The early bird gets the worm: foraging strategies of wild songbirds lead to the early discovery of food sources

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Animals need to manage the combined risks of predation and starvation in order to survive. Theoretical and empirical studies have shown that individuals can reduce predation risk by delaying feeding (and hence fat storage) until late afternoon. However, little is known about how individuals manage the opposing pressures of resource uncertainty and predation risks. We suggest that individuals should follow a two-part strategy: prioritizing the discovery of food early in the day and exploiting the best patch late in the day. Using automated data loggers, we tested whether a temporal component exists in the discovery of novel foraging locations by individuals in a mixed-species foraging guild. We found that food deployed in the morning was discovered significantly more often than food deployed in the afternoon. Based on the diurnal activity patterns in this population, overall rates of new arrivals were also significantly higher than expected in the morning and significantly lower than expected in the afternoon. These results align with our predictions of a shift from patch discovery to exploitation over the course of the day.

1. Introduction

Small birds exhibit predictable management of body mass in order to manage overnight survival. Under high perceived predation risk, individuals employ a strategy whereby they trade-off their starvation risk by reducing fat storage to maintain greater flight ability [1,2], delaying weight gain until later in the day [3,4]. During winter months, birds are under increased time and energy constraints resulting from shorter day length and colder temperatures. Therefore, they must ensure that they have access to enough resources to meet a higher rate of energy intake late in the day. Despite considerable work on body-mass strategies, the process relating to the discovery and sampling of resources has received much less attention.

Models dealing with resource uncertainty predict that individuals should increase fat storage linearly during the day [3,5], a strategy that is clearly incompatible with avoiding predation [6]. Existing work highlights the ability of individuals to locate the most profitable food sources using optimal sampling [7]. Thus, by sampling a number of sites earlier in the day, individuals should be able to exploit the most profitable site later in the day as the risk of overnight starvation increases. This would be particularly important for individuals employing a body-mass delay strategy; rather than exploiting known patches in the morning, birds could be searching (either socially or asocially) for new resource locations while they are light or when predation risk is low. Models of caching behaviour suggest high rates of caching in the morning with high retrieval rates late in afternoon [8].

Taken in combination, these models suggest that knowledge of the location of a reliable food source is paramount for individuals to optimally manage the risks of predation and starvation. Yet, models have not incorporated strategies that gather information about food availability as a way of dealing with resource uncertainty.
Here, we propose a new hypothesis; individuals should prioritize discovery and assessment of potential resources early in the day, before switching to exploitation as the day progresses.

In this study, we tested for temporal dependence in food discovery behaviours. We predicted that if individuals are shifting strategies from exploration to exploitation, we should observe a non-random pattern of within-day-discovery, with higher probabilities of discovering food earlier in the day. Given the presence of multiple species in the population, we then tested for species-level differences, testing the prediction that caching species should be more likely to discover novel food sources earlier given their need to accumulate food earlier than non-cachers [8].

2. Material and methods

(a) Discovery of foraging patches

We ran 36 independent trials at 18 unique sites within Wytham Woods in Oxfordshire, UK (51°46’ N, 1°20’ W) in a fully balanced experimental design. Sites were chosen by randomly selecting coordinates within the boundaries of the woodland ensuring that they were sited at least 150 m apart and 100 m away from any permanent feeding locations. Each day, three feeders (sites) fitted with radio-frequency identification (RFID) antennae were placed at different sites in the morning (from 07.00) and three more at other sites in the afternoon (from 12.00), for 5 h each. Two weeks later, each site was deployed during the other time period. Thus, each of the 18 sites was sampled twice, once in morning and once in the afternoon. Feeders detected individual great tits (Parus major), blue tits (Cyanistes caeruleus), marsh tits (Poecile palustris), coal tits (Periparus ater) and nuthatches (Sitta europaea) that had been fitted with PIT-tags either as nestlings or during extensive pre-winter catching as part of on-going research into social behaviour in this population [9,10]. We tested whether sites were more likely to be discovered early in the day by recording the arrival of first individual at each site in each treatment (a ‘discovery’). Subsequent arrivals by new individuals were used to test whether a greater number of individuals arrived in morning treatments, using 1000 randomizations of the data that controlled for social effects (see the electronic supplementary material). We calculated 95% confidence intervals (CIs) using 1000 bootstraps on each treatment.

(b) Population-level patterns

In order to assess the relationship with activity levels in the population, we used data from a permanent grid of 65 feeders fitted with RFID antennae. These feeders are placed approximately 250 m apart and designed to open concurrently 2 days per week (from pre-dawn to post-dusk), providing a snapshot of the population structure and activity pattern. We used data from this grid over the three weeks that discovery feeders were deployed (but opened on different days and kept spatially separated from these sites). In order to avoid effects of changing day lengths when combining data, we scaled the daily foraging data to fit into 20 evenly spaced segments that were approximately half-an-hour long (range 28.8 min to 31.2 min long). Finally, we tested the alternative hypotheses that arrivals to novel feeders were related to activity levels by dividing the probability of arriving at feeders by the independent feeding and movement rates at those times. All statistical analyses were conducted in R [11].

(c) Species effects

In order to assess whether there was a non-random distribution of discoveries according to species, we calculated the odds of each species discovering the novel food site given the frequency of species visiting the feeders in the population. The CIs were estimated using 1000 jackknife simulations of the data where one data point was removed in each simulation. We then tested for a non-random distribution in arrival order of the different species by calculating the mean for each species. We estimated two-tailed significance by running 1000 permutations of the arrival order (randomizing orders between individuals within sites and days) and calculated the number of mean randomized orders that were greater or less than the observed mean order in each species.
3. Results

(a) Discovery of food patches
There was a clear difference in site discovery events across the day. In total, 22 of the 36 feeders were discovered (14 in the morning and eight in the afternoon treatments; paired $t$-test: $t = 2.92$, d.f. = 17, $p = 0.01$; figure 1a). No site, which was discovered in an afternoon treatment, had not discovered in its paired morning treatment. Furthermore, the number of new individuals arriving at sites was significantly higher throughout the morning than the afternoon (180 individual morning discoveries versus 64 in the afternoon; figure 1b). This is unlikely to have occurred due to environmental differences between sites as the experimental design was fully balanced with both morning and afternoon treatments conducted at each.

(b) Relationship with activity pattern
We found that morning discoveries occurred significantly more often than expected from the foraging activity (figure 2a). The odds of arriving given the feeding activity was greater in the morning and dropped to below expected in the afternoon (dashed line shows expected 1-to-1 ratio, shading are 95% bootstrapped CIs, significance is calculated from the number of bootstraps overlapping 1). Asterisks represent significance (**$p < 0.01$, *$p < 0.05$). (c) The pattern was general across species.

(c) Species effects
The patterns of new arrivals were similar across all species (linear models: all $p > 0.05$, figure 2c). However, there were proportionally fewer blue and great tits than expected given their relative abundance in the population (odds $\pm$ 95% CIs 0.75 $\pm$ 0.19 and 0.95 $\pm$ 0.30, respectively, expected = 1). By contrast, coal tits, marsh tits and nuthatches all had higher numbers of individuals finding feeders (odds $\pm$ 95% CIs 2.22 $\pm$ 1.50, 2.42 $\pm$ 1.34 and 2.09 $\pm$ 2.26, respectively). The same pattern held with the order of arrival after a site had been discovered (expected range is 95% of the posterior distribution). Both blue (mean 12.5, expected 9.6–12.5, $p = 0.05$) and great tits (mean 13.6, expected 9.4–12.8, $p < 0.01$) arrived later than expected. Coal tits (mean 8.6, expected from 13.00 onwards the odds dropped below the value expected from foraging activity. Although arrivals by individuals at feeders may be mediated by social mechanisms such as local enhancement [9], group sizes were larger in the afternoon than in the morning (see electronic supplementary material, figure S1) and therefore unlikely to explain the observed pattern.
8.0–14.5, \( p = 0.09 \), marsh tits (mean 5.6, expected 8.4–13.8, \( p < 0.001 \)) and nuthatches (mean 5.7, expected 5.8–17.8, \( p < 0.05 \)) mostly arrived earlier than expected.

4. Discussion

Using experimental deployment of novel food patches combined with automated detection, we demonstrated that birds exhibit clear differences in foraging strategy over the course of a day. Patterns of discoveries closely matched our predictions with sites having a greater probability of being discovered in the morning than the afternoon. These patterns were not explained by the general feeding activity.

An alternative explanation for the observed daily patterns in patch discovery is that there is a switch between the marginal values of foraging and gaining information in the early morning. Under this hypothesis, individuals need to replenish energy lost overnight, thereby increasing the marginal value of known patches early in the morning. As patches are exploited and the value of acquiring energy decreases, the marginal value of a bird’s current patch decreases; consequently causing all individuals to leave their patches in search for new ones. However, while this would result in a high rate of morning discoveries, it should also be accompanied by a morning peak in between-site movements as individuals refresh their information and relocate to the richest remaining patches. Analysis of movements between known feeding sites by individuals in the permanent grid does not support this hypothesis (see electronic supplementary material, figure S2).

The second part of our hypothesis relates to the exploitation of better patches late in the day. Movements by individuals between known feeders showed a clear burst of relocations approximately 2 h before dusk, followed by a drop in movements (see electronic supplementary material, figure S2) that were not related to the pattern of site discoveries (see electronic supplementary material, figure S3). A recent study on closely related species also found a peak in feeding activity at known food sources approximately 2 h before sunset [12]. These results are inconsistent with our hypothesis; as individuals should preferentially forage immediately before sunset. However, this could emerge from a trade-off with several other competing pressures on survival strategies, including: (i) time spent searching for or guarding roosting sites, and (ii) exclusion from high-quality patches by socially dominant individuals. End-of-day foraging strategies warrant further investigation, and experiments using varying patch qualities is a clear future step.

This study shows clear differences in the behaviour of individuals over the course of a day. We found that individuals partitioned foraging into searching and feeding behaviour, potentially enabling optimal management of the opposing predation and starvation risks. This implies that behavioural plasticity plays an important role in mediating survival in a way that has not previously been considered by existing studies.

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Data accessibility. We provide the data of patch discovery via the Dryad repository (doi:10.5061/dryad.9g6q2) [13].

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References

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