The influence of density on frequency-dependent selection by wild birds feeding on artificial prey

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Previous work has demonstrated frequency-dependent selection by wild garden birds when feeding on green and brown pastry 'baits'. When the density of baits is low, the common colour is eaten disproportionately more than the rare colour (apostatic selection), and when the density is very high, the rare colour is eaten disproportionately more than the common (anti-apostatic selection). We explored the relationship between frequency-dependent predation and density in an experiment at 16 separate sites, using four levels of density and two frequencies of green and brown. Analysis of estimates of log relative risk ratios showed little evidence for frequency-independent selection, but frequency-dependent selection changed gradually from apostatic at low density to anti-apostatic at high density. The validity of these conclusions in terms of individual bird behaviour was confirmed by Monte-Carlo simulations. We thus conclude that selection by wild birds feeding on green and brown artificial prey is frequency dependent, and that the strength and direction of this selection changes with prey density in a gradual and predictable manner.

Keywords: frequency-dependent selection; apostatic selection; anti-apostatic selection; predation; wild birds; artificial prey

1. INTRODUCTION

When green and brown pastry artificial 'prey' are presented at low density (2 m^{-2}) on grass lawns, wild passerine birds tend to eat disproportionately more of the common colour (Allen & Clarke 1968; Allen 1972, 1976). By contrast, when the 'baits' are presented at very high density ($>10\,000\text{ m}^{-2}$), they remove disproportionately more of the rare form (Allen 1972; Horsley *et al.* 1979; Allen & Anderson 1984). Thus, the selection by wild birds is frequency dependent and its direction is influenced by prey density. At a low density of green and brown prey, selection is 'pro-apostatic' (with the potential to maintain variation within prey species; Clarke 1962), while at very high prey density it is 'anti-apostatic' (with the potential to reduce variation; Greenwood 1984, 1985). Similar effects of density on frequency-dependent selection have been observed in other predator-prey systems (e.g. Sherratt & Harvey 1989).

The emphasis of early experiments on green and brown baits was on the effect of selection on the prey, rather than on the behaviour of the birds (Allen & Clarke 1968; Allen 1972, 1976; Horsley *et al.* 1979). In all of these studies, wild birds in their normal surroundings were offered populations of baits with brown baits being nine times as common as green (9B:1G), or green nine times as common as brown (1B:9G). Typically, at a given site we offered one of the two types of population (e.g. 9B:1G) for a number of days and then 'crossed-over' the frequen-

cies and presented the second type (e.g. 1B:9G), again for several days. In some experiments the sites were observed continuously and data obtained for different bird species, while in others the birds were not observed and selection was recorded from their pooled predation.

The cause of frequency-dependent selection by wild birds is unclear. Several proximate mechanisms can lead to individual predators selecting either pro- or anti-apostatically (Greenwood 1984, 1985; Allen 1988). In the past, we tended to assume that birds selected pro-apostatically because they acquired 'search images' to frequently encountered cryptic prey and hence overlooked rare ones (Allen & Clarke 1968; Allen 1972, 1976). This explanation now seems unlikely, given that the green and brown prey were conspicuous (at least to the human eye). Moreover, the concept of the search image itself has come under question (Guilford & Dawkins 1987). One possible cause of anti-apostatic selection is that individual predators tend to remove rare forms because they stand out from the background of the rest (Allen 1972). Another possible cause of anti-apostatic selection at the population level is from variability in frequency-independent selection among individual predators (P. Chesson 1984; Sherratt & MacDougall 1995), and there is some evidence for such variability from the behaviour of wild blackbirds feeding on pastry prey at very high density (Allen & Anderson 1984).

We now describe an experiment, again focused on the prey, designed to explore further the influence of density on frequency-dependent selection by wild birds feeding on brown and green pastry baits. Our aim was to test

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whether the change with density is gradual, and to identify the point at which selection is neutral as it switches from pro- to anti-apostatic selection. We also wished to examine more closely the role of variability in selective behaviour among predators on the type and degree of frequency-dependent selection taking place.

2. METHODS

(a) *Experimental design*

We used a cross-over experimental design employed at 16 separate sites (at least 0.5 km apart) in and around Yeovil, Somerset, and Southampton, Hampshire, UK. At each site, prey populations were presented either with initial frequencies of 90% brown prey and 10% green (9B:1G), or with 10% brown prey and 90% green (1B:9G). Six sequential feeding trials were performed at the given prey frequency. The frequency was then crossed-over and another six sequential feeding trials were completed.

Feeding trials ran in July, September, October and December 1988 and January and March 1989. Each site featured one of the four possible density levels (10 m^{-2} , 100 m^{-2} , 1000 m^{-2} or $10\,000\text{ m}^{-2}$) and one of the two possible presentation orders (9B:1G first or 1B:9G first). This allowed each one of the eight possible between-site treatment combinations to be replicated at two different sites. Treatment combinations were allocated randomly to sites, and sites were used in a random order.

(b) *Prey*

The prey were brown and green cylindrical 'baits' of pastry (ca. 6 mm $\times$ 7 mm (diameter $\times$ length)), made from flour and lard in a 3:1 ratio (Allen & Clarke 1968; Allen *et al.* 1987, 1990). The colours were made by the addition of 16 ml of brown culinary dye (K6024, Pointing Ltd) or 10 ml of green (K6027) to every 1 kg of dough. Scored on the Munsell Color System, the green had a hue of 7.5 GY and a Value/Chroma of 7/10 while the brown had a hue of 5YR and a Value/Chroma of 6/6. The coloured pastry was extruded through the circular holes of a modified mincer, resulting in cylindrical tubes which were cut by hand into 7 mm lengths and stored in a cold room before use.

(c) *Feeding trials*

Populations of 200 prey were presented on grass lawns in plots of areas 20 m^2 , 2 m^2 , 0.2 m^2 and 0.02 m^2 , corresponding with densities equivalent to 10 m^{-2} , 100 m^{-2} , 1000 m^{-2} , and $10\,000\text{ m}^{-2}$. Each plot was a square or rectangular grid (plot shape varied slightly for practical reasons) marked with wooden skewers either at the corners of each metre square or, for the two high-density populations, at the four corners of the grid. The baits were dropped singly from waist height, and were distributed randomly within the grid with respect to both colour and position (following the method of Allen 1974).

During a feeding trial, each population was revisited every 2 h until between 50 and 150 of the baits had been removed. Trials where the total number removed was outside this range were disregarded. We abandoned sites where the predation rate was persistently slow.

The sites were not observed continuously, but birds seen feeding included the blackbird (*Turdus merula*; all sites), song thrush (*T. philomelos*), dunnock (*Prunella modularis*), house sparrow (*Passer domesticus*), wood pigeon (*Columba palumbus*), magpie (*Pica pica*), starling (*Sturnus vulgaris*), great tit (*Parus major*), and robin (*Erithacus rubecula*). Sites where the major predators were domestic

cats, grey squirrels, or foxes were abandoned in favour of new sites.

(d) *Analysis*

We modelled relative selective preference for brown baits over green ones using estimates of the log relative risk ratio $\theta = \log_e(r_B/r_G)$: r_B and r_G can be interpreted as the instantaneous per-item consumption rates of brown and green baits, respectively (Manly 1985; J. Chesson 1983), or alternatively as the respective probabilities that a brown (or green) prey item is consumed given that it has been encountered, where 'encounters' are defined such that per-item encounter rates are independent of prey type (J. Chesson 1978; Gendron 1987). If $\theta > 0$, then brown is preferred to green; if $\theta < 0$, then green is preferred. 'Preference' in this context need not necessarily mean active choice on the part of the predator, but could also be the result of, say, differences in prey visibility (Gendron 1987).

The index θ can also be interpreted as a logit transformation, $\theta = \log(\beta_B/(1-\beta_B))$, of Manly's beta index β_B for brown baits. One reason why such a transformation is advantageous is that a linear model fitted to β_B can produce 'forbidden' predictions ($\beta_B < 0$ or $\beta_B > 1$). Another is that a given change (Δ) in θ always corresponds to the same multiplicative change x in the ratio r_B/r_G , whereas for β_B this is not so.

We used two analytical approaches. In the first we fitted generalized linear models (GLMs) (Nelder & Wedderburn 1972) to θ using a complementary log-log link to the proportion of each prey type eaten in each trial. This method assumes a proportional hazards model in which the ratio r_B/r_G remains constant throughout a trial; the numbers of each prey type eaten in each trial come from independent binomial distributions; and the ratio r_B/r_G is the same among replicate trials. This last assumption was violated, however, because significant overdispersion was found among replicate trials.

In our second approach, estimates of θ for each block of six sequential replicate trials at each site were found using the GLM approach outlined above (in one, block convergence on a solution was impossible because all the brown baits were eaten in each trial, so here 0.5 of a brown bait was assumed to remain in the trial with the least green baits eaten). We then analysed these θ estimates by conventional least-squares methods. The mean value of θ for both sequential blocks $((\theta_{9B:1G} + \theta_{1B:9G})/2)$ was used as a measure of the frequency-independent preference for brown at each site. The difference $\Delta\theta = (\theta_{9B:1G} - \theta_{1B:9G})$ between the 9B:1G block and the 1B:9G block was used as a measure of the degree (and type) of frequency-dependent selection at each site. The error source for the least-squares analysis was found from the two replicate sites with the same treatment and presentation order, since the GLM analysis had shown that variation among sites was the greatest source of overdispersion. We checked the validity of our least-squares approach using Monte-Carlo simulations.

3. RESULTS

(a) *Overdispersion*

We fitted three highly parameterized GLM models, to look for different sources of overdispersion. The first model looked at variation among temporal replicates (i.e. sequential trials at each site). A separate θ value was allowed for each block of six similar trials (i.e. with the same frequency of prey types presented) at each site. The deviance of this model (a measure of its 'lack of fit') is

624.6 with 160 degrees of freedom (d.f.). This is highly significant when tested as a χ^2 statistic ($p \ll 0.001$), being 3.9 times larger than its d.f. The second model also looked at variation among temporal replicates, and sought to minimize the effects of any systematic trends in θ -values over a block of six trials by splitting it into three pairs of sequential trials. A separate value of θ was allowed for each pair in each block at each site. The deviance of this model is 287.5 with 96 d.f., which is also highly significant ($p \ll 0.001$, the deviance being 3.0 times larger than d.f.). The third model looked at variation among site replicates. Trials were paired (in the same sequential order) between replicate sites (those with the same prey density and the same presentation order of prey frequencies) and a separate θ value was allowed for each pair. The deviance of this model is 472.9 with 96 d.f., which is also highly significant ($p \ll 0.001$, the deviance being 4.9 times larger than d.f.). These models indicated that substantial sources of overdispersion existed, and that it was somewhat greater among replicate sites than it was among replicate trials within sites.

(b) Frequency-independent selection

The mean θ -values for each site were estimated according to the method outlined in the analysis section, and are displayed in figure 1 plotted against prey density on a log scale. Figure 1 suggests that there was little influence of prey density on mean selective preference. It also suggests that (i) there was a tendency to prefer brown over green prey (more points lie above zero than below it); and (ii) that there was, perhaps, a tendency for mean preference for brown to be greater in sites where brown was presented at a high frequency first. However, an analysis of variance (ANOVA) revealed no significant difference among sites with different presentation orders ($F_{4,8}=1.66$, $p>0.1$); no significant difference among sites with different prey densities ($F_{3,8}=9.78$; $p>0.1$); and the overall preference for brown, although nominally significant (mean θ over all sites = 0.197; $F_{1,8}=9.78$, $p<0.05$), was not significant if one used an experiment-wise error rate designed to keep overall type I errors at less than 5%.

(c) Frequency-dependent selection

The difference values, $\Delta\theta$, between the 9B:1G block and the 1B:9G block at each site are displayed in figure 2 plotted against prey density on a log scale. Figure 2 suggests little influence of presentation order on the magnitude of $\Delta\theta$, but a very strong influence of prey density. A steady change occurs between low-density sites (10 m^{-2} and 100 m^{-2}), where selection is generally propostatic (i.e. where preference for brown is greater in trials with a high frequency of brown), and high-density sites (1000 m^{-2} and 10000 m^{-2}), where selection is antiapostatic (i.e. where preference for brown is less in trials with a high frequency of brown). One of the sites at 10000 m^{-2} appears to have an anomalous difference value when compared with the other three, but we felt it was unwise to remove this outlier from the analysis when the paucity of data points made drawing conclusions about the correct distribution of difference values uncertain. An ANOVA confirmed that there was no significant difference among sites with different presentation orders ($F_{4,8}=1.01$, $p>0.1$), but a very highly significant difference among

Figure 1. Frequency-independent selection for brown baits at each site. Mean $\theta = (\theta_{9B:1G} + \theta_{1B:9G})/2$. Solid circles are sites where 9B:1G trials were performed first; open circles denote sites where 1B:9G trials were performed first. The horizontal dotted line represents the case of no frequency-independent selection.

Figure 2. Frequency-dependent selection at each site $\Delta\theta = \theta_{9B:1G} - \theta_{1B:9G}$. Solid and open circles are as for figure 1. The horizontal dotted line represents the case of no frequency-dependent selection.

sites with different prey densities ($F_{3,8}=51.45$, $p \ll 0.001$), even if one uses an experiment-wise error rate to keep overall type I errors at less than 5%. A linear regression model of difference values on $\log(\text{prey density})$ proved to be a good fit to the data (goodness-of-fit test; $F_{2,8}=0.59$, $p>0.1$). The regression line ($\Delta\theta = 3.12 - 1.47 \log_{10}(\text{prey density})$) is shown in figure 2. The linear regression model suggests that selection switches from being propostatic to antiapostatic at a prey density of about 131 m^{-2} . The 95% confidence limits for this x -intercept are 61 m^{-2} and 248 m^{-2} (Zar 1984, equation (17.33)).

(d) Simulations

We performed Monte-Carlo simulations to check the validity of our conclusions. In our first simulation we assumed a 'true' mean θ value for each block of six trials at each site (using the same values as those used for figures 1 and 2), and assumed that overdispersion was due

to 'true' θ -values being normally distributed among replicate trials with a common variance term σ^2 . Using the weighted linear regression method of Manly (1978, equations (9–12)), σ^2 was estimated to be 0.274. We generated 200 simulated data sets, assuming a proportional hazards model for the number of each prey type eaten in each trial. We checked the assumption of constant variance in our model of overdispersion by comparing the observed range of the 32 GLM deviances for each block of six trials at each site with the simulated distribution of this range. The observed range was within the 95% confidence limits of the simulated distribution, suggesting that there was no strong evidence to reject the idea of a single σ^2 term for all blocks. We then generated 200 versions of figures 1 and 2 from our simulated data sets and compared them with our observed results. The simulated distributions of mean θ -values over both blocks at each site agreed well with the 'true' values displayed in figure 1, but the simulated distributions of $\Delta\theta$ -values between blocks at each site were consistently biased above the 'true' values displayed in figure 2. Under our model of overdispersion, therefore, the analytical method that produced figures 1 and 2 tends to overestimate the degree of apostatic selection and to underestimate the degree of anti-apostatic selection. However, the maximum bias in $\Delta\theta$ of +0.133 produced by our simulation is still small compared with the overall range of 5.623 in $\Delta\theta$ values shown in figure 2.

In our second simulation, we assumed that mean θ -values at each site were the same for both 9B:1G and 1B:9G blocks, being the same mean values as those in figure 1. We thus removed any systematic source of frequency-dependent selection from our model. We generated 200 versions of figures 1 and 2, using the same model of overdispersion among replicate trials as above, to see whether variation in predator preference alone could generate patterns of frequency-dependent selection. We found again that the simulated distributions of mean θ -values over both blocks at each site agreed well with the 'true' values displayed in figure 1, but that the simulated distributions of $\Delta\theta$ -values between blocks at each site were consistently biased above the 'true' value of zero, with a maximum bias of +0.160 (see figure 3). However, figure 3 shows that our model produced no consistent trend in $\Delta\theta$ -values with prey density, which suggests that the observed trend in figure 2 is the result of a real change in the selective behaviour of wild birds with prey density, and not an artefact of variable selective preferences.

4. DISCUSSION

Our results confirm that selection by wild birds feeding on brown and green pastry prey is frequency-dependent and that the strength and direction of this selection changes with prey density in a gradual and predictable way. Cook & Miller (1977) have shown that the strength of frequency-dependent selection by captive quail (*Coturnix virginianus*) feeding on pastry prey also decreases with increasing density but never becomes anti-apostatic (perhaps because the maximum density, 7.5 m^{-2} , was too low?). Other experiments, with domestic chicks and coloured bread crumbs (Willis *et al.* 1980), and with humans searching for images on computer screens (Tucker & Allen 1991), have demonstrated effects of

Figure 3. The effect of variable selective preferences on measured frequency-dependent selection. $\Delta\theta$ -values are the means from 200 Monte-Carlo simulations of a variable selection model featuring no systematic frequency-dependent selection. Solid and open circles are as for figure 1. The dotted line is as for figure 2.

density on frequency-independent selection, but not on the frequency-dependent component.

In our experiment, the prey population size was kept constant (at 200 baits), and density was altered by changing the plot size. An alternative protocol would be to keep the plot size constant and vary the population size. It would be useful to see if, and how, the results of an experiment using this second protocol would differ from ours. Church *et al.* (1997), again using wild birds and green and brown pastry prey, have shown that the effects of prey dispersion (random versus clumped distributions) on frequency-dependent selection may not be the same as the effects of varying plot size.

The results revealed significant variability in predator preferences among replicate trials, and the χ^2 tests on GLM deviances are a useful way of testing for this formally. However, our Monte-Carlo simulations suggested that this variability could not account for the trend in frequency-dependent selection with prey density, indicating that a systematic change in individual predator behaviour was responsible instead. The exact causes of this change remain uncertain.

Our Monte-Carlo simulations also revealed a bias towards pro-apostatic selection, whereas the effects of variable preferences are generally expected to lead to population-level anti-apostatic selection (P. Chesson 1984; Sherratt & MacDougall 1995). At first, we thought that this might be due to some difference between situations of prey-replacement, as addressed by P. Chesson (1984) and Sherratt & MacDougall (1995), and the situation of prey-depletion as encountered in this experiment. Further reflection revealed, however, that the real difference was between situations in which food selection is stopped after a fixed number of prey have been eaten (as addressed by Sherratt & MacDougall 1995) and situations in which food selection is stopped after a fixed time-period. Under proportional hazards conditions, it is only in the former situation that population-level anti-apostatic selection is expected as a consequence of variable preferences. P. Chesson (1984) showed that in the latter situation

(corresponding to a type I linear functional response model), there can be no population-level frequency-dependent selection effects. While P. Chesson's (1984) result was derived from a consideration of prey-replacement situations only, it is a relatively simple matter to show that the same is also true in prey-depletion situations.

This means our Monte-Carlo simulations cannot be influenced by population-level anti-apostatic selection, because they simulated trials that were stopped after a fixed period of time. Instead, the tendency towards pro-apostatic selection they produced must be a bias effect only. In reality, the stopping condition for our trials was a mixture between checking that an adequate number of prey had been eaten and stopping after a fixed time. However, the variation in total number eaten among trials indicates that the latter effect was probably dominant over the former.

It would, of course, be unwise to extrapolate the fitted linear relationship of figure 2 to prey densities beyond the range of $10\text{--}10\,000\text{ m}^{-2}$ used in this experiment. In any case, it would make little sense to extrapolate upwards beyond $23\,810\text{ m}^{-2}$, as this represents the maximum possible density of our baits before they start to overlap. Of more interest ecologically are the prey densities (unbounded on a log scale) below 10 m^{-2} , corresponding to those often found naturally in prey of this size (e.g. Tinbergen 1960). It has been suggested that below a certain prey density (perhaps $0.1\text{--}2\text{ m}^{-2}$) frequency-dependent selection will revert to zero because predators will eat whatever items they chance to encounter (Tinbergen 1960; Clarke 1962; Owen 1965). Greenwood (1969) has pointed out that one cannot use indirect evidence concerning the relationship between prey polymorphism and density to test this, because the overall selective pressure exerted by predators can also be expected to be proportionately less at low densities. A direct experimental test is difficult precisely because overall predation rates decrease as prey densities decrease. Such ideas must therefore remain speculative until more is known of the behavioural mechanisms underlying frequency-dependent selection by wild birds.

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REFERENCES

- Allen, J. A. 1972 Evidence for stabilizing and apostatic selection by wild passerines. *Nature* **237**, 348–349.
- Allen, J. A. 1974 Further evidence for apostatic selection by wild passerine birds: training experiments. *Heredity* **33**, 361–372.
- Allen, J. A. 1976 Further evidence for apostatic selection by wild passerine birds—9 : 1 experiments. *Heredity* **36**, 173–180.
- Allen, J. A. 1988 Frequency-dependent selection by predators. *Phil. Trans. R. Soc. Lond. B* **319**, 485–503.
- Allen, J. A. & Anderson, K. P. 1984 Selection by passerine birds is anti-apostatic at high prey density. *Biol. J. Linn. Soc.* **23**, 237–246.
- Allen, J. A., Anderson, K. P. & Tucker, G. M. 1987 More than meets the eye—a simulation of natural selection. *J. Biol. Education* **21**, 301–306.
- Allen, J. A., Anderson, K. P. & Tucker, G. M. 1990 An improved method for demonstrating visual selection by wild birds. *J. Biol. Education* **24**, 262–266.
- Allen, J. A. & Clarke, B. 1968 Evidence for apostatic selection by wild passerines. *Nature* **220**, 501–502.
- Chesson, J. 1978 Measuring preferences in selective predation. *Ecology* **59**, 211–215.
- Chesson, J. 1983 The estimation and analysis of preference and its relationship to foraging models. *Ecology* **64**, 1297–1304.
- Chesson, P. L. 1984 Variable predators and switching behaviour. *Theor. Popul. Biol.* **26**, 1–26.
- Church, S. C., Jowers, M. & Allen, J. A. 1997 Does prey dispersion affect frequency-dependent predation by wild birds? *Oecologia* **111**, 292–296.
- Clarke, B. 1962 Balanced polymorphism and the diversity of sympatric species. In *Taxonomy and geography* (ed. D. Nichols), pp. 47–70. Systematics Association publication no. 4. Oxford, UK: Systematics Association.
- Cook, L. M. & Miller, P. 1977 Density-dependent selection on polymorphic prey—some data. *Am. Nat.* **111**, 594–598.
- Gendron, R. P. 1987 Models and mechanisms of frequency-dependent predation. *Am. Nat.* **130**, 603–623.
- Greenwood, J. J. D. 1969 Apostatic selection and population density. *Heredity* **24**, 157–161.
- Greenwood, J. J. D. 1984 The functional basis of frequency-dependent food selection. *Biol. J. Linn. Soc.* **23**, 177–199.
- Greenwood, J. J. D. 1985 Frequency-dependent selection by seed predators. *Oikos* **44**, 195–210.
- Guilford, T. & Dawkins, M. S. 1987 Search images not proven: a reappraisal of recent evidence. *Anim. Behav.* **35**, 1838–1845.
- Horsley, D.T., Lynch, B. M., Greenwood, J. J. D., Hardman, B. & Moseley, S. 1979 Frequency-dependent selection by birds when the density of prey is high. *J. Anim. Ecol.* **48**, 483–490.
- Manly, B. F. J. 1978 Regression models for proportions with extraneous variance. *Biometrie-Praximetrie* **18**, 1–18.
- Manly, B. F. J. 1985 *The statistics of natural selection*. London: Chapman & Hall.
- Nelder, J. A. & Wedderburn, R. W. M. 1972 Generalized linear models. *J. R. Statist. Soc. A* **135**, 370–384.
- Owen, D. F. 1965 Density effects in polymorphic land snails. *Heredity* **20**, 312–315.
- Sherratt, T. N. & Harvey, I. F. 1989 Predation by larvae of *Pantala flavescens* on tadpoles of *Phyllomedusa trinitatis* and *Physalaemus pustulosus*: the influence of absolute and relative density of prey on predator choice. *Oikos* **56**, 170–176.
- Sherratt, T. N. & MacDougall, A. D. 1995 Some population consequences of variation in preference among individual predators. *Biol. J. Linn. Soc.* **55**, 93–107.
- Tinbergen, L. 1960 The natural control of insects in pine woods. 1. Factors influencing the intensity of predation by songbirds. *Arch. Néerl. Zool.* **13**, 265–343.
- Tucker, G. M. & Allen, J. A. 1991 Selection by humans searching for computer-generated prey images: the effect of prey density. *Biol. J. Linn. Soc.* **44**, 169–174.
- Willis, A. J., McEwan, J. W. T., Greenwood, J. J. D. & Elton, R. A. 1980 Food selection by chicks: effects of colour, density, and frequency of food types. *Anim. Behav.* **28**, 874–879.
- Zar, J. H. 1984 *Biostatistical analysis*. 2nd edn. Englewood Cliffs, NJ: Prentice-Hall.