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Does prey dispersion affect frequency-dependent predation by wild birds?

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Abstract Despite the fact that the vast majority of natural prey items are dispersed in a non-random manner, few studies of frequency-dependent selective predation have explicitly examined the effect of prey dispersion on selectivity. We examined the effect of prey dispersion on the direction and strength of frequency-dependent selection by wild birds feeding on artificial prey (green or brown pastry baits). In a series of four experimental manipulations, we tested for the occurrence of frequency dependence with two different dispersion patterns (random or clumped). Manipulations were carried out at one of two absolute densities (25 prey m⁻² or 100 prey m⁻²), and were repeated at different sites in Southampton, England and Aljarafe, Spain. Our results suggest that prey dispersion has no effect on either frequency-dependent or -independent preferences. One possible explanation for this is that the birds had virtually complete information about prey frequencies at the relatively high densities used and based their preferences on their overall perception of availability. However, we cannot rule out the possibility that dispersion may influence selectivity when prey are cryptic or available at lower absolute densities. Although there was no effect of dispersion, frequency-dependent selection was, overall, significantly anti-apostatic (i.e. rare baits were more preferred than common baits). This anti-apostatic effect was stronger in Southampton than Aljarafe and stronger at 100 prey m⁻² than 25 prey m⁻². The differences in the strength of selection between the two locations was interpreted in terms of (i) whether the avian predators foraged in flocks or not, and (ii) the

number of different species present (and, consequently, the variation in preference among individual birds).

Key words Frequency dependence · Selective predation · Bird · Dispersion · Density

Introduction

It is well known that frequency-dependent selective predation has important consequences for the stability of prey populations (Murdoch and Oaten 1975; Hassell 1978), or morphs within a population (Clarke 1962). In studies using wild birds as predators, numerous experiments (see Allen 1988 for review) have demonstrated that, broadly speaking, over-predation on common prey types or morphs (“apostatic” selection) occurs at relatively low prey densities and over-predation on rare prey types (“anti-apostatic” selection) occurs at high densities. These two types of selection have very different consequences for prey populations; apostatic selection tends to promote genetic diversity within a population or species diversity within a community, while anti-apostatic selection tends to promote uniformity.

Much of the research in this field has focused on the effects of prey density and crypsis on frequency-dependent predation (Allen 1988) or the proximate mechanisms of frequency-dependent predation, such as search image formation and search rate modification (Guilford and Dawkins 1987; Plaisted and Macintosh 1995; Reid and Shettleworth 1992). However, almost nothing is known about the influence of prey dispersion on selectivity, either from the point of view of the predator or the prey. In virtually all studies of frequency dependence by wild birds experimenters have presented baits to the predators in a randomly dispersed manner (or an approximation thereof). This would usually be considered to be good experimental practice since it removes a potentially confounding dispersion effect. Yet a random dispersion represents only a small part of a natural continuum of dispersion

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which ranges from uniform (repulsive), through randomness to a clumped (contagious) dispersion. Attempts to characterise the dispersion of wild species suggest that most invertebrate prey populations are highly clumped (Taylor 1961, 1984), perhaps due to habitat preference or as an anti-predator strategy. Indeed, truly random distributions may be very rare in natural systems (Taylor et al. 1978).

How might prey dispersion affect frequency-dependent predation? Since the first few prey encountered by a predator in a foraging period may affect subsequent selection decisions (Cook 1965) it is conceivable that any deviation from randomness could affect the strength and direction of selection. Gianino and Jones (1989) have demonstrated, using pastry baits at a density of 2 m^{-2} , that changes in dispersion can reverse the direction of frequency-dependent selectivity by vertebrate foragers. Clearly, it is necessary to understand the effects of dispersion on prey selection before any generalisations can be made from experiments with random distributions to real-world situations. Here, we present the results of a series of experimental manipulations that examine how the dispersion of artificial pastry baits affects frequency-dependent predation by wild birds at high densities (25 and 100 baits m^{-2}). Our study also offers some insight into the way in which differences in selectivity between territorial and flocking bird species may have differing consequences for prey populations.

Methods

Our experiments were carried out in Southampton, United Kingdom, during February and early March 1996, and Aljarafe, near Seville, Spain, during late March and April 1996. Four different sites were used in each location. In Southampton, these consisted of two sites in the grounds of the Biomedical Sciences Building, University of Southampton and two within the University's Botanical Gardens. In Aljarafe, the four sites were located in olive groves within a private residence. In both locations, at least 200 m separated all sites.

Prey consisted of small green or brown pastry baits. The pastry was made from plain flour and lard in a 3:1 ratio by weight. Green baits were made by adding 15 ml of Apple Green food dye (k6027, Pointing Ltd) to 1000 g of pastry, while brown baits were produced by adding 27 ml of brown dye (k6024, Pointing Ltd) to 1000 g of pastry. After mixing the colours, the pastry was rolled into a flat sheet of height 5 mm, then cut into small cuboids ($10 \times 7 \times 5 \text{ mm}$).

In each trial, 100 prey (10 of one colour and 90 of the other) were placed within a square plot. Experimental manipulations were conducted with plots of two different sizes; either $1 \times 1 \text{ m}$ (100 prey m^{-2}), henceforth referred to as "high density", or $2 \times 2 \text{ m}$ (25 prey m^{-2}), henceforth referred to as "low density". In Southampton, these were short grass plots, while in Aljarafe they consisted of semi-barren earth with low weeds.

In total, four experimental manipulations were carried out: (i) Southampton, high density, (ii) Southampton, low density, (iii) Aljarafe, high density, and (iv) Aljarafe, low density. The same four sites were used at each location. Apart from prey density and location, each manipulation followed an identical protocol. This involved testing the selectivity of predators at two different frequencies (10% brown and 90% brown baits) and two different dispersions ("random" and "aggregated"). In each manipulation, there were four treatments, representing the four possible combi-

nations of frequency and dispersion: (i) random dispersion with 10% brown prey, (ii) random dispersion with 90% brown prey, (iii) aggregated dispersion with 10% brown prey, and (iv) aggregated dispersion with 90% brown prey.

In the random dispersion treatments, prey items were scattered haphazardly over the experimental area (Fig. 1a), following the techniques of Allen et al. (1990), Allen and Anderson (1984) and Greenwood et al. (1984). In the "aggregated" treatments, the prey were arranged into five high-density clumps (one in the centre and one near to each corner), with a frequency of 9:1 (18:2) present in each clump (Fig. 1b). The two prey types were haphazardly dispersed within each clump.

Each manipulation lasted for 12 days, with data being collected from all four sites on each day. We used a Latin square design, with all four treatments carried out each day at different sites. Each treatment was repeated three times at each of the four sites. Birds were attracted to the experimental sites and familiarised with the baits for several days prior to the start of each manipulation.

Trials in the United Kingdom commenced at 0900 hr, and those in Spain at 1000 hours (local times). Sites were checked every hour. A trial was terminated when, in the judgement of the experimenters, between 30% and 50% of the available prey items had been consumed, although the exact number was difficult to control. Data were discarded from days when predation rates were very low (less than 10 baits consumed) since these would tend to produce poor estimates of selectivity (Murdoch et al. 1975). Baits which were heavily pecked (with a piece missing) were counted as predated.

Data were analysed using the β index of Manly (1974). When prey are not replaced during experimental trials the preference for brown prey, β_{brown} is estimated by:

$$\beta_{\text{brown}} = \frac{\log(b/B)}{\log(b/B) + \log(g/G)}$$

where B and G are the number of pieces of brown and green prey present at the start of a trial and b and g are the numbers remaining at the end of a trial. β lies in the range 0–1, with $\beta_{\text{brown}} = 1$ representing exclusive preference for brown prey, and $\beta_{\text{brown}} = 0$ representing total rejection of brown prey. β cannot be calculated when all of one type of prey are eaten. On the few occasions when this occurred, a β value was calculated by setting the number of remaining prey equal to 0.0001.

In order to statistically examine the effects of density and location in addition to the effects of frequency and dispersion, we analysed all four experimental manipulations in a single analysis. To avoid the risk of pseudoreplication (Hurlbert 1984) we used a nested analysis of variance, with the eight different sites considered as repeated measures (i.e. independent experimental units) nested within locations.

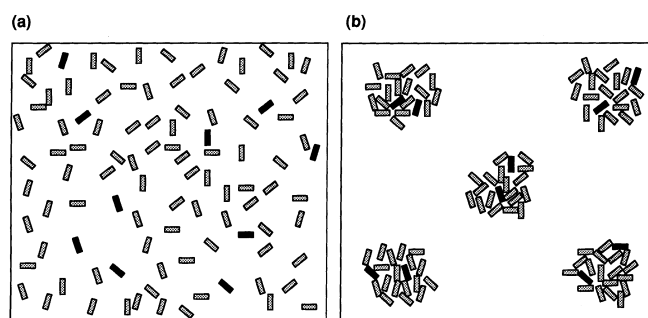


Fig. 1 Schematic representation of a random, and b aggregated distribution of baits used in our experiments. Note that relative to the experimental plot the baits appear larger in our figure than they did in reality. The exact sizes of the baits and experimental plots are given in the text

Results

Predators

The main predators in these experiments were wild passerine birds. In the Southampton experiments, the species observed feeding were the blackbird (*Turdus merula*), songthrush (*T. philomelos*), robin (*Erithacus rubecula*) and starling (*Sturnus vulgaris*). At the sites in Aljarafe, only flocks of house sparrows (*Passer domesticus*) were observed feeding on the baits.

Number of baits consumed

The number of baits consumed in experimental trials may bias estimates of selectivity (Manly 1974; Weale 1992; Church et al. 1996). In particular, there is a bias towards apostatic selection when fewer than 50% of available prey are consumed. In such cases, the probability of a predator completely overlooking rare baits by chance is increased. This results in a β value of 0 for the rare prey. This stochastic process will, when averaged over a number of trials, tend to produce an apostatic bias, and the fewer the total number of baits consumed, the stronger the bias. In the two Aljarafe experiments, approximately 50% of baits were consumed (Table 1); this will give rise to virtually unbiased β values. However, only 20–30% of baits were eaten in the Southampton experiments. The simulations of Weale (1992) and Church et al. (1996) suggest that this will result in a slight bias towards apostatic selection.

Analysis of β values

Overall, selection was significantly anti-apostatic, with β_{brown} values being significantly higher when brown baits were rare than when common (frequency main effect: $F_{1,6} = 49.4$, $P < 0.001$; Fig. 2a–d). The anti-apostatic effect was significantly stronger in Southampton than it was in Aljarafe (frequency \times location: $F_{1,6} =$

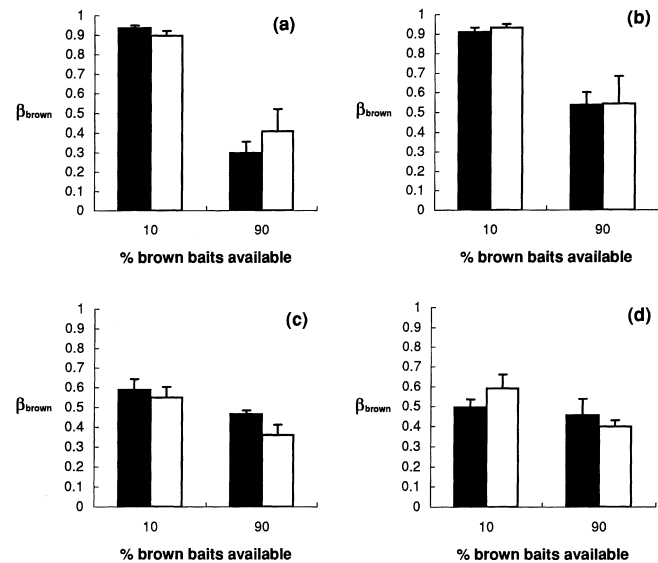


Fig. 2a–d Effect of prey frequency and dispersion on selectivity (mean $\beta_{\text{brown}} \pm \text{SE}$, calculated from mean values for each of the four sites in a given experimental manipulation) by avian predators. *Black bars* represent random and *white bars* aggregated prey distributions. **a** Southampton, high prey density (100 baits m^{-2}), **b** Southampton, low prey density (25 baits m^{-2}), **c** Aljarafe, high prey density (100 baits m^{-2}), **d** Aljarafe, low prey density (25 baits m^{-2})

15.8, $P < 0.01$). It was also stronger at a density of 100 baits m^{-2} than at 25 baits m^{-2} (frequency \times density: $F_{1,6} = 26.9$, $P < 0.01$). This density effect was more pronounced in the Southampton manipulations than in Aljarafe (frequency \times density \times location: $F_{1,6} = 11.3$, $P < 0.05$).

Prey dispersion had no effect on either frequency-independent bait preferences (dispersion main effect: $F_{1,6} = 0.0$, $P > 0.9$) or frequency-dependent selection (frequency \times dispersion: $F_{1,6} = 0.1$, $P > 0.5$). In addition, the effect of dispersion on frequency-dependent selection was not influenced by density (frequency \times dispersion \times density: $F_{1,6} = 0.7$, $P > 0.1$) or location (frequency \times dispersion \times location: $F_{1,6} = 2.9$, $P > 0.1$).

Table 1 Number of artificial baits (mean \pm SE) consumed in each frequency-dispersion combination in the four experimental manipulations; $n = 4$ sites in all cases

Experiment	10% Brown baits available		90% Brown baits available	
	Random	Aggregated	Random	Aggregated
Southampton high density	20.3 \pm 2.8	25.5 \pm 2.4	32.5 \pm 4.5	29.7 \pm 2.5
Southampton low density	23.5 \pm 4.1	23.8 \pm 1.9	24.7 \pm 3.4	29.6 \pm 2.1
Aljarafe high density	48.0 \pm 6.1	46.3 \pm 5.4	47.6 \pm 5.0	48.0 \pm 6.0
Aljarafe low density	43.6 \pm 4.1	50.9 \pm 4.2	48.4 \pm 1.6	50.9 \pm 3.0

Discussion

In this study, we found significant anti-apostatic selection by wild birds feeding on a dimorphic population of artificial prey items. However, the strength of this frequency-dependence was stronger in Southampton than it was in Aljarafe and stronger at 100 baits m^{-2} than 25 baits m^{-2} . Broadly speaking, these data are consistent with those of Raymond (1987), who found anti-apostatic selection by garden birds foraging on similar pastry prey at a density of 30 m^{-2} . Other experiments with wild birds which have demonstrated this type of selection have generally presented baits at much higher, and perhaps unrealistic, densities. For example, Horsley et al. (1979) used a density of 800 m^{-2} , while Allen and Anderson (1984) used 11 800 m^{-2} . The implication of

our data is that, at moderate prey densities, selection by wild birds would tend to promote colour pattern monomorphism, rather than polymorphism, in natural prey populations (other things being equal).

Our results also suggest that prey dispersion has no effect upon the direction or strength of frequency-dependent predation by wild birds. In contrast, Gianino and Jones (1989) found apostatic selection at a density of 2 baits m^{-2} when prey were randomly distributed and anti-apostatic selection when aggregated (although it must be noted that their "aggregated" dispersion was qualitatively different to ours and probably less realistic, consisting of a line of rare prey types along one side of their experimental plot). We suggest that the non-significant effect of dispersion in our study resulted primarily from the way in which the small experimental plots and high prey densities influenced prey perception by the avian foragers. In general, birds may be capable of perceiving prey scattered over a relatively wide area (Blough 1979), although there is bound to be some effect of distance on prey detectability (Getty and Pulliam 1993). In a small "patch" of high-density, relatively conspicuous prey (as in our experiments), it is likely that most prey items can be detected simultaneously by the predator. In other words, the foragers may have complete information about prey availabilities. If preferences depend upon the overall perception of prey availability in a patch, this would tend to obscure any effects of dispersion on frequency-dependence. In our experiments, therefore, the birds might have preferentially consumed rare prey regardless of the actual dispersion of the prey due to other mechanisms such as a confusion effect (Allen and Anderson 1984), or because there are benefits to consuming a mixed diet (Greenwood 1984). We suggest that prey dispersion is more likely to influence preference when prey are cryptic and/or encountered sequentially. In such cases, the perceived availabilities of prey items by foragers are more likely to differ under different prey dispersions.

We must also sound a note of caution with regards to the statistical analysis of Gianino and Jones (1989). They treated each foraging trial as independent, even though data were obtained from only two experimental sites, albeit over a period of 2 years. As a result, it is likely that some foraging birds would have been present in a number of different trials. Treating trials as independent under such circumstances leads to a degree of pseudoreplication (Hurlbert 1984; Lombardi and Hurlbert 1996), in which degrees of freedom are increased and, consequently, the type I error rate is inflated. We suggest that the appropriate analysis is, as we have performed here, to treat sites as experimental units and perform a repeated measures ANOVA. Such an analysis would certainly reduce the *P*-values of Gianino and Jones (1989) results; indeed, it is worth noting that our data produces significant effects of dispersion on frequency-dependence if individual foraging trials are treated as independent. On a broader scale, there is a risk of pseudoreplication in many analyses of selective

predation carried out in the wild (including those previously performed by us). The solution is clearly to replicate foraging trials at as many different sites as possible, and to treat different sites as independent experimental units in subsequent statistical analyses (see Greenwood (1985) for further discussion of the design and analysis of such experiments).

Our results should also be interpreted in the light of potential biases in β . Estimates of β were virtually unbiased in the Aljarafe experiments since approximately 50% of baits were consumed (Weale 1992). In contrast, the Southampton data were likely to have a slight apostatic bias since only 20–30% of baits were, on average, consumed in trials (Weale 1992, Church et al. 1996). As a result, the significant difference in the magnitude of anti-apostatic selection between the two locations is likely to be an underestimate of the true difference. However, a note of caution must be sounded; in general, it is not clear what effect dispersion might have on bias in β since assessment of β bias is based on the assumption of randomly dispersed prey. We suspect that, if anything, β should be less biased when prey are aggregated since the five identical clumps, each containing two rare baits, would tend to reduce "runs of bad luck" (whereby stochastic effects might result in rare prey being under-predated relative to common prey types).

Overall, the strength of anti-apostatic selection was markedly lower in the Aljarafe experiments than the Southampton experiments. We suggest two possible explanations, both of which relate to the nature of the predators at the two sites. The first is that selection will depend to some extent on whether predators are foraging individually, as in the Southampton experiments, or in flocks, as with the house sparrows in the Aljarafe experiments. Given that prey preferences may result from individuals modifying their behaviour as successive prey are encountered (Cook 1965), we would have expected to see stronger preferences from the Southampton birds since our data were obtained from long foraging bouts by relatively few individuals. Conversely, in Aljarafe there were few opportunities for individual sparrows within a flock to consume more than a few prey items before trials were terminated. This would tend to make selection more random (i.e. less anti-apostatic). Our second explanation is that the difference between the two locations is due to between-species variation in the frequency-independent component of preference. In the Southampton experiments, several different species frequently visited the experimental sites, while in Aljarafe only house sparrows were seen. If some of the species present in Southampton had strong opposing preferences for brown or green baits then anti-apostatic selection would tend to be the overall result (Chesson 1984; Sherratt and Macdougall 1995). This is because whichever species prefers the rare prey items will consume proportionately more of their preferred prey than will the species which has an overall preference for common foods (assuming that individuals of both species consume roughly equal numbers of prey). Since

between-species variation in preference is likely to be greater than individual variation within a species, it follows that this type of effect would have been markedly reduced in the Aljarafe experiments, where house sparrows were the only species observed foraging.

The justification for these experiments lies, ultimately, in their ability for us to understand real-world predator-prey systems, and in such systems prey are rarely dispersed randomly. Our results suggest that, at high densities at least, prey dispersion does not greatly influence frequency-dependent selective predation. On a broader scale, though, we do believe that consideration of prey dispersion has generally been neglected in studies of foraging behaviour. Future research programs may benefit from attempting to characterise the dispersion of prey species and also from theoretical and empirical considerations of the behavioural responses of predators to deviations from random dispersion between and within patches (e.g. Iwasa et al. 1981; Dall and Cuthill 1997).

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