

Sound improves visual discrimination learning in avian predators

Candy Rowe

Department of Psychology, The Henry Wellcome Building for Neuroecology, Framlington Place, University of Newcastle, Newcastle upon Tyne NE2 4HH, UK (candy.rowe@ncl.ac.uk)

Aposematic insects use warning colours to deter predators, but many also produce odours or sounds when attacked by a predator. One possible role for these additional components is that they promote the association between the warning colour and the non-profitability it signals, thus reducing the chance of future attacks from visually hunting predators. This experiment explicitly tests this idea by looking at the effects of sound on a visual discrimination task. Young domestic chicks were trained to look for food rewards under coloured paper cones scattered in an experimental arena. In a subsequent visual discrimination task, they learned to discriminate between rewarded and non-rewarded hats on the basis of colour. Half the chicks performed this task in silence, whilst the other half had a tone played when they attacked non-rewarded hats. The presence of the tone improved the speed of colour discrimination learning. This demonstrates that there could be a selective advantage for aposematic coloured insects to emit sounds when attacked, since avian predators will learn to avoid their coloration more quickly. The role of psychological interactions between signal components in receivers is discussed in relation to the evolution of multimodal displays.

Keywords: evolution; aposematism; multimodal signals; domestic chick

1. INTRODUCTION

Aposematic insects use bright coloration to advertise their non-profitability or unpalatability to would-be predators. Conspicuous coloration is particularly effective as a warning signal, as avian predators learn to avoid unpalatable prey faster if they are conspicuously coloured rather than if they are cryptic (Gittleman & Harvey 1980; Roper & Redston 1987), and there is also evidence that birds may instinctively avoid food that has colour typical of aposematic prey (Schuler 1982; Schuler & Hesse 1985; Roper & Cook 1989; Gamberale-Stille & Tullberg 2001). However, many aposematic insects do not just use colourful signals, but also often emit odours or sounds when they are approached or attacked by a predator (Cott 1940; Rothschild 1961; Rothschild & Haskell 1966; Edmunds 1974). These warning displays, consisting of components in more than one sensory modality, have been called 'multimodal' signals (Partan & Marler 1999; Rowe 1999). The question is, given that conspicuous colour patterns are effective warning signals against avian predators, why have aposematic insects also evolved these additional signal components?

Recent experiments have investigated the signalling significance of pyrazine, an odour commonly found in multimodal insect warning displays (Rothschild 1961; Moore *et al.* 1990; Marples *et al.* 1994; Marples & Roper 1996; Rowe & Guilford 1996, 1999; Roper & Marples 1997; Jetz *et al.* 2001; Lindström *et al.* 2001). Birds can detect pyrazine, and learn to avoid unpalatable prey by odour alone (Guilford *et al.* 1987; see Roper (1999) for a review of birds' olfactory capabilities), but pyrazine can also evoke unlearned colour biases in naive avian predators. Pyrazine odour causes naive domestic chicks (*Gallus gallus domesticus*) to reduce their intake of prey that share visual characteristics typical of aposematic insects, such as prey that are red or yellow (Rowe & Guilford 1996, 1999), con-

spicuous against the background (Lindström *et al.* 2001), or novel in appearance (Jetz *et al.* 2001). Further results show that such biases are not elicited by pyrazine alone and that other odours, and even sounds, can elicit these unlearned biases (Jetz *et al.* 2001; Rowe & Guilford 2001).

Therefore, there is evidence that non-visual components could enhance prey survival through eliciting unlearned visual biases in naive avian predators, but it is also possible that they could enhance the learning process. Claridge (1974), and later Rothschild *et al.* (1984), proposed that sounds and odours could promote the association between the colour pattern of the prey and its unpalatability, thus avian predators would learn to avoid aposematic prey more quickly. Kaye *et al.* (1989) showed that pyrazine odour could enhance the association between visual environmental cues and water palatability in rats (*Rattus norvegicus*). For birds, Roper & Marples (1997) showed that chicks learned to avoid unpalatable water that was a familiar colour if a novel odour (almond) was presented alongside. Although one interpretation is that the odour enhanced the colour avoidance learning, an alternative interpretation is that the learning proceeded more quickly because the chicks associated the novel odour with the unpalatability; there is as yet no conclusive evidence supporting the idea that a non-visual component can promote the learning of prey coloration in avian predators.

This experiment is, to my knowledge, the first to explore how a sound produced upon attack can enhance the speed of discrimination learning in avian predators. I used sound rather than odour since it is easier to use in a laboratory setting, but more importantly, it also allowed me to control the order of presentation of visual and auditory components. In previous experiments using pyrazine, the odour was detected before any attack to the prey had been made: in this experiment sound is only produced when an unrewarded prey item is actually attacked, mimicking natural insect warning displays. Naive predators had to

learn to discriminate between two colours of prey, one that was rewarded and one that was not. For half the birds, a simple tone was played when they mistakenly attacked the unrewarded prey, in order to investigate the effect on the speed of learning. Throughout the experiment I used colours and sounds that are not typically associated with warning signals, to prevent any unlearned aversive reactions to the stimuli. This experiment is concerned with whether there are any general psychological mechanisms that could help explain the evolution of auditory (and possibly also olfactory) components of aposematic displays.

2. MATERIAL AND METHODS

(a) *Subjects and housing*

Seven batches of mixed-sex domestic chicks (*Gallus gallus domesticus*, Goldline strain) hatched in the laboratory between 8 August 2000 and 15 May 2001. The chicks were kept in cages measuring *ca.* 100 cm × 50 cm × 50 cm, and maintained at 20–22 °C using heat lamps. They were subject to a 14 L : 10 D cycle. Water was provided *ad libitum*, as were chick starter crumbs when the chicks were not being food deprived during the experiment (all food deprivation was in accordance with ethical guidelines issued by the Home Office). Chicks were kept for 10–14 days and were subsequently donated to free-range farms.

(b) *Training*

Each week, I trained chicks using the same general procedure. On days 1 and 2 post-hatch, I trained single chicks to eat brown chick starter crumbs scattered on the white floor of a walled circular arena (*ca.* 1 m in diameter). Chicks were food deprived, initially, for 1–2 h before being given a series of training sessions. They were allowed to eat to satiation in the arena in each session before being returned to the home cage. By the end of day 2, all chicks were eating from the arena on their own.

On day 3, I gave individual chicks three sessions with the first type of training stimuli. These were discs of coloured paper, 2 cm in diameter, under which I placed a small pile of chick crumbs (*ca.* 10–15 crumbs under each disc). There were six discs in each session, three each of two different colours, which were changed between sessions so that chicks became accustomed to the presence of novel colours. The colours I used were merely selected to look different since I was not training the chicks to any particular set of colours, but attempting to eliminate any neophobic responses that might occur towards the novel experimental colours when they were presented. Colours were selected from a panel of 14, ranging from violet (peak reflectance measured with a PR650 spectrosan was 420 nm) to red (peak reflectance was 600 nm). There was no ultraviolet component to these colours due to the lighting in the experimental room. Chicks rapidly learned to find food under the paper discs, and also to attack them regardless of novel coloration.

After a further training session with these discs on day 4, I gave chicks three sessions with shallow cones or 'hats' under which food could now be hidden (these were the circles that had been made into 'hat'-like shapes). Although I left the food visible underneath these hats at first, by the end of day 5 and a further four to five training sessions, I could hide the food completely and chicks flipped them over to look for food underneath.

(c) *Experiment*

On day 6, I gave chicks a visual discrimination-learning task. They were given six hats of two different colours (*i.e.* 12 in total)

arranged randomly in the arena where only hats of one colour had three chick crumbs hidden underneath. I used two novel colours, purple and green, which were selected in order to reduce any colour biases that chicks might show: these colours are not commonly associated with warning signals, and chicks show no biases against them (Rowe & Guilford 2001). Chicks were given eight sessions; in each session they were allowed to attack six hats before they were removed from the arena, and the colours of these hats were recorded. An attack was defined as a chick pecking a hat, whether they were rewarded or not. There were 30–50 min between each session (depending upon the number of chicks being tested), except for a break halfway through the trials, when the chicks were fed chick crumbs and left for *ca.* 1 h.

On day 7, all chicks were given two further sessions to make a total of 10. I considered chicks to have learned the task if they attacked only the six rewarded hats in a given session, and by the end of these 10 sessions, nearly all the chicks (77 out of 81) had achieved this learning criterion. These chicks were then given an extinction session to ensure that they had learned the colours of the hats, and had not used any other visual or olfactory cues to find the food. In this session, three chick crumbs were put under all 12 hats, regardless of colour, and the colour choices of the chicks were recorded. Any chick that had not achieved the learning criterion was given further trials spaced 30 min apart until it attacked only the rewarded hats in a session (no chick needed more than four further sessions). These chicks were then also given an extinction trial.

Eighty-five chicks were trained in total. In each week, chicks were assigned to four groups before the start of the experiment. For approximately half the chicks, food was placed under the purple hats, whilst for the other half it was under the green hats. Within each colour treatment, chicks were divided into two further groups, one that heard a tone when they attacked an unrewarded hat, whilst the other performed the task in silence. It was impossible to have equal numbers in each group since different numbers were hatched and trained each week, and some chicks were excluded; three chicks refused to attack six hats in a given session on the first day, whilst the other had an extreme preference for green hats and attacked only these in the very first session. However, across all seven weeks, the number of chicks in each experimental group was virtually equal: rewarded purple hats, no sound, $n = 21$; rewarded purple hats, sound, $n = 20$; green hats rewarded, no sound, $n = 20$; green hats rewarded, sound, $n = 20$.

The sound played was a simple alert beep, played at maximum volume, from a Macintosh CS1400 laptop situated adjacent to the arena. I used this instead of a warning buzz or rattle to reduce the likelihood of eliciting an aversive reaction, and during this experiment (and others using sound: C. Rowe, unpublished data; Rowe & Guilford 2001), chicks did not aver- sely react to the novel sound. Groups where food was hidden under the purple hats were always tested first before the two groups where it was under the green hats. Within each colour treatment, in weeks 1–4 the groups that had a sound played were tested first, whilst in weeks 5–7 this order was reversed and these groups were tested second.

3. RESULTS

Although green and purple were selected to reduce the chance of a colour bias in this experiment, chicks showed an initial preference for green hats. Looking at the first

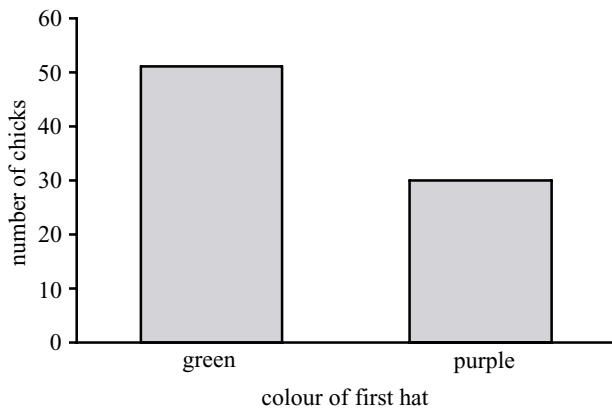


Figure 1. The number of chicks that initially attacked green and purple hats in the first session.

hat attacked in the very first session, chicks showed a significant tendency to attack a green hat initially (binomial test, $p < 0.05$; see figure 1).

I assessed the relative speeds with which the different groups learned the task by comparing the number of sessions that it took for chicks to show 'perfect discrimination' (i.e. attack only those six hats that were rewarded). No chick took more than 14 sessions to achieve perfect discrimination, and all individual scores therefore ranged from 2 to 14. There were apparent differences between weeks in how quickly chicks learned this task, and in order to plot and analyse the data I needed to control for among-week differences. I standardized the data by calculating the mean and standard deviation number of sessions taken to achieve perfect discrimination by all chicks in a given week, and then calculated the number of standard deviations that each individual chick's score lay from this mean (this could be either positive or negative). I performed a three-way ANOVA using sound (present or not), colour (purple or green as the rewarded colour) and order (sound or silent groups tested first) as the three factors. A check of the residual plots showed that the data were approximately normally distributed and had equal variance among groups. Sound significantly improved the speed with which chicks learned to avoid unrewarded hats (table 1; figure 2). There was no other significant main effect or interaction.

In the extinction session, I predicted that if the chicks had learned to detect food rather than learned coloration, choices should be random with regard to colour. The mean scores of the last test session and the extinction session did not significantly differ (mean number and standard error of rewarded hats attacked for all chicks in the session preceding extinction was 5.58 ± 0.07 , and for the extinction session was 5.49 ± 0.08 ; Wilcoxon signed-rank test, $n = 81$, $Z = 0.796$, $p > 0.1$), and the scores in the extinction session were significantly above random (one-sample t -test, expected value of 3, $t = 28.90$, d.f. = 80, $p < 0.001$).

4. DISCUSSION

These results clearly demonstrate that sound can improve the speed of visual discrimination learning in birds. This occurs regardless of the direction of the colour discrimination, despite a bias for the first hat colour to be

attacked to be green. This colour bias could be unlearned (Roper & Cook 1989; Gamberale-Stille & Tullberg 2001), or have been caused by the colours used in the training set; fewer colours occurred at shorter wavelengths around the purple stimuli than at longer wavelengths around the green. This may have made purple test stimuli relatively more novel when they were initially presented, thus creating a bias for green.

However, regardless of the initial colour bias, there is no significant effect on the speed of learning between the two colour treatments, and the only main effect is that of sound. But how does sound enhance colour discrimination learning? What is not known from this experiment, or from observations of wild birds, is whether the sound functions as a conditioned or an unconditioned stimulus in the learning process. The coloration is a conditioned stimulus, in that it becomes associated with a valued outcome (the unconditioned stimulus), which in this case is the reward, or lack of it. The role of sound in this process is more ambiguous, and it could be working in one of two ways.

The first is that it is perceived as an additional unconditioned stimulus, with learning proceeding faster because those groups with sound have additional negative reinforcement. However, tones are regularly used in psychological experiments (Mackintosh 1974; Pearce 1997), including those investigating compound learning (Kehoe *et al.* 1994), and no aversive behaviour towards the tone was evident (see also Rowe & Guilford 2001).

Alternatively, it could be acting as an additional conditioned stimulus, which promotes the strength of colour aversion learning. Such a mechanism would be similar to that of 'potentiation', which occurs when two conditioned stimuli predict an outcome and where one conditioned stimulus promotes the association between the other conditioned stimulus and the outcome (Durlach & Rescorla 1980; Honey & Bolhuis 1997). For example, in the context of multimodal warning signals, rats make a stronger association between visual environmental cues and water palatability if the warning odour, pyrazine, is also present in the environment (Kaye *et al.* 1989). In a different context, visual filial imprinting in chicks can be improved by the presence of a simultaneous auditory signal, as can auditory imprinting by a visual stimulus (Van Kampen & Bolhuis 1991, 1993). In my experiment, although learning about the colour may be promoted by the sound, this is not potentiation in the strict sense, as the two conditioned stimuli are not presented together, with the sound being presented after the coloration. In some attacks, the coloured hats remained upright rather than being flipped over, and in these cases perhaps the sound and the coloration could be said to have occurred together. However, in most cases, the sound would have been perceived after a hat had been flipped over (all hats were white underneath), and possibly even after the lack of reward had been realized. Further experiments, under more controlled presentation conditions, will be required to determine the importance of the order and timing of the stimulus presentations.

Sound has also been shown to help animals in discrimination tasks, where it is played during a long delay between the presentation of a visual stimulus and the reward or punishment that it predicts (Spence 1947;

Table 1. Results of three-way ANOVA performed on the standardized data.

source	sum of squares	d.f.	mean square	F-value	p-value
sound	4.923	1	4.923	6.154	0.015
colour	1.932	1	1.932	2.415	0.124
order	0.299	1	0.299	0.374	0.543
sound × colour	0.115	1	0.115	0.144	0.705
sound × order	0.009	1	0.009	0.011	0.916
colour × order	0.245	1	0.245	0.306	0.582
sound × colour × order	0.218	1	0.218	0.272	0.604
error	58.39	73	0.800		

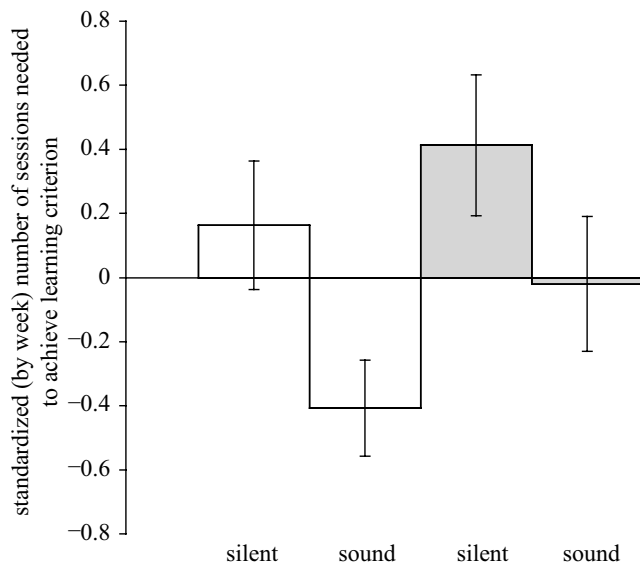


Figure 2. The standardized (by week) number of sessions (\pm s.e.) taken by chicks in each experimental group to achieve perfect discrimination (see § 3 for further details). Open bars are the scores for two groups where food was hidden under purple hats, and shaded bars are where food was rewarded under green hats. Sample sizes for each group are as follows: rewarded purple hats, no sound, $n = 21$; rewarded purple hats, sound, $n = 20$; green hats rewarded, no sound, $n = 20$; green hats rewarded, sound, $n = 20$.

Thomas *et al.* 1987; Williams 1991). However, in this experiment, the delay between pecking the colour and its profitability was almost instantaneous. One proposed mechanism for this effect is that the sound alerts the animal to pay more attention to the visual stimulus, and thus the association with the delayed punishment would be made more readily (Rothschild *et al.* 1984). Hulstsch *et al.* (1999) highlighted the potential importance of the role of attention in signal learning by showing that a synchronous flashing light was sufficient to enhance song learning in nightingales (*Luscinia megarhynchos*). However, other operant experiments with zebra finches (*Taeniopygia guttata*) have not found any evidence that the presentation of a visual stimulus improves song learning (Bolhuis *et al.* 1999; Houx & ten Cate 1999), although this could possibly be due to the nature of the visual stimulus. It is possible that in this experiment sound is alerting the birds to the association between the visual stimulus and the lack of reward and making it more salient in the birds' memories, but further experiments will be needed to fully identify the mechanism behind this intersensory interaction.

Regardless of the specifics of the psychological mechanism, this effect will have important implications for insects in the wild. What is important for multimodal warning signals is that the speed of learning is improved by the sound being played after an attack. Therefore, sound is not being used by the birds to discriminate between differently coloured prey before an attack, but instead enhances the avoidance of unrewarded prey types, purely on the basis of their visual signals. This mimics the natural situation where insects produce sounds and odours when approached or attacked by a predator. Therefore, aposematic insects that produce sounds could improve birds' abilities to learn their colour patterns, thus enhancing their survival prospects (Claridge 1974). This intersensory interaction could be more general and work between other sensory modalities, and it is possible that odours that are produced after attack will also enhance colour discrimination learning (Rothschild *et al.* 1984).

Multimodal displays are common in nature, and yet we are still at an early stage of understanding how signal receivers process multiple components. In some instances, auditory and visual signal components may simultaneously transmit redundant information (Møller & Pomiankowski 1993; Johnstone 1996), as in the case of signals of need in reed warbler chicks (*Acrocephalus scirpaceus*) (Kilner *et al.* 1999). However, not all signal components need be informative, and psychological interactions between signal components in different sensory modalities could enhance signal efficacy (Guilford & Dawkins 1991; Rowe 1999). These results demonstrate how an auditory signal component can enhance the efficacy of a visual warning signal through enhanced discrimination learning. Of course, it is also possible that sounds could increase the detection and discrimination of visual signals (see Rowe (1999) for a review). Therefore, signal components need not necessarily evolve solely to transmit information, but instead could be under selection to promote the perception of an informative signal component in signal receivers.

This work was supported by a Sir James Knott Research Fellowship from the University of Newcastle, and a Royal Society Dorothy Hodgkin Research Fellowship. I thank Michelle Waddle for training some of the chicks, and also for her help in finding homes for the chicks at the end of the experiment. Thanks also to Gabi Jordan for her colour measurements of paper stimuli, and Melissa Bateson, Marion Petrie and Craig Roberts for their comments on the manuscript.

REFERENCES

- Bolhuis, J. J., Van Mil, D. P. & Houx, B. B. 1999 Song learning with audiovisual compound stimuli in zebra finches. *Anim. Behav.* **58**, 1285–1292.
- Claridge, M. F. 1974 Stridulation and defensive behaviour in the ground beetle, *Cychrus caraboides* (L.). *J. Entomol.* **A 49**, 7–15.
- Cott, H. B. 1940 *Adaptive coloration in animals*. London: Methuen.
- Durlach, P. J. & Rescorla, R. A. 1980 Potentiation rather than overshadowing in flavour-aversion learning: an analysis in terms of within-compound associations. *J. Exp. Psychol. Anim. Behav. Process.* **6**, 175–187.
- Edmunds, M. 1974 *Defence in animals*. Harlow: Longman.
- Gamberale-Stille, G. & Tullberg, B. S. 2001 Fruit or aposematic insect? Context-dependent colour preferences in domestic chicks *Proc. R. Soc. Lond. B* **268**, 2525–2529. (DOI 10.1098/rspb.2001.1814.)
- Gittleman, J. & Harvey, P. H. 1980 Why are distasteful prey not cryptic? *Nature* **286**, 149–150.
- Guilford, T. & Dawkins, M. S. 1991 Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1–14.
- Guilford, T., Nicol, C., Rothschild, M. & Moore, B. P. 1987 The biological roles of pyrazines: evidence for a warning odour function. *Biol. J. Linn. Soc.* **31**, 113–128.
- Honey, R. C. & Bolhuis, J. J. 1997 Imprinting, conditioning, and within-event learning. *Q. J. Exp. Psychol. B* **50**, 97–110.
- Houx, B. B. & ten Cate, C. 1999 Do stimulus–stimulus contingencies affect song learning in zebra finches (*Taeniopygia guttata*)? *J. Comp. Psychol.* **113**, 235–242.
- Hultsch, H., Schless, F. & Todt, D. 1999 Auditory-visual stimulus pairing enhances perceptual learning in a songbird. *Anim. Behav.* **58**, 143–149.
- Jetz, W., Rowe, C. & Guilford, T. 2001 Non-warning odors trigger innate color aversions—as long as they are novel. *Behav. Ecol.* **12**, 134–139.
- Johnstone, R. A. 1996 Multiple displays in animal communication: ‘backup signals’ and ‘multiple messages’. *Phil. Trans. R. Soc. Lond. B* **352**, 329–338.
- Kaye, H., Mackintosh, N. J., Rothschild, M. & Moore, B. P. 1989 Odour of pyrazine potentiates an association between environmental cues and unpalatable taste. *Anim. Behav.* **37**, 563–568.
- Kehoe, E. J., Horne, A. J., Horne, P. S. & Macrae, M. 1994 Summation and configuration between and within sensory modalities in classical conditioning of the rabbit. *Anim. Learn. Behav.* **22**, 19–26.
- Kilner, R. M., Noble, D. G. & Davies, N. B. 1999 Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature* **397**, 667–672.
- Lindström, L., Rowe, C. & Guilford, T. 2001 Pyrazine odour biases food selection in avian predators against conspicuously coloured prey. *Proc. R. Soc. Lond. B* **268**, 357–361. (DOI 10.1098/rspb.2000.1377.)
- Mackintosh, N. J. 1974 *The psychology of animal learning*. London: Academic Press.
- Marples, N. M. & Roper, T. J. 1996 Effects of colour and smell on the response of naive chicks towards food and water. *Anim. Behav.* **51**, 1417–1424.
- Marples, N. M., Van Veelen, W. & Brakefield, P. M. 1994 The relative importance of colour, taste and smell in the protection of an aposematic insect *Coccinella septempunctata*. *Anim. Behav.* **48**, 967–974.
- Møller, A. P. & Pomiankowski, A. 1993 Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* **32**, 167–176.
- Moore, B. P., Brown, M. V. & Rothschild, M. 1990 Methyl-alkylpyrazines in aposematic insects, their hostplants and their mimics. *Chemoeology* **1**, 43–51.
- Partan, S. & Marler, P. 1999 Communication goes multimodal. *Science* **283**, 1272–1273.
- Pearce, J. M. 1997 *Animal learning and cognition*, 2nd edn. Hove: Psychology Press.
- Roper, T. J. 1999 Olfaction in birds. *Adv. Stud. Anim. Behav.* **28**, 247–332.
- Roper, T. J. & Cook, S. E. 1989 Responses of chicks to brightly coloured insect prey. *Behaviour* **110**, 276–293.
- Roper, T. J. & Marples, N. M. 1997 Odour and colour as cues for taste-avoidance learning in domestic chicks. *Anim. Behav.* **53**, 1241–1250.
- Roper, T. J. & Redston, S. 1987 Conspicuousness of distasteful prey affects the strength and durability of one-trial avoidance learning. *Anim. Behav.* **35**, 739–747.
- Rothschild, M. 1961 Defensive odours and Mullerian mimicry among insects. *Trans. R. Entomol. Soc. Lond.* **113**, 101–121.
- Rothschild, M. & Haskell, P. T. 1966 Stridulation of the garden tiger moth *Arctia caja* L. audible to the human ear. *Proc. R. Soc. Lond. A* **41**, 167–170.
- Rothschild, M., Moore, B. P. & Brown, W. V. 1984 Pyrazines as warning odour components in the monarch butterfly, *Danaus plexippus*, and in moths of the genera *Zygaena* and *Amata* (Lepidoptera). *Biol. J. Linn. Soc.* **23**, 372–380.
- Rowe, C. 1999 Receiver psychology and the evolution of multi-component signals. *Anim. Behav.* **58**, 921–931.
- Rowe, C. & Guilford, T. 1996 Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature* **383**, 520–522.
- Rowe, C. & Guilford, T. 1999 Novelty in a multimodal warning signal. *Anim. Behav.* **57**, 341–346.
- Rowe, C. & Guilford, T. 2001 The evolution of multimodal warning displays. *Evol. Ecol.* **13**, 655–671.
- Schuler, W. 1982 Zur Funktion von Warnfarben: die reaktion junger Stare auf wespenähnlich schwarz-gelbe Attrappen. *Z. Tierpsychol.* **58**, 66–78.
- Schuler, W. & Hesse, E. 1985 On the function of warning coloration: a black and yellow pattern inhibits prey attack by naïve domestic chicks. *Behav. Ecol. Sociobiol.* **16**, 249–255.
- Spence, K. W. 1947 The role of secondary reinforcement in delayed reward learning. *Psychol. Rev.* **54**, 1–8.
- Thomas, G. V., Robertson, D. & Lieberman, D. A. 1987 Marking effects in Pavlovian trace conditioning. *J. Exp. Psychol. Anim. Behav. Process.* **13**, 126–135.
- Van Kampen, H. S. & Bolhuis, J. J. 1991 Auditory learning and filial imprinting in the chick. *Behaviour* **117**, 303–319.
- Van Kampen, H. S. & Bolhuis, J. J. 1993 Interaction between auditory and visual learning during imprinting. *Anim. Behav.* **45**, 623–625.
- Williams, B. A. 1991 Marking and bridging versus conditioned reinforcement. *Anim. Learn. Behav.* **19**, 264–269.