the level of the chemical defence the prey contain (Skelhorn and Rowe 2006b). The current study adds the predators' energy reserves as another factor involved in determining asymptotic attack levels. These findings have implications for the evolution of warning patterns and chemical defences.

First, warning signals may not just be designed to be easily associated with chemical defences by naive predators (e.g., Gittleman and Harvey 1980; Guilford 1992) but may need to be effective for recognition by educated predators. This idea is not new; for example, it has previously been suggested that warning signals could be designed to facilitate recognition or cautious sampling by experienced predators (Guilford 1985, Guilford 1994) or to be more memorable (Speed 2000). We have shown that educated birds continue to attack and consume defended prey even after they have learned the association between the color signal and the defence level. Therefore, perhaps more emphasis should be given to understanding how warning signals result from selection from educated predators and how they are designed to facilitate avoidance after the initial color association has been made.

Second, this result has ramifications for the recent debate surrounding the evolutionary dynamics of mimicry. It indicates that defended prey can be "moderately defended" in the sense that predators do not always eat or always avoid a defended prey species but can have an intermediate level of attack and ingestion according to the balance between nutrients and toxins and the energetic needs of predators (Speed 1993a; Brower et al. 1968). Whether prey can be moderately defended and attacked at intermediate rates are important for recent debate concerned with the evolution of mimicry (Speed 1999; Joron and Mallet 1998). If our data reflect how birds deal with prey under natural foraging conditions, predatory behavior will allow for the evolution of quasi-Batesian mimicry, where a moderately defended mimic is parasitic on a more defended mimic (Speed 1993a). Indeed, the fact that birds have evolved this strategic behavior might even point to the widespread occurrence of defended prey in nature that attract intermediate levels of attack from predators. This would be an interesting area for future research.

Finally, given that prey acceptability changes according to the fat reserves and masses of the birds, selection on the warning signals, chemical defences, and behavior of prey may vary across the year according to food availability or the birds' energetic needs. For example, defended 7-spot ladybirds (*Coccinella septempunctata*) are solitary in the warm summer months but are often found in aggregations in the winter months (Majerus and Kearns 1989). An increase in attacks from avian predators when food is scarce could lead to individuals enhancing their survival chances in winter from dilution or saturation effects of being in an aggregation (Lindström et al. 2001; Turner and Speed 1999). Prey might also strategically adjust their investment in chemical defences and conspicuous coloration in response to predation pressure (Darst et al. 2006). Studying annual mass and fat fluctuations in birds from ringing data may lead to further testable hypotheses. In addition, we may have to consider these effects when experimenting on natural bird populations because the time of year of prey presentation or food availability at different sites may affect prey choices. It will be important to control for these effects in future experiments.

Overall, our data suggest that we may need to reevaluate our current approach to studying aposematism and mimicry and include more fully the role of cognitive processes of educated predators in the evolutionary dynamics of aposematism and mimicry. It is perhaps also time to develop a new approach to the study of aposematism in the wider context of optimal diet choice and the potential benefits and trade-offs faced by foraging animals (Stephens and Krebs 1986; Speed 1993b; Yearsley et al. 2006). It will be interesting to further investigate how predators perceive defence chemicals and how they make foraging decisions in relation to what they have learned about a prey's nutritional content and defence chemistry. Decisions could be based on not only the need for protein and energy but also for rare trace elements or perhaps even the toxins themselves (e.g., Turner and Speed 1999; Saporito et al. 2004). The cognitive processes underlying the assessment of nutritional and toxic properties of prey are likely to be complex, but this study provides a rare insight into the decision-making strategies that predators might employ.

We would like to thank Lin Hedgecock and Michelle Waddle for husbandry; John Skelhorn for helpful advice; and Mike Speed, Anne Houde, and 2 anonymous referees for their helpful comments on our manuscript. C.A.B. was supported by a departmental studentship and an ORS Award, M.B. held a Royal Society University Research Fellowship, and C.R. held a Royal Society Dorothy Hodgkin Fellowship during this study. The work was supported by the Royal Society and the BBSRC.

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