

## COMPETITIVE FORAGING IN MALLARDS: 'IDEAL FREE' DUCKS

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**Abstract.** Mallards (*Anas platyrhynchos* L.) distribute themselves between two patches of food in a close approximation to the distribution predicted by the ideal free model. However an important assumption of this model is violated since the despotic behaviour of some individuals results in different birds receiving unequal payoffs. The distribution of the birds between the food patches is influenced by the distribution of these despots. Evidence is presented to suggest that the ducks initially use the frequency of supply of food items at a patch to assess its profitability, but they can, over a longer time scale, use other cues.

Although a great deal of work has been done on the exploitation by animals of patchy resources, especially food (see review by Krebs 1978), most of this work has dealt with the utilization of a single resource patch by a single individual. Hence the important question of how competing individuals should distribute themselves between several different resource patches has been comparatively neglected. The theoretical discussion of this problem has centred on two possible distributions: the 'ideal free' and 'despotic' (Fretwell & Lucas 1970; Fretwell 1972). In the ideal free model it is assumed that competing individuals distribute themselves between resource patches in such a way that each individual receives the same payoff. This equality of payoff can be achieved by individuals distributing themselves between resource patches in the ratio of the patch profitabilities: more animals utilize the most profitable patch. The model assumes that the animals are 'ideal' in their assessment of the patch profitability ratio and that they are 'free' to go to the patch of their choice, no individual being able to prevent another from doing so. In contrast, the despotic model assumes that some individuals are able to monopolize an unfair share of the available resources through dominance and/or territorial behaviour; in this case different individuals will receive different payoffs.

To distinguish between these two hypotheses we need to know individual payoffs in different resource patches of known quality, and it is therefore not surprising that the models have proved difficult to test empirically (Fretwell 1972). One example of a study providing results relating to these theories is that of Milinski (1979). This study used a simple laboratory set-up to demonstrate that three-spined sticklebacks (*Gasterosteus aculeatus*) distribute themselves between two patches of their prey

*Daphnia magna* in the ratio of the patch profitabilities. This is exactly what would be predicted from the ideal free model; unfortunately, individual payoffs were not recorded. In my study I have been throwing pieces of bread to ducks on a garden pond and recording both the distribution of the birds between food patches and the individual food intake of some of the ducks at one of these patches.

### General Methods

The experiments described in this paper were carried out on a flock of 33 free-living mallards (*Anas platyrhynchos* L.) on a lake in the University Botanic Garden, Cambridge, in the winter of 1979-1980. Since the ducks exhibited considerable variation in plumage and in bill pattern (the latter is most obvious in females), it proved possible to recognize them individually. However some of the birds were difficult to identify rapidly, and only 24 individuals (13 males, 11 females) could be reliably identified on sight. I will refer to these ducks as the 'recognizable birds'.

The resource patches used in the experiments were pre-cut and pre-weighed pieces of white bread being thrown by two observers at fixed points on the lake surface 20 m apart, called site A and site B. Patch profitability was varied by changing either the rate at which the items were thrown into the patches, or the weight of the food items. The pieces of bread were thrown singly and at regular intervals: for instance a frequency of supply of 12 items per minute was achieved by throwing an item every 5 seconds.

In every one of the experiments described, a total of 33 birds were on the lake surface and all 24 recognizable birds were present. As soon as a trial was terminated, by stopping the input of food, the ducks very rapidly swam away from the observers and a new trial was not started

until all the ducks had dispersed from the feeding sites.

It is obvious that ideal free distribution models can only apply in cases where the resource in question is actually limiting. Therefore it was important that food was not provided in excess abundance and that individuals were not becoming satiated during the experimental trials. No single trial of an experiment used more than 550 g of food and no more than three trials were conducted daily (the mean daily input over the whole winter was 896 g). The individual food items weighed 2 or 4 g: these weights were chosen because with larger items the handling time and consequent risk of kleptoparasitism by other ducks were increased. On no occasion did any duck fail to respond to food when it was offered, and no individuals swam away from the two feeding sites until feeding ceased.

Another potential problem with the experiments described here was that of learning: for instance it was important that the ducks could not learn that one patch was always the most profitable, and for this reason the site (A or B) of the most profitable patch was varied on a random basis. In addition, although I have found it easier to describe this study as four discrete experiments, they were performed on a common randomized schedule: in other words, they were all done during the same period of time.

### Experiment 1

#### Methods

If ducks distribute themselves between two food patches in an ideal free manner we would expect to be able to verify two hypotheses. Firstly, we would predict that the distribution of ducks between the food patches would match the patch profitability ratio: for example, if the least profitable site has one third of the total food available (patch profitability ratio of 2:1), we would predict that one-third of the flock would be at that site. The second prediction is that the individual ducks will, on the average, gain access to the same amount of food.

These two hypotheses were tested in a series of feeding trials in which the food items thrown onto the two patches all weighed 2 g. The profitability of the patches was determined by the frequency with which the items were being thrown. During each trial a continuous tape recording was made in order to monitor the distribution of the flock between the two feeding sites, a particular note being made of the location of the 24 recognizable birds. In addition,

at one of the two sites the amount of bread eaten by each of the recognizable birds at that site was recorded.

#### Results

When offered two food patches, the flock rapidly came to a dynamic equilibrium in their distribution between them. The rapidity and stability of the observed equilibrations were striking, even during the first trial. In 29 trials the two patches were equally profitable, with 2-g food items being thrown at each site every 5 s (24 g per minute). In this case the ideal free model predicts that half of the flock (16.5 birds) should go to each patch.

Figure 1 shows the mean number of ducks at site A plotted against time since the first food item was thrown, for these trials. The predicted flock size at this site is represented by the horizontal line on the figure, and it can be seen that the mean flock size observed comes to closely approximate to this prediction. For all times after 80 s, the observed number of birds does not significantly differ from the ideal free prediction ( $t$  tests,  $df = 28$ ,  $P > 0.05$ ). For each individual trial, the number of birds at site A was plotted against time (just as in Fig. 1) and

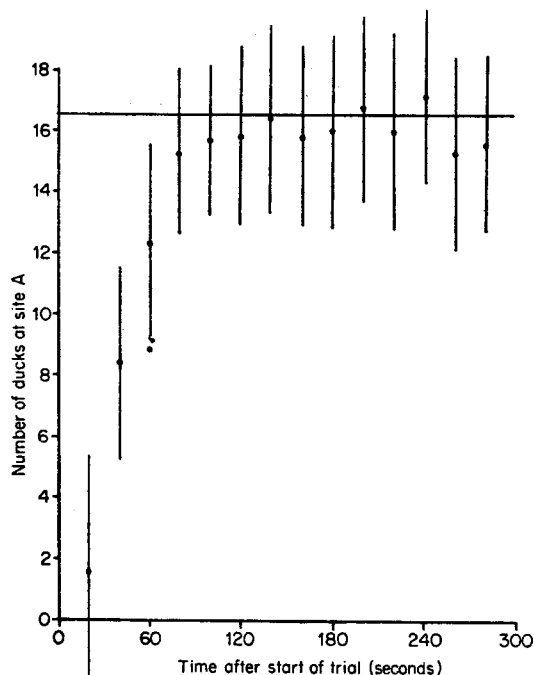


Fig. 1. Mean number of ducks at site A plotted against time since start of trial, when patch profitability ratio was unity. The horizontal line is the ideal free prediction.

an equilibrium number (to the nearest whole duck) judged by eye. These values ranged from 10 to 23 birds in these trials; a further indication of the variation observed between trials is given by the standard deviations shown in Fig. 1.

Similarly close approximations to the distribution predicted by the patch profitability ratio were found in cases where the patches were not equally profitable. For example, Fig. 2 shows the mean number of ducks at the least profitable of two patches with a profitability ratio of 2:1 during 24 trials. Since one-third of the total food is available at this site, the ideal free model predicts that one-third of the flock (11 birds) will go to this patch. This prediction seems to be borne out by the observations, since for all times after 80 s the observed number of birds does not differ significantly from the predicted value ( $t$  tests,  $df = 23$ ,  $P > 0.05$ ). The equilibrium number at the least profitable patch during individual trials ranged from 8 to 13 birds.

The observation that the ducks distribute themselves between two food patches in a good approximation to the patch profitability ratio is necessary, but not sufficient, evidence in support of the ideal free model. If the ducks were

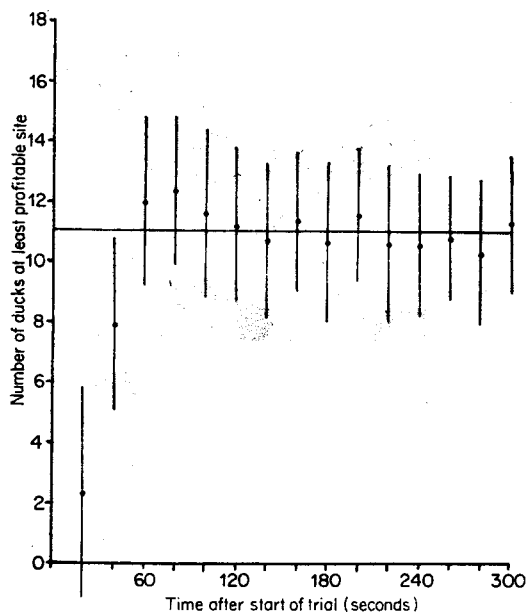


Fig. 2. Mean number of ducks at least profitable site plotted against time since start of trial, when patch profitability ratio was 2:1. The horizontal line is the ideal free prediction.

behaving in an ideal free manner we would also predict that every individual received the same payoff, and this prediction was not confirmed by the observations during these feeding trials. Some individuals took a large proportion of the available food and did so consistently throughout the study period. For all the trials mentioned above (a total of 53 trials) I determined which individual had taken the most food items from the food patch at which I was recording how many items each of the recognizable birds had taken. Only seven individuals were found ever to have taken the most food items from a patch during a trial, and one of these ducks only did so once. These results are shown in Table I.

## Experiment 2

### Methods

Direct observation of the birds feeding at the food patches in experiment 1 revealed that the individuals taking disproportionate amounts of the available food were involved in numerous aggressive interactions with other ducks. It seemed reasonable to hypothesize that the inequality in payoffs observed was caused by the despotic behaviour of dominant flock members. If this is correct, then it not only matters to each individual how many other ducks are at the same food patch (as in the density-dependent effect in the ideal free model) but it also matters who those other ducks are. To examine the influence of dominance rank on the ability of individuals to gain access to food, it is clearly important to be able to compare the payoffs received by different individuals under the same conditions. In particular it is important that each individual is studied competing against the same other individuals. Since I was unable to manipulate the composition of the groups of

Table I. Number of Trials during which Each Particular Individual Ate More Items than Any Other Individual in the Flock

Bird	Number of trials involved
A	12
B	12
C	8
D	8
E	7
F	5
G	1

Total no. of trials\* 53

\*No other bird in the flock of 33 ate the most items in any trial.

ducks at the two feeding patches, I did a series of trials in which all the flock were competing at a single feeding site (site A of experiment 1). The hypothesis I wished to test was that the ability of individuals to gain access to food in competitive situations was related to their dominance rank within the flock. To assess the ability of individuals to gain access to food, I performed 11 trials through the winter, in which about 100 items weighing 2 g were thrown onto the feeding site, and recorded the number of items eaten by each of the 24 recognizable birds. In order to determine the dominance relationships within the flock, I watched aggressive behaviour within the flock in non-feeding contexts, throughout the winter. Each dyadic encounter was scored as a 'win' for one individual and a 'defeat' for the other. These data were used to arrange the recognizable birds into a peck order.

### Results

The single site trials revealed that, just as in the previous experiment, a few individuals took a disproportionate amount of the food thrown to the flock. I drew the 24 recognizable birds up into a rank according to the number of items they had eaten in all the 11 trials. Figure 3 shows the cumulative frequency of items eaten (as a proportion of the total of 1204 items) plotted against increasing rank on this measure. The proportion of items below the horizontal line (15% of the total) was taken by the nine birds that were not recognized individually. If each of the recognizable birds took an equal share of the available food, the plotted points would follow the diagonal line. In fact the plotted points diverge widely from this line and it is notable that six individuals took nearly 60% of the available items, each one of these ducks taking at least 8% of the total. No other recog-

nizable bird took more than 3% of the total and the mean intake of the 'unrecognizable birds' was under 2%. The number of items taken by each of the six most successful individuals is shown in Table II, which uses the same identification letters for the individuals as is used in

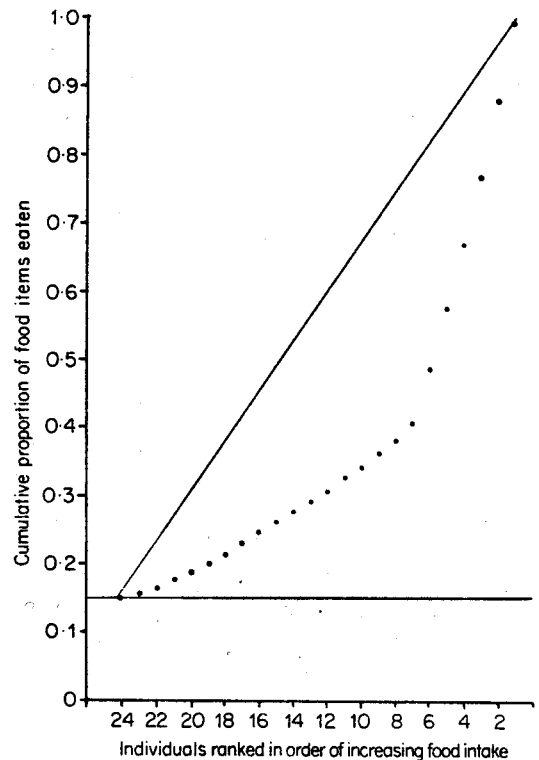


Fig. 3. Cumulative frequency of proportion of food items taken by individuals ranked in order of increasing food intake (total number of food items = 1204). See text for further details.

Table II. Food Monopolization by the Six Most Successful Members of a Flock of 33 Ducks Competing at a Food Patch

Bird	Number of food items eaten in each trial											% Available food eaten in all trials
	1	2	3	4	5	6	7	8	9	10	11	
A	11	9	16	21	12	14	14	10	10	9	12	11.5
B	8	12	18	11	11	8	22	11	10	8	13	11.0
C	14	7	9	9	8	19	11	12	7	12	12	10.0
D	10	12	8	12	11	12	9	6	15	12	9	9.6
E	12	11	18	8	9	9	5	9	10	9	7	8.9
F	7	8	18	13	11	10	7	6	4	7	7	8.1
Total A to F	62	59	87	74	62	72	68	54	56	57	60	59.1
Total flock	111	107	102	114	119	100	121	117	100	104	109	100.0

Table I; comparison of these two tables shows that the same six ducks were eating a disproportionate amount of the food in experiments 1 and 2.

The peck order drawn up by watching aggressive encounters outside the feeding context is not very linear, having a Landau index of 0.63 (Chase 1974). To produce a linear rank for calculations all reversals were treated as ties. Two important factors contributing to the high number of reversals in peck order were the very limited sample sizes for most dyads (four were never seen to interact) and the long time scale over which the data were collected (in order to increase the sample sizes). The ability of individuals to monopolize food as measured by the rank order depicted in Fig. 3 is correlated with the linearized peck order (Fig. 4, Kendall's Coefficient of Rank Correlation,  $\tau = 0.57$ ,  $N = 24$ ,  $P < 0.001$ ). The same six individuals (A-F in Tables I and II) head both ranks, and I will refer to these birds as 'dominants'. These individuals appear to monopolize food in competitive contexts through despotic behaviour.

### Experiment 3

#### Methods

The distribution of ducks between the two food patches in experiment 1 varied in relation to the patch profitability ratio and approximated closely to the predictions of the ideal free model. It is important to remember that the distribution

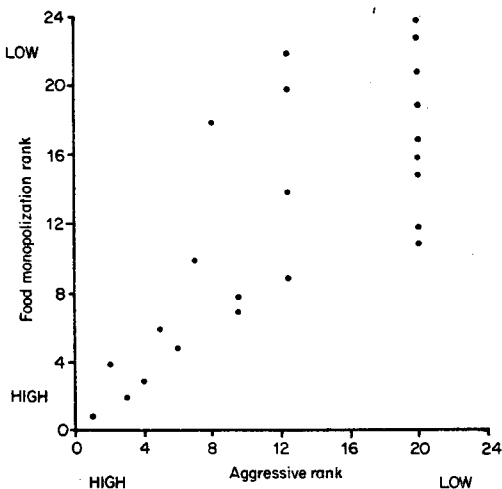


Fig. 4. Rank ability of individuals to monopolize food, plotted against aggressive rank in non-feeding contexts.

of the flock is the result of decisions made by individual ducks. The results of experiment 1 show that these decisions are made rapidly (see Figs 1 and 2), and direct observation suggested that they were made independently, no individuals seeming to hang around waiting to see where other individuals went. However it is obvious that the 'right' answer to the problem each duck faces depends upon the responses made by the other flock members. Below I intend to outline a simple (-minded) model to suggest how an individual could make an independent decision rapidly, and then to compare the predictions of this model with some further trials similar to those in experiment 1.

In a competitive situation it seems likely that rapid responses to ephemeral resources will be favoured: 'rapid, quite good' decisions about what to do (for example which of two food patches to go to in these experiments) may well be better than 'slow, very good' decisions. The model outlined below supposes that it is to the advantage of each individual duck for the overall flock distribution to be ideal free and that each duck behaves in a way to make this more likely to occur than if it behaved in a random fashion. If individuals can assess (in some unspecified way) the patch profitability ratio, then one possible rule for them to follow would be to move to each patch with a probability determined by this ratio. For example if one-third of the food available is at site B (patch profitability ratio 2:1), ducks following this rule would move to site B with a probability of one-third and to site A with a probability of two-thirds.

If all the individuals in the flock use this rule, the distribution of flock sizes at a feeding site obtained over a number of different independent experiments will be a binomial curve centred upon the flock size for that site predicted by the ideal free model. As long as the overall flock size is not too small, the resultant distribution between the two food patches is usually close to that predicted by the ideal free model. If an individual using this rule is present in a flock of ducks which distribute themselves at random, it is at an advantage since it is more likely to end up at the most profitable site.

A further series of trials exactly similar to those in experiment 1 were carried out, in which the patch profitability ratio was 2:1 (item weight 2 g, food input at most profitable site 48 g per minute). For each separate trial the equilibrium number of ducks at the least profitable site was

estimated as explained above. If the model proposed holds, these equilibrium flock sizes should be binomially distributed around the value of 11, predicted by the patch profitability ratio. Further variation is likely to occur owing to other factors influencing the birds' decisions. For example, the ducks may not be able to make consistent or accurate assessments of the patch profitability ratio.

### Results

The distributions of equilibrium flock sizes at the least profitable site (one-third of the total food available) for November, December and January, are shown separately in Fig. 5. During November (Fig. 5a) and January (Fig. 5c), the observed distributions do not differ significantly from the binomial curve predicted by the model (Kolmogorov-Smirnov test,  $D = 0.097$ ,  $N = 41$ ,  $P > 0.2$  and  $D = 0.125$ ,  $N = 37$ ,  $P > 0.1$  respectively). If anything, the observed data are even more closely clumped around the binomial curve than the model suggests: for instance the three most frequent flock sizes in November occur more frequently than expected ( $\chi^2 = 4.61$ ,  $P < 0.05$ ). This suggests that the ducks are either using a better rule to decide which patch to visit, or that they are modifying initial choices made by such a rule of thumb.

The distribution of equilibrium flock sizes during December (Fig. 5b) is strikingly different from that observed in the other months, and differs significantly from the binomial distribution predicted by the model (Kolmogorov-Smirnov test,  $D = 0.361$ ,  $N = 35$ ,  $P < 0.001$ ). These data demonstrate that there must be other factors influencing the distribution of ducks between resource patches, and that these factors exhibit temporal variation.

While examining my observations in an attempt to suggest reasons why the December data in these trials differed from those of the other two months, it became apparent that the social interactions of the six dominants were different in December compared to the rest of the winter. If one calculates dyad affinities for the birds in the flock, it is clear that individuals do not associate at random, being seen frequently with certain individuals and hardly at all in association with other individuals. The dyad affinities of the six dominants, between themselves, ranged from close association to nearly total avoidance. Dyad affinities calculated for these birds during the feeding experiments

were found to be correlated with the dyad affinities observed in other (non-feeding) contexts.

Figure 6 illustrates this correlation for the December data (Kendall's Coefficient of Rank Correlation,  $\tau = 0.784$ ,  $N = 15$ ,  $P < 0.001$ ). The six points in the top right-hand corner of Fig. 6 show statistically significant associations (binomial test,  $P = 0.001$  level). This group of four dominants fed together at one feeding site during 33 of the 35 trials depicted in Fig. 5b.

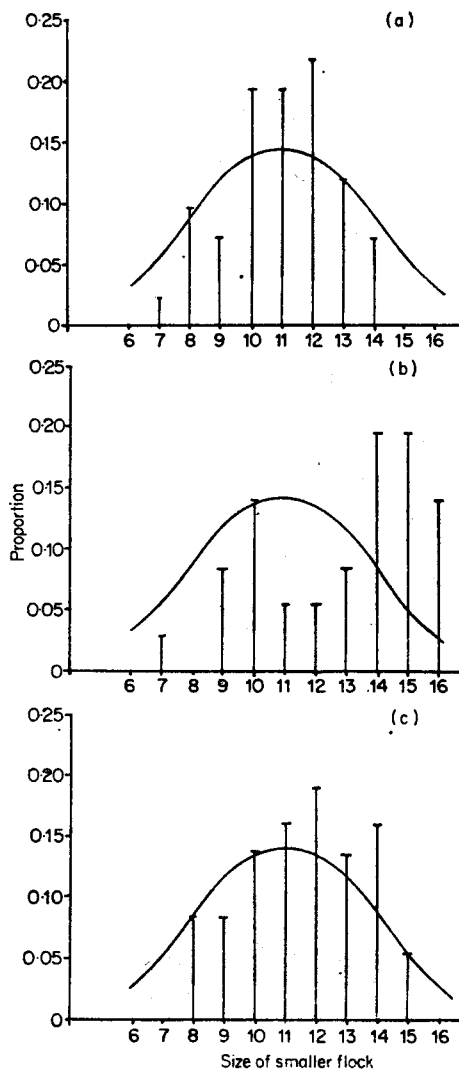


Fig. 5. Distribution of flock sizes observed at least profitable site when patch profitability ratio was 2:1, during (a) November, (b) December, (c) January.

Interestingly, the group were feeding at the least profitable site on only seven of these occasions, a significant preference for the most profitable site (binomial test,  $P < 0.001$ ). During trials when the group of four dominants were at the least profitable site, the mean flock size at this site was significantly smaller than during trials when they were at the most profitable site, as shown in Table III.

These results suggest that the other birds were tending (sensibly) to avoid the resource-monopolizing dominants. It is indeed tempting to suggest that the distribution shown in Fig. 5b is the result of the superposition of two curves, one centred on the mean flock size when the group of four were present at that site (9.3) and the other centred on the mean flock size when they were absent (14.0). This must remain speculative; however further evidence is available to support the hypothesis that the other ducks tend to avoid the dominant individuals. The data shown in Fig. 1 relate to 29 trials, in which the

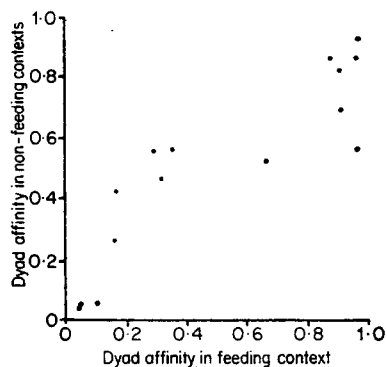


Fig. 6. Dyad affinity in non-feeding contexts plotted against dyad affinity in feeding contexts, for the six dominants.

patch profitability ratio was unity. In Fig. 7 the total size of the smaller flock (with 33 birds, the flock at one of the two feeding sites must be smaller) has been plotted against the number of dominants at the food patch. A highly significant negative correlation was found (Kendall's Coefficient of Rank Correlation,  $\tau = 0.587$ ,  $N = 29$ ,  $P < 0.001$ ).

#### Experiment 4

##### Methods

The observation that the distribution of ducks between two food patches is influenced by the patch profitability ratio (experiment 1) raises the question of how the ducks assess the patch profitability ratio. Milinski (1979) found that three-spined sticklebacks took about 4 min to equilibrate between two prey patches, and it seems likely that at least some of the fish were sampling both prey patches before making a choice between them. This contrasts with the situation found in this study, where it is clear that sampling is unlikely to be involved in the assessment of the patch profitability ratio by ducks, since very few individuals have eaten food at either patch, let alone both, in the time taken for equilibration! One potential means of assessing patch profitability at a distance would be the frequency with which food items are thrown onto the lake surface. During the experiments described above, the frequency of food input would have been an unusually accurate measure of patch profitability compared to its accuracy during the ducks' everyday feeding by the public.

To test the hypothesis that the ducks were using the frequency of food input as a measure of the patch profitability ratio, a series of feeding trials were performed in which throwing frequency was sometimes a completely accurate or 'true' indicator of patch profitability and

Table III. Flock Size at the Least Profitable Site in relation to the Location of the Group of Four Dominants Observed during December

Group of four	Number of trials	Size of flock at least profitable site			<i>t</i> -test
		Range	Mean	SD	
At least profitable site	7	7-11	9.29	1.25	} $t_{31} = 7.95$ $P < 0.001$
At most profitable site	26	10-16	13.96	1.78	
Divided between sites	2	10-14	—	—	

sometimes a 'false' indicator. During all the trials the patch profitability ratio was 2:1 (48g per minute at the most profitable patch). In some trials 2-g food items were thrown at the most profitable patch at twice the frequency they were being thrown at the least profitable patch, and therefore frequency was a true indicator of patch profitability. In the remaining trials, food items were thrown at the same frequency at the two patches, but those at the most profitable site weighed 4 g compared to 2 g at the least profitable site. In these trials the frequency of food input was a false indicator of patch profitability. The distribution of the flock between the two patches was monitored during each trial as a continuous tape recording.

### Results

The results are summarized in Fig. 8. In those trials in which throwing frequency was a true indicator of patch profitability, the number of ducks at the least profitable site became very close to 11, the number predicted by the ideal free model. For all times after 80 s from the start of the trials, the difference between the mean number of ducks at the least profitable site and the predicted number was not statistically significant ( $t$ -test,  $P = 0.05$  level). On the other hand, in those trials in which throwing frequency was a false indicator of patch profitability the number of ducks at the least profitable site initially rose higher than the figure of 11 predicted by the patch profitability

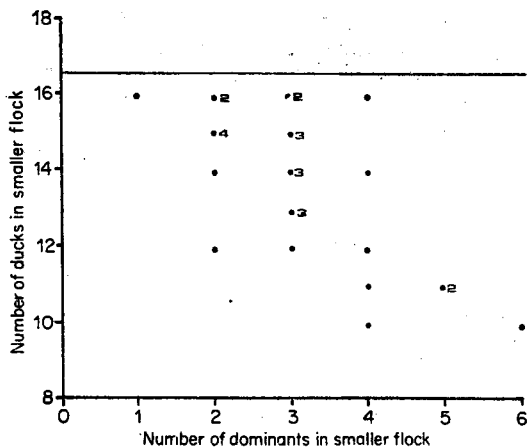


Fig. 7. Number of ducks in smaller flock when patches were equally profitable, plotted against the number of dominants in that flock. The horizontal line is the ideal free prediction.

ratio. For all times from 60 to 320 s after the trials had started, the mean number of ducks at the least profitable site was significantly higher than in the trials in which throwing frequency was proportional to patch profitability ( $t$ -test,  $P = 0.05$  level). If the ducks were using throwing rate to assess patch profitability we would expect that they would treat the two food patches in these 'false rate' trials as if they were of equal profitability, and the predicted number of birds at each site would be 16.5 (half the

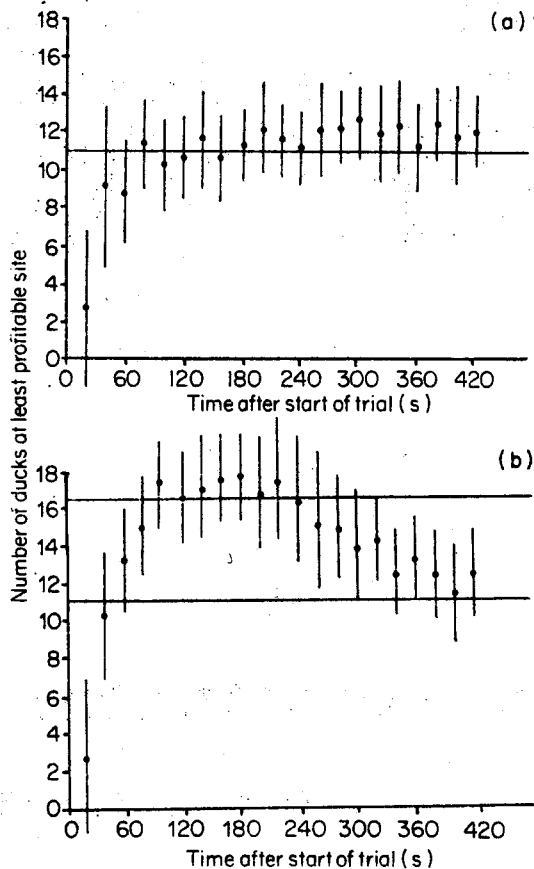


Fig. 8. Mean number of ducks at the least profitable of two food patches with a profitability ratio of 2:1 plotted against time since start of trial.

(a) Difference in profitability caused by different frequencies of supply of food items (11 trials). The horizontal line is the ideal free prediction.

(b) Difference in profitability caused by different food item weights (14 trials). The lower horizontal line is the ideal free prediction and the upper horizontal line is the predicted flock size if rate of food input is used to assess profitability.



flock). This expectation seems to be supported by the data, since for all times between 80 and 260 s after the start of the trials, there is no significant difference between the mean number of ducks at the least profitable site and this prediction of 16.5 ( $t$ -test,  $P = 0.05$  level). The number of ducks at the least profitable site then declined, and within 380 s of the start of the trials it was not significantly different from the figure of 11 predicted by the patch profitability ratio ( $t$ -test,  $P = 0.05$  level). These observations suggest that although the ducks do use the frequency of food input to assess the patch profitability ratio, other factors can also be used, over a longer time scale, to detect differences in patch profitability in the absence of differences in the rate of food input. The time scale involved is certainly long enough for direct sampling of both patches by individuals to be plausible.

### Discussion

The distribution of the flock between two food patches was very similar to that predicted by the ideal free model. However one of the assumptions of this model was violated by the despotic behaviour of dominant individuals, who monopolized a disproportionate amount of the food by restricting access by other individuals to the point where food was being thrown.

Whitham (1980) has found a similar case in his study of habitat selection by *Pemphigus* aphids. In this instance the patches were leaves which the aphids colonized, and the relative fitness of different individuals was measured by the number of progeny produced. Although it was observed that the individuals in different patches had the same average fitness (i.e. like the ideal free model), there was individual variation in fitness within each patch. This was due to the fact that each leaf (patch) was highly heterogeneous in its suitability for the aphids, and some individuals defended the optimum sites. Whitham (op. cit.) points out that a common assumption of both the ideal free and despotic models is violated by heterogeneity within resource patches. Differences between individuals have a similar effect: since the ability to kleptoparasitize other ducks is positively correlated with dominance rank (personal observation), it seems probable that even if the patch was so large and homogeneous that individuals could not restrict other birds' access to food, individuals would still achieve unequal payoffs (as long as food was a limiting resource).

The despotic individuals in the flock also seem to influence the distribution of other flock members between food patches. This response to the number of despots is presumed to be due to the decrease in the food availability experienced by the other ducks, although other factors (such as the avoidance of damaging fights) may be involved. If this assumption is correct, it seems probable that the ducks are correcting their assessment of the patch profitability ratio according to the location of the dominants. Each additional dominant at a food patch increases the pressure on the available food: if one calculates a linear regression from Fig. 7 one gets a slope of  $-1.2$  birds in the smaller flock per dominant present, which could be interpreted as suggesting that each dominant imposed as great a pressure on food availability as 2.2 other birds. This raises the possibility that defining flock size in terms of bird-units, which allow weighting of each dominant by a factor of 2.2, might improve the fit to the ideal free model.

If this proved to be the case it would imply that the despotic model was a variant upon the density-dependent effect modelled by the ideal free hypothesis. However, re-analysis of the data in this manner does not improve the fit to the ideal free model. As an illustrative example, Fig. 9 shows the data from Fig. 5b (the December data which seemed to depart from the predictions of the ideal free model because of an association between four of the dominants), re-analysed in this manner. The flock of

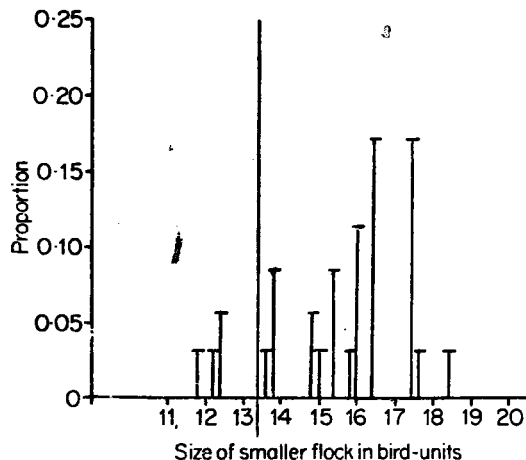


Fig. 9. Distribution of flock sizes expressed as bird-units, observed at least profitable site when patch profitability ratio was 2:1 (see text).

six dominants (weighted by a factor of 2.2) and 27 other birds comprises a total of 40.2 bird units, and since the least profitable site had one-third of the food available, the ideal free distribution would result in 13.4 bird units being present at the least profitable site, as shown by the vertical line in the figure. It is clear that the observations do not cluster very convincingly around this prediction. Similar results were obtained when other sets of data were re-analysed in this manner. This does not prove that the despotic model is not a variant of the density-dependent model, but implies that the suggested interpretation of Fig. 7 is incorrect. Not only are the data in Fig. 7 not entirely suitable for a linear regression analysis, but the 95% confidence limit for the value of the slope is rather large ( $\pm 0.52$ ). Clearly, further observations are required to test the hypotheses that the avoidance of dominants by other ducks (Fig. 7) is a response to the pressure which dominants impose on food availability (Table 1), and that the despotic model is a variant on the ideal free model.

The experiments described above mimic the problems that the ducks face every day when being fed by the public. Except when being controlled by experimenters the rate of food item input is likely to be erratic and to be an imperfect indication of patch profitability. However it has the advantage of being detectable from a distance, and the results of experiment 4 show that other cues can be used by the ducks to correct

their assessment of the patch profitability ratio. It is clear that the behaviour of ducks being fed bread on a park pond is more complicated than might be thought.

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