CONTRAFREELOADING IN STARLINGS:
TESTING THE INFORMATION HYPOTHESIS

by

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Summary

Contrafreeloading (CFL) behaviour, in which animals forage persistently in patches that require effort to exploit when patches containing *ad lib.* food are easily available, seems to contradict the predictions of optimal foraging theory. However, it has been proposed that contrafreeloaders are in fact exploiting a hidden resource, namely information about patches that may be useful in future foraging attempts. We performed two experiments on starlings *Sturnus vulgaris* to test this hypothesis by determining the circumstances in which CFL occurs and assessing whether any useful information is acquired by animals performing the behaviour. In accordance with previous results we found that CFL is reduced when foragers are previously deprived of food and also when there are means of gathering information aside from sampling (namely when patches that require effort to exploit can be visually inspected). We also found that useful information is acquired by birds that perform CFL, in that when subsequently tested in extinction with the best patch removed they reliably chose the patch that had been the second best. These results are consistent with the information gain hypothesis. However, birds with low levels of CFL did not perform discernably worse in this test of patch knowledge and experimental reductions in CFL achieved through deprivation treatments did not produce apparent reductions in useful information possessed.

Introduction

Many optimal foraging models are based on the assumption that animals behave so as to maximise their average net long-term rate of energy intake (for

a review see Stephens & Krebs, 1986). This currency is assumed because it combines energy gained from foraging, energy expended during foraging and time spent foraging in a manner that seems likely to relate closely to fitness in most vertebrates. Despite much experimental support for models based on rate maximisation (*e.g.* Kacelnik, 1984), research on operant conditioning frequently produced observations that animals will work for food even when the same food is freely available (Osborne, 1977). Indeed, many of these observations come from animals of the same species more recently used to produce evidence supporting rate maximisation, *e.g.* starlings (Inglis & Ferguson, 1986), laboratory rats *Rattus norvegicus* (Jensen, 1963) and laboratory pigeons *Columba livia* (Neuringer, 1969). This phenomenon, which is in apparent contradiction to the predictions of classical optimal foraging theory and most other accounts of instrumental performance, is known as contrafreeloading (CFL) (D'Amato, 1974; Osborne, 1977; Inglis *et al.*, 1997).

Some feeding from sub-optimal patches is inevitable in animals attempting to identify the best patch of a range. For example, Krebs *et al.* (1978) found that when presented with two novel patches of differing profitability, great tits *Parus major* began by sampling both patches, before switching to almost exclusive exploitation of the most profitable patch. Such behaviour was shown to be consistent with an optimal foraging strategy. However, CFL has been contrasted to this form of sampling since it occurs both in the presence of obviously abundant and continuously available free food, and when animals performing the behaviour demonstrate whilst hungry that they know the location of the best food source (D'Amato, 1974; Osborne, 1977). CFL has also been defined as showing a preference greater than 50% for taking food from sub-optimal sources though this seems to be a rather arbitrary threshold (D'Amato, 1974; Osborne, 1977; Forkman, 1991, 1996; Inglis *et al.*, 1997).

CFL has been explained in terms of various reinforcement effects. Species-typical behaviour can be reinforcing in its own right regardless of any observed purpose or association (Kacelnik, 1987), so a behaviour such as probing by starlings could be performed merely because it is inherently reinforcing. However, species-typical behaviour may be elicited as a foraging technique (Kacelnik, 1987), possibly as an obligatory appetitive response (Gardner & Gardner, 1988) or as a more arbitrary response that becomes reinforced when it is associated with acquiring food (Osborne,

1977), ultimately becoming reinforced in its own right (Bindra, 1959). This secondary reinforcement effect may also apply to the performance of operant behaviours rewarded by the experimenter, *e.g.* lever-pressing for food pellets in rats (Osborne, 1977). Further causal explanations of CFL account for it in terms of faulty methodology. For example, in a training period prior to an experiment the subjects could be exposed to the various food sources at different frequencies which could result in differential neophobia during the experiment (Osborne, 1977). Thus if *ad lib.* food was introduced without prior training this could result in CFL. Conversely, lack of prior training could result in attraction to new sources of food in an experiment; if food that required work appeared as a novel source this could also result in CFL.

Recent functional explanations of CFL have invoked the idea of information primacy (Inglis & Ferguson, 1986; Forkman, 1991, 1993; Inglis *et al.*, 1997). This seeks to explain CFL in terms of animals seeking information about alternative food sources by sampling them, a hypothesis consistent with previous evidence that animals find information gain reinforcing (D'Amato, 1974). Such information would be valuable in the wild, improving the efficiency of relocating profitable patches in the future. To date, three approaches have been used to test the information hypothesis. These have been: manipulating food deprivation prior to foraging (Inglis & Ferguson, 1986); varying the potential usefulness of information gained through the constant changing of patch quality (Forkman, 1991); and providing alternative methods of assessing patch quality without requiring extensive sampling (Forkman, 1996).

Inglis & Ferguson (1986) reasoned that information gathering decreases when it is supplanted by more intense motivational states such as hunger and attempted to manipulate CFL in starlings *Sturnus vulgaris* by food deprivation; they found that increasing deprivation decreased CFL. However, this did not provide conclusive verification of the information hypothesis because the experiment did not disprove explanations of CFL based on differential attraction to the food sources as proposed by Osborne. The experiment was also criticised by Kacelnik (1987) on the grounds that it did not account for the operant response being reinforcing in its own right.

Forkman (1991) investigated CFL in Mongolian gerbils, *Meriones unguiculatus*, by looking at the effect of uncertainty (high variance in patch quality from session to session). He reported that high uncertainty reduced CFL. This was explained as a change from exploratory to exploitative food

gathering since information gained would have little applicable use in an environment expected to be variable by the gerbils. However, the opposite result, in which low uncertainty reduced CFL, could also be explained by the information hypothesis, in that in this case repeated sampling would cease to yield new information in a constant environment.

Forkman (1996) used Mongolian gerbils *Meriones unguiculatus*, to test the information hypothesis. He suggested that foragers engaged in CFL because they cannot gather information about food sources by other means. Hence, if the information about a food source is signalled and can be assessed without work, then CFL should cease. This was tested by comparing the choices foragers made between food sources that can or cannot be assessed visually and freely available food. Forkman found that foragers fed by a significantly greater amount from food sources that cannot be assessed visually rather than on freely available food and that they fed by a significantly greater amount on freely available food rather than food that can be assessed visually. These findings cannot be explained by reinforcement effects. An alternative means of testing the information hypothesis is based on the assumption that if useful information about the environment is gathered during CFL, then the forager should reveal this improved knowledge about alternative food sources when tested. Bell (1991) proposed that animals that have the opportunity to learn the location of the best patch in their environment improve their efficiency in relocating those patches. The information hypothesis could thus be tested by means of a 'knowledge test' in which animals given the opportunity to establish the location of the best patch could then be tested in future foraging attempts to see whether they possessed this information. We therefore used this approach, and that of providing alternative methods of assessing patch quality without requiring extensive sampling, to test the information hypothesis in starlings, a species known to reliably display CFL (Inglis & Ferguson, 1986).

Experiment 1: Does CFL vary when the content of food sources are signalled and unsignalled?

The aim of this experiment was to replicate Forkman's (1996) experiment on contrafreeloading to see if CFL is reduced when information can be gathered

by an alternative method to sampling the food itself. In this experiment the preferences of starlings for *ad lib.* food versus food that requires work is examined. In one case the starlings are able to evaluate the food content of the latter by sight and in the other case they must actually sample the food in order to evaluate it. According to the information hypothesis one would predict the starlings to perform CFL to a greater extent when they cannot evaluate the content of work-dependent food by sight. We used a foraging task similar to that of Inglis & Ferguson (1986), exploiting the propensity of starlings to probe for food, but with an experimental design not used on this species before.

Method

Eight adult (> 1 yr) starlings of mixed sex were used. These individuals were caught in the wild and initially kept as an experimentally naive group. For the purposes of the experiment they were transferred to individual wire cages (l × h × w: 143 × 44 × 36 cm) resulting in visual but not acoustic isolation. The laboratory conditions included a controlled cycle of 8 hrs light per day during the experiment which reflected the winter conditions at the time of the experiment. Temperature fluctuated with the outdoor conditions though the building provided shelter from wind. The starlings were habituated to this regime for a week prior to the experimental procedures during which water and food were available *ad lib.* from dispensers in the cage walls. Water was available *ad lib.* during the experiments. The starlings could be observed through one way mirrors. After the experiments were completed the birds were retained for future experiments.

   Prior to the main experimental session a pre-trial period was used to test whether the birds could distinguish the contents of bowls by sense of smell, as well as to accustom the birds to feed through both opaque and transparent plastic membranes. Sense of smell was tested in order to verify the assumption that an opaque membrane blocks sensory information about the content of a dish. The bowls were 15 cm in diameter, 5 cm deep and made of plastic.

Pre-trial training
The birds were presented with two dishes of food for four hours each morning during which period no *ad lib.* food was available. The birds were not deprived outside the four hour training periods. Both dishes had identical contents, a mixture of 400 g of sieved sand and 50 g of sieved turkey crumbs. One dish was covered with an opaque plastic membrane and the other with a transparent plastic membrane. The membranes were weak enough to be pierced with equal ease by the beaks of the starlings in order for them to search in the sand underneath for the turkey crumbs. On the first day of the pre-trial session the membranes were pre-pierced in order to encourage probing by the birds and the session was continued until the birds fed readily from the dishes. Each dish was weighed in order to record the amount eaten. The point at which birds fed readily was judged by comparing their intake to their normal daily intake of turkey crumbs which was estimated to be 18 g (D. Wilson, pers. comm.). If feeding readily then the birds could be expected to eat approximately 4.5 g from each dish in the time available assuming they fed equally from each dish. Weighing the sand separately showed that it was not spilt or eaten in significant quantities.

Pre-trial test of sense of smell
The birds were presented with two dishes, both covered in transparent plastic membranes consistent with presentations through the rest of the experiment. One dish contained 50 g of turkey crumbs and 400 g of sand and the other contained a volume of sand equal to the volume of the materials in the other dish. Both dishes appeared identical since the food was entirely covered by sand in the first dish. The first dish to be probed by each bird was recorded and the dishes were removed. This presentation was repeated seven more times on the same day, each time the position of the dishes was swapped in order to randomise the effect of position.

Experimental session
The eight birds were split into two experimental groups of four. In the first block of four days members of one group were individually presented with a dish of *ad lib.* turkey crumbs accompanied by a dish containing an even mixture of 50 g of turkey crumbs and 400 g of sand covered in an opaque plastic membrane. The other group was given a dish of *ad lib.* turkey crumbs accompanied by a dish of the sand/food mixture covered in a transparent plastic membrane so that the food content could be evaluated visually. The trial period each day lasted for four hours and the amount of food eaten from each dish was recorded. In the second block of four days the same treatments were carried out but the two groups of birds exchanged treatments. At each presentation the position of the dishes was randomised.

Results

Pre-trial training
By the 5th day of training, all the subjects had reached required level of feeding of > 4.5 g from each dish, this indicating that the birds had become habituated to this method of foraging. Birds were found to take the same average amount of food from dishes covered in opaque plastic membrane as from dishes covered in transparent plastic membrane over the five days of training: Mean amount of food eaten on the fifth day = 5.19 g; Wilcoxon test: $T = 20$, $N = 8$, NS, indicating no prior preference for one membrane over the other.

Pre-trial test of sense of smell
Over eight trials, birds were equally likely as a group to approach the dish containing food and the dish not containing food: Mean number of approaches in the group to the dish containing food = 4.25 and mean number of approaches in the group to the dish without food = 3.75: Wilcoxon test: $T = 10$, $N = 8$, NS.
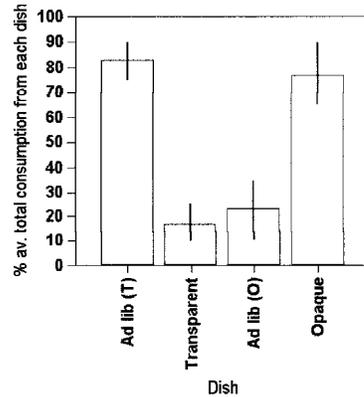
Fig. 1. Graph comparing the average % total consumption in experiment 1 across a group of birds ($n = 8$) from dishes when choosing either between dishes containing *ad lib.* food and a food-sand mix with a transparent covering (first two columns of graph) or between dishes containing *ad lib.* food and a food-sand mix with an opaque covering (second two columns of graph). Bars indicate inter-quartile ranges.

Experimental session

On average over eight days the birds chose to eat a significantly greater proportion of food from *ad lib.* dishes than from transparently covered dishes: See Fig. 1: Wilcoxon test: $T = 2.52$, $N = 8$, $p < 0.05$. In contrast, on average over eight days the birds chose to eat a significantly greater proportion of food from opaquely covered dishes than *ad lib.* dishes: Wilcoxon test: $T = 2.38$, $N = 8$, $p < 0.05$. Overall, the birds chose to eat a significantly larger amount of food from the opaquely covered dishes than from the transparently covered dishes: Wilcoxon test: $T = 2.52$, $N = 8$, $p < 0.05$. Individual birds also showed variation in day to day levels of CFL. When feeding from transparently covered dishes the mean range between maximum and minimum % CFL values of individual birds was 28.3%, when feeding from opaquely covered dishes this value was 41.2%.

Discussion

The results indicate that CFL levels are significantly lower when information about a food source can be visually assessed, compared with CFL levels when sampling is necessary for information to be acquired. Sampling was established as the sole means of acquiring information about opaquely covered bowls since the opaque membrane was shown in the pre-trial test of

sense of smell to be an effective sensory block. These findings are therefore consistent with the information primacy hypothesis which predicts that if CFL is for the purpose of acquiring information, it should lessen when information can be acquired by alternative behaviours. Our results also show that starlings will perform CFL when foraging for food in sand. These observations of the performance of a novel task add to previous data on starling CFL behaviour (Inglis & Ferguson, 1986).

The explanations of CFL based on the reinforcing properties of foraging or work (Kacelnik, 1987; Gardner & Gardner, 1988) are rejected. If foraging in sand was reinforcing in itself then one would not expect any significant difference between the amount of foraging based on the type of membrane covering the food/sand mixture. The differential neophobia explanation of CFL (Osborne, 1977) is also rejected, since the results show that both types of bowl were approached equally readily in the pre-trial acclimatisation period. Furthermore, if differential neophobia was a cause of CFL in the experimental session then one would predict that the birds would preferentially approach the membrane covered dishes rather than the *ad lib.* food since they had experienced acclimatisation to the former. This was not the case.

Experiment 2: Does CFL result in improved knowledge about alternative food sources?

The aim of this experiment was to see if CFL behaviour results in the gain of useful information about alternative food sources. If this is the case then birds should readily switch, without any further sampling, to the second best food source available when the best food source is removed from a range of patches. In order to investigate the effect of CFL on information gain we used two sources of variation in CFL levels: First, individuals show wide variation as found in experiment 1 (maximum range of 82.9%). Second, CFL may be manipulated via prior food deprivation (Inglis & Ferguson, 1986).

Method

For this experiment twelve different birds were used which were caught and kept under the same conditions as in experiment 1.

Experiment 2a: Is CFL accompanied by information gain?

Experimental sessions were run that lasted four days during which the activities of twelve subjects were observed through mirrored glass. On the first three days the birds were deprived of food for 3 hours and then presented with food for one hour. The food was presented in four identical dishes varying in food content, each one having a different colour-coded rim that allowed the birds to distinguish them. They had the following contents making up the total volume of 250 ml:

— Sand — 250 ml of sand
— High — 250 ml of turkey crumbs (sieved)
— Medium — 62.5 ml (25%) of food, 187.5 ml (75%) of sand
— Low — 31.25 ml (12.5%) of food, 118.75 ml (87.5%) of sand.

Dishes *Medium* and *Low* were filled so that none of the food content was visible on the surface. Throughout the experiment the dishes were arranged in the same position for each bird at every presentation but position of colour and contents was randomised between birds so that any preferences of position or colour common to all birds would not affect the results. The contents of the dishes containing food were weighed before and after each presentation. CFL was calculated as the percentage of the total food eaten from dishes *Medium* and *Low*. After each presentation the birds were given *ad lib.* food from dispensers.

On the third day after the morning presentation the birds were deprived at 2 pm in order that they would be motivated to feed on the fourth day. In order to discover whether the birds had gained information about the dishes they were 'knowledge tested' as follows. On the fourth day they were presented with three dishes at 10 am for fifteen minutes, the dish containing *ad lib.* food having been removed. The three dishes were identical in appearance to dishes *Sand*, *Medium* and *Low* used in the first three days of the session, but the test was carried out in extinction, *i.e.* with all the three dishes containing sand only, so that birds could not distinguish between them by smell. The behaviour of the birds was then observed through one-way glass. If the birds had gained information about the dishes then they would be expected to attempt to feed first from the best dish in this test, *i.e.* the dish resembling dish *Medium*. The first dish sampled during the knowledge test was therefore recorded for each bird. This marked the end of one experimental session; after a break of one day a replicate session was carried out.

Experiment 2b: Does reducing CFL via food deprivation reduce information gain?

After a break of two weeks, the experiment was repeated with the same birds in a modified form in which prior food deprivation was used to manipulate CFL. In this case the same experimental procedure was followed, except that just one day of presentation of dishes was followed by one day of knowledge testing. The colour and contents of the dishes for each bird were changed from those of experiment 2a. On the day prior to the presentation the birds were divided into three groups of four birds and were deprived for either 8, 4 or 0 hours following the methodology of Inglis & Ferguson (1986). This excluded deprivation time overnight and was repeated three times so that each bird experienced each period of deprivation. The presentation occurred at 10 am the next morning.

The following day the birds were deprived for 2 hours and then knowledge tested. The first dish sampled in the knowledge test was recorded for each bird. This was one experimental session, a break of two days being taken before any further sessions were commenced.

Results

Experiment 2a

As in experiment 1, the levels of CFL fluctuate quite heavily between and in individual birds. The mean % CFL levels of individual birds ranged between 0.0% and 100% and the mean range between maximum and minimum % CFL values of each bird was 29.3%. The mean CFL of individual birds did not significantly correlate between the 1st and 2nd sessions, however Spearman rank correlation: $r_s = 0.503$, $n = 12$, $0.10 > p > 0.05$.

In order to test for significance in the choice of dish in the knowledge test we used a G test as the expected results are greater than the expected results minus the observed results (see Table 1). In both sessions a significant number of birds selected the best available dish as first choice: 1st session, $G = 12.87$, df $= 2$, $p < 0.01$; 2nd session, $G = 13.74$, df $= 2$, $p < 0.01$.

To investigate the role of individual variation in CFL, the mean prior % CFL values for birds that did and did not choose the best dish in the knowledge probe were compared. A separate analysis was carried out for each session and no significant differences were found. Session 1: Mean prior % CFL of birds choosing best dish $= 51.0$, mean prior % CFL of birds not choosing best dish $= 33.9$, Mann-Whitney U-test: $U = 64.0$, $N_1 = 9$, $N_2 = 3$, NS. Session 2: Mean prior % CFL of birds choosing best dish $= 33.2$, mean prior % CFL of birds not choosing best dish $= 18.0$, Mann-Whitney U-test: $U = 63.0$, $N_1 = 9$, $N_2 = 3$, NS.

TABLE 1. *A comparison of the observed and expected results when groups of birds were tested for knowledge of the location of the most profitable food patch following two sessions of contrafreeloading during experiment 2a*

	Best available dish	Second best available dish	Empty dish	No of tests
Session 1				
Observed results	9	3	0	12
Expected results	4	4	4	
Session 2				
Observed results	9	2	0	11
Expected results	3.7	3.7	3.7	

Experiment 2b

The mean % CFL values were compared between birds that were deprived for 4 or 8 hrs and undeprived birds (see Fig. 2). The average CFL levels of birds that were deprived for 8 hrs was significantly lower than when birds were deprived for 0 hrs: Mann-Whitney U-test: $U = 32.5$, $N_1 = N_2 = 12$, $p < 0.05$. In contrast there was no significant difference between the average CFL levels of birds that were deprived for 0 hrs and birds that were deprived for 4 hrs: Mann-Whitney U-test: $U = 63$, $N_1 = N_2 = 12$, NS. The latter values were therefore not used in subsequent analyses since the treatment was ineffective at reducing CFL.

In order to test for significance in the choice of dish in the knowledge test birds were grouped according to common deprivation treatments. After 0 hrs deprivation a significant proportion of the birds chose the best dish available as first choice: $G = 9.76$, df $= 2$, $p < 0.01$. However, this was also true after the 8 hr deprivation treatment that significantly lowered CFL: $G = 20.14$, df $= 2$, $p < 0.001$. In addition, there was no significant difference in the proportion of birds choosing the best dish available in the knowledge test between the 0 hr and 8 hr deprivation treatments: $G = 0.015$, df $= 1$, NS.

As in experiment 2a, the mean prior % CFL values of birds that chose the best dish in the knowledge probe were compared with the values of those that did not chose the best dish. Birds that did not approach any dish during
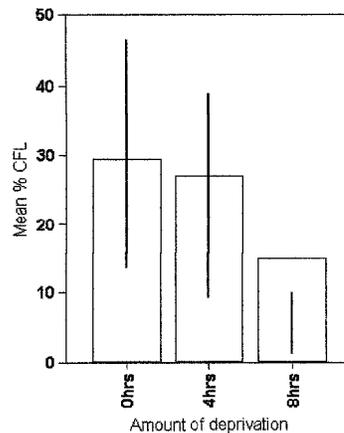

Fig. 2.   Graph comparing the effect to deptivation treatments of 8, 4 and 0 hours on subsequent mean % contrafreeloading across a group of birds ($n = 12$) in Expt. 2b. Bars indicate inter-quartile ranges.

the knowledge probe were excluded from the analysis. A separate analysis was carried out for each deprivation treatment and no significant effects were found: 0 hrs deprivation: Mean prior % CFL of birds choosing best dish = 35.5, mean prior % CFL of birds not choosing best dish = 29.9, Mann-Whitney U-test: $U = 8, N_1 = 7, N_2 = 3$, NS. 4 hrs deprivation: Mean prior % CFL of birds choosing best dish = 25.5, mean prior % CFL of birds not choosing best dish = 34.8, Mann-Whitney U-test: $U = 8, N_1 = 6, N_2 = 4$, NS; 8 hrs deprivation: Mean prior % CFL of birds choosing best dish = 18.0, mean prior % CFL of birds not choosing best dish = 2.4 Mann-Whitney U-test: $U = 13.0, N_1 = 9, N_2 = 3$, NS.

The data for all three deprivation periods were then pooled and each bird's performance across the three knowledge tests was used to investigate whether an individual bird's failure in the knowledge test was preceeded by lower CFL than when the same bird passed. Of the twelve subjects, five passed all three knowledge tests, one failed all three and six sometimes passed and sometimes failed. For these six birds the mean CFL the day before a failure and the day before a pass was compared: Wilcoxon test: $T = 0.105, N = 6$, NS.

Discussion

The results of both experiments 2a and 2b show that CFL is accompanied by information gain, as demonstrated by the results of the knowledge test in which birds demonstrated their knowledge of the second best food source in extinction. The results of experiment 2b also confirm Inglis & Ferguson's (1986) findings that deprivation reduces levels of CFL. However, the reduction of CFL seen in birds deprived for 8 hrs did not significantly affect the birds' ability to select the best dish in the knowledge test.

General discussion

In order to test the hypothesis that CFL is a mechanism for gaining information about alternative food sources we used two alternative methods: The first approach rests on the assumption that if CFL is for the purpose of collecting information, it should not occur in circumstances where information gathering would either not yield useful information or prejudice immediate survival. The second approach is based on the assumption that if CFL

is for the purpose of information gain, then this gain should be measurable through changes in the animal's behaviour when appropriately challenged. As discussed in the introduction, previous attempts to investigate CFL have been based round the first approach (Forkman, 1996).

We adopted the first technique for Experiment 1 and produced results that were consistent with the information hypothesis: Birds preferentially fed from dishes that required sampling rather than dishes containing *ad lib.* food but only when the contents of the former could not be visually assessed. However, a puzzling aspect of these results was that during pre-trial training the birds fed equally from both dishes. The information hypothesis would predict that the birds would feed more from the dish covered in opaque material since information could be gained from the other dish without sampling. It may be the case that information was gained on the first and second days of the trial, after which the birds had learnt that both dishes were equally profitable. However, this raises the question of why CFL is maintained in the four day long experimental session if adequate information can be acquired within the first few days.

One possible explanation is that information is more valuable when variance between patches is greater (Bell, 1991). In the pre-trial training period variance is small (nil) so the value of information is low. This suggests that extensive sampling is worthless in this situation and gives way to randomly distributed feeding from either dish. In the experimental session variance is great, therefore accurate information about patch profitability is more valuable and requires constant reappraisal. An alternative explanation for the failure of CFL to decrease over time proposes that assessing the information content of patches may be an ongoing process in a medium containing a finite amount of food since the act of CFL itself results in alteration of the food content of the patch. This would result in the subject initiating a behavioural loop of continual patch content reassessment. In the case of this experiment this would require an ability on the part of starlings to detect subtle changes in food content of under a gram in a patch of 450 g total mass containing 50 g of food and 400 g of sand.

Our second approach, of measuring information gain by means of a behavioural test, has not previously been used in the context of foraging, though Renner (1988) used a similar approach for spatial exploration. Stephens (1986) states that the value of information depends on its use, *e.g.* an ability

to influence future foraging behaviour and therefore any test of the information hypothesis should look for useful information. Our knowledge test determined whether a bird has gained the information necessary to forage effectively in partially altered conditions. We found that CFL was accompanied by the acquisition of useful information since a significant number of birds that had performed CFL demonstrated knowledge of alternative food sources in the knowledge test. Thus, our second approach was also consistent with the information gain hypothesis. However, evidence that animals gain information from CFL does not mean that this is the cause of the behaviour. Furthermore, an experimental reduction of CFL resulting in a corresponding reduction in apparent information gain would have provided considerably stronger support for the hypothesis. Experiment 2b, in which CFL levels were reduced by means of 8 hr food deprivation, did not find such an effect. Neither did inter and intra-individual differences in CFL levels have any obvious effects on performance in the knowledge test. These non-significant results may be explained by an insufficient sample size. Other possible explanations require further examination of the best way to experimentally assess information gain, and of the mechanisms by which CFL may be involved in the acquisition of information.

For example, one possible explanation is that our knowledge test was not subtle enough to register quantitative differences in the quality of information acquired by the birds. Another problem of the knowledge test was that we only recorded which dish the birds chose first without attaching any cost to choosing the wrong dish. The ease of changing to the correct dish could result in low motivation to choose the correct one first. Future work might develop the knowledge test by encouraging subjects to make the correct choice first, for example by making it more costly to move between the dishes.

A second possible explanation is that levels of CFL do not in fact correlate with levels of information gained. For example, it could be that the case that birds with low CFL levels acquire information about patch quality more efficiently than birds performing extensive amounts of this behaviour. Alternatively, CFL could merely be one of a suite of behaviours involved in acquiring information about patch quality; others might include visual inspection or sifting the sand in each patch and pecking at food without ingesting it. If this is the case, merely measuring the amount eaten as we did would be unlikely to fully reflect the birds' exploratory activity.

Overall, we have demonstrated that the contrafreeloading behaviour of starlings is affected by the ability of sub-optimal patches to be visually assessed, just as predicted by the information hypothesis. We also demonstrated that the performance of CFL is accompanied by the acquisition of useful information about patch quality. However, further work is needed to explain why individuals vary so much in their CFL levels, and to investigate the nature of the relationship between the levels of CFL and the quality of information gained. Current knowledge of the mechanism of CFL is not sufficient to say whether the distinction between it and the exploitative sampling described by Krebs *et al.* (1978) is qualitative or quantitative. It may be found that certain conditions cause extensive exploitative sampling which has previously been defined as CFL.

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