

# Foraging rate versus sociality in the starling *Sturnus vulgaris*

Rodrigo A. Vásquez† and Alex Kacelnik\*

Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

It is well established that social conditions often modify foraging behaviour, but the theoretical interpretation of the changes produced is not straightforward. Changes may be due to alterations of the foraging currency (the mathematical expression that behaviour maximizes) and/or of the available resources. An example of the latter is when both solitary and social foragers maximize rates of gain over time, but competition alters the behaviour required to achieve this, as assumed by ideal free distribution models. Here we examine this problem using captive starlings *Sturnus vulgaris*. Subjects had access to two depleting patches that replenished whenever the alternative patch was visited. The theoretical rate-maximizing policy was the same across all treatments, and consisted of alternating between patches following a pattern that could be predicted using the marginal value theorem (MVT). There were three treatments that differed in the contents of an aviary adjacent to one of the two patches (called the 'social' patch). In the control treatment, the aviary was empty, in the social condition it contained a group of starlings, and in a non-specific stimulus control it contained a group of zebra finches. In the control condition both patches were used equally and behaviour was well predicted by the MVT. In the social condition, starlings foraged more slowly in the social than in the solitary patch. Further, foraging in the solitary patch was faster and in the social patch slower in the social condition than in the control condition. Although these changes are incompatible with overall rate maximization (gain rate decreased by about 24% by self-imposed changes), if the self-generated gain functions were used the MVT was a good predictor of patch exploitation under all conditions. We discuss the complexities of nesting optimal foraging models in more comprehensive theoretical accounts of behaviour integrating functional and mechanistic perspectives.

**Keywords:** optimal foraging; social foraging; starlings, *Sturnus vulgaris*; marginal value theorem; gain function; constraints

## 1. INTRODUCTION

Animals may differ in foraging behaviour when observed in individual or group contexts, and this may happen for various (not mutually exclusive) reasons. On one hand, the social setting may change the foraging priorities of the forager, for example, by modifying the maximized currency either towards or away from energy rate maximization (e.g. Caraco 1981; Clark & Mangel 1984; Ydenberg *et al.* 1986; Koops & Giraldeau 1996; Giraldeau & Caraco 1999). On the other, the presence of other foragers may change the availability or distribution of foraging opportunities, so that even though the same energetic currency is maximized, observed behaviour is different (e.g. Ranta *et al.* 1993, 1995; Livoreil & Giraldeau 1997; Rita & Ranta 1998; see also Beauchamp 1998; Giraldeau & Beauchamp 1999). We present an attempt to elucidate some of these effects using starlings (*Sturnus vulgaris*) in the laboratory.

An example of a complex interaction of the first kind is when foragers in a social context reduce the amount of vigilance, tilting the balance between allocating behaviour between predator avoidance and food searching (e.g. Elgar 1987; Lima 1987). Social companionship then should lead

to higher feeding rates because each individual may spend less time looking for predators. While the ultimate currency (fitness) is presumably unaltered, the drop in vigilance leads to feeding behaviour being more closely predicted by classical (rate-maximizing) optimal foraging theory in social than in individual circumstances. When alone, energy gain should not be a sufficiently important component of fitness gain to be sufficient to predict behaviour. A conceptually very different effect is when nearby foragers alter food availability by altering feeding productivity, as in the cases of prey depression, kleptoparasitism, or provision of public information (e.g. Barnard & Sibly 1981; Valone 1993; Ranta *et al.* 1995; Templeton & Giraldeau 1995; Sutherland 1996; Livoreil & Giraldeau 1997; see also Beauchamp 1998; Giraldeau & Beauchamp 1999). Under these scenarios the predator may behave as a rate maximizer both socially and individually, but observed behaviour differs because foraging constraints are modified. In the lexicon of experimental psychology (and this is useful to relate laboratory to field observations), the first route leaves the (feeding) schedule of reinforcement unaltered, but a contextual, non-foraging factor changes the way the subject responds to its schedule, while the second route alters the schedule of reinforcement. Under the second scenario, at a mechanistic level an observed change in behaviour correlated with the presence of foraging companions cannot be attributed to a response to sociality *per se*. The behavioural change may be identical whether the feeding opportunities are modified by specifics or by any other variation of the food supply.

\* Author for correspondence (alex.kacelnik@zoology.oxford.ac.uk).

† Present address: Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile (rvasquez@abello.dic.uchile.cl).

The distinction we draw is important in linking individual strategies to population consequences, an important goal of much current work in behavioural ecology. Most work in this area assumes that competitors' density affects feeding opportunities by altering the relative profitability of different food patches. This is the foundation of most of the models derived from the ideal free distribution (Fretwell & Lucas 1969; Bernstein *et al.* 1988; Sutherland 1996; but see McNamara & Houston (1990) and Houston & McNamara (1999) for a more inclusive approach with fitness rather than a single maximized dimension as currency). To validate these models empirically, feeding rates are measured under various consumer densities and are then used, together with the assumption of foraging-rate maximization, to predict the spatial mapping of consumers to resource distributions. With suitable simplifying assumptions, these models (with the exception of the fitness-based stochastic dynamic models of McNamara & Houston) lead to equilibria where consumers could not do better in foraging terms by changing feeding patch. This approach needs considerable rethinking in cases where foraging companions exert influence on foraging not by altering feeding opportunities but because the subject itself modifies its behaviour.

We are arguing from a mechanistic perspective, but similar points can be made by functional analysis. As McNamara & Houston (1990) and Houston & McNamara (1999) have shown, if there is a compromise between two fitness components such as energy gain and predation risk none of the components is maximized or equalized across patches. From a mechanistic point of view, if the subjects actively seek companionship for safety or any other unknown reason and are ready to pay a foraging cost to be in company the very labelling of feeding companions as competitors is inappropriate.

Although the issue may give the impression of being an arcane subtlety, it connects with a fundamental and recognized difficulty in empirical applications of the adaptationist approach: the fact that animals themselves to some extent create their own ecological circumstances, and it is hard to know when the constraints end and the strategy deployment starts. For instance, if a subject chooses to be in company for safety reasons and pays an energetic cost for it, is it still valid to use energy-gain maximizing models to predict its behaviour within the social circumstances?

Our study illustrates this problem by comparing the foraging behaviour of starlings within or without the proximity of conspecifics, while ensuring that there is no change in the objective feeding opportunities of our target animal.

## 2. METHODS

### (a) *Subjects and experimental set-up*

The subjects were eight male starlings, housed in individual experimental cages (150 cm × 50 cm × 50 cm). Experimental cages were designed to provide birds the opportunity of choosing between foraging alone, in close proximity to a flock of conspecifics, or close to a control stimulus (flock of zebra finches, *Taeniopygia guttata*, see figure 1). Subjects were trained to forage in their cages with two feeding patches located at opposite ends of the cage (each patch section measured 60 cm

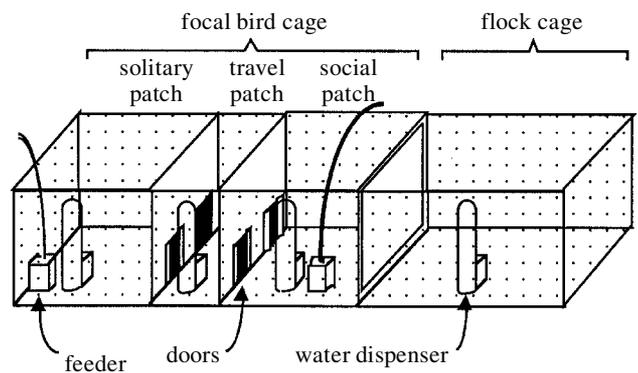


Figure 1. Experimental set-up. The focal bird cage was 130 cm long, 50 cm high and 50 cm deep. The two patch sections were similar, and the middle section (the travel patch) was 30 cm long. The flock cage was 80 cm long, with similar height and depth as the focal bird cage. All sections of the cage had perches (not in figure) and water dispensers.

× 50 cm × 50 cm). Patches were separated by a middle section (the travel patch; 30 cm × 50 cm × 50 cm) and birds had to go through doors to move from one section to the other. In one extreme of the experimental cage, a separate 'flock cage' (80 cm × 50 cm × 50 cm) was located. A wire mesh screen separated the experimental cage from the flock cage. This allowed focal birds to have visual, acoustic and some physical contact with flock members but ensured that there was no physical interference with foraging opportunities (Vásquez 1995). The section of the experimental cage adjacent to the flock cage was called the 'social' patch, the other section the 'solitary' patch. One computer-controlled feeder was located in each patch. Feeders and doors had microswitches connected to the recording system. An ACORN microcomputer running ARACHNID experimental control language (Paul Fray Ltd, Cambridge, UK) controlled the stimulus events and response contingencies, and recorded the data. The experimental cages were located in an indoor aviary which was acclimatized with temperature ranging between 15 and 18 °C, and a light cycle of 10L:14D. Feeders consisted of a food dispenser, a pecking window and a white light bulb (Campden Instruments, Sileby, Leicestershire, UK). Each reward (a 'prey' item) consisted of about 0.03 g of sieved turkey crumbs. While not in experimentation or training, birds were fed *ad libitum* turkey crumbs, and small quantities of mealworms (*Tenebrio* sp.) and commercial bird food. During training and experimentation the subjects were in a closed economy, namely they obtained all the daily food from the working regime. Before training, all subjects had been living together in an outdoor aviary for several weeks.

### (b) *Experimental procedure*

Both patches were programmed with the same schedule of food delivery. Each feeder delivered a reward after the subject made a number of responses in the pecking window. The number of responses required to obtain a prey increased as the bird persisted in the same patch according to a progressive ratio schedule, delivering the  $n$ th prey after  $2^n$  cumulative responses. A response in one patch set  $n=1$  in the opposite patch. This schedule simulates an environment where resources are gradually depleted or just harder to get in a patch as the patch is exploited (Charnov 1976; Kacelnik 1984). The experimental design comprised three treatments: (i) no birds in the flock cage (control treatment), (ii) three zebra finches in the flock cage

(control-zebra-finch treatment), and (iii) three starlings in the flock cage (social treatment). The control-zebra-finch treatment was designed to test whether the presence of a flock of conspecifics had a different effect from that of any generalized, attention-grabbing, disturbance. The sequence of conditions was randomized across subjects and treatments. Each subject experienced all three treatments and each treatment lasted five sessions. Recording sessions started at 08.00 and lasted 30 min. Additional sessions were run each day to keep the birds in the same regime, without data collection: one 30 min session at 11.00, and a 4 h session at 13.00. Thus, subjects were food deprived for 15 h (17.00 to 08.00) before each experimental session. Water was provided *ad libitum*. Flocks were food deprived during experimental sessions, but had water and food *ad libitum* the rest of the time. Flocks were housed in another room while not in experimentation, and hence subjects only experienced a social environment during the appropriate experimental trials.

We recorded the number of prey captures, the amount of time spent by individuals in both patches, and the travel time between patches during each session. ANOVAs were carried out to test significance levels. Data sets satisfied the assumptions of the ANOVA.

### 3. RESULTS

Because both patches were programmed equally, the rate-maximizing policy consisted of spending equal times in each of the two patches, switching between them regularly. The visit length that results in maximum gain per unit of time can be calculated according to the marginal value theorem (Charnov 1976), but this requires translating the progressive ratios required to collect food into time schedules or gain functions, with cumulative number of prey expressed as a function of patch time. This translation requires information about work rates, which is provided and discussed below. Under the assumption of overall rate maximization, work rate and hence patch times should be equal across patches and treatments.

Figure 2*a* shows the mean time per visit for different experimental treatments. There is a significant effect of treatment (repeated measures ANOVA,  $F_{5,7}=28.55$ ,  $p<0.001$ ). Patch visits did not differ when foraging in both patches was solitary (control treatment, figure 2*a*), nor when the social patch contained a control flock of zebra finches (figure 2*a*). When there were conspecifics next to the social patch, patch time was longer in the social than in the solitary patch, mostly because of a reduction in patch time in the solitary one (figure 2*a*). The mean number of prey per visit did not differ between patches nor among conditions ( $F_{5,7}=0.489$ ,  $p>0.5$ ; see figure 2*b*). The biased allocation of time between patches in the flock condition could be due to different components of the patch visit, both foraging and non-foraging. It is conceivable that the birds may have separated drastically 'work time' from 'playtime' and behaved as rate maximizers during work time. To examine this, we computed the durations of two potentially non-foraging periods and the shape of the gain functions. Figure 2*c* shows the average pre-response intervals (i.e. the time since the bird enters to the patch until it makes the first pecking response in the feeder). There is a significant effect of treatment ( $F_{5,7}=7.943$ ,  $p<0.001$ ), and birds

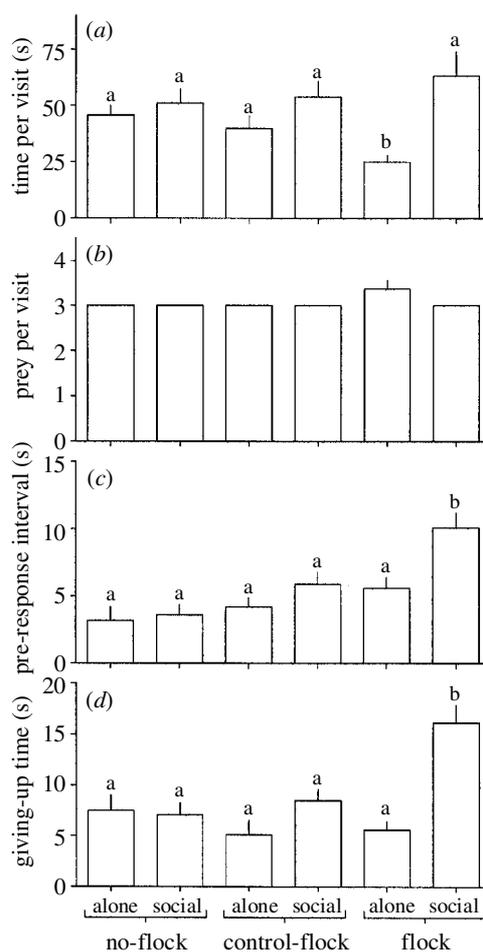


Figure 2. (a) Time per visit; (b) mean of individual modal number of prey per visit; (c) pre-response interval; and (d) giving-up time. Values are means ( $\pm$  s.e.). Different letters on columns indicate significant differences among means (Tukey test,  $\alpha=0.05$ ).

present longer pre-response intervals in the social patch when the flock cage is occupied by conspecifics (figure 2*c*). This observation excludes a possible interpretation of the result shown in figure 2*a*, namely that patch visit was only affected by shorter times in the solitary patch. A similar result occurs in the giving-up times (i.e. the time since the bird captured the last reward until it actually abandons the patch; figure 2*d*). Analogous to the pre-response result, there is a significant effect of condition ( $F_{5,7}=7.523$ ,  $p<0.001$ ), and birds show longer giving-up times in the social patch during flock conditions (figure 2*d*). Notice that the effects in the non-foraging components cannot explain the significant reduction in patch visit to the solitary patch shown in the fifth column in figure 2*a* because of their magnitude and direction. Since this reduction is not associated with a reduction in number of prey captured (prey per visit is actually slightly higher, see figure 2*b*), it must obey to faster working rate between the first response and the last capture, namely within foraging time.

Figure 3 shows the average gain functions for each subject and averaged across subjects. Under control conditions, birds showed similar gain functions in solitary and social patches. In control-zebra-finch conditions there is a similar pattern, but some subjects show a tendency to

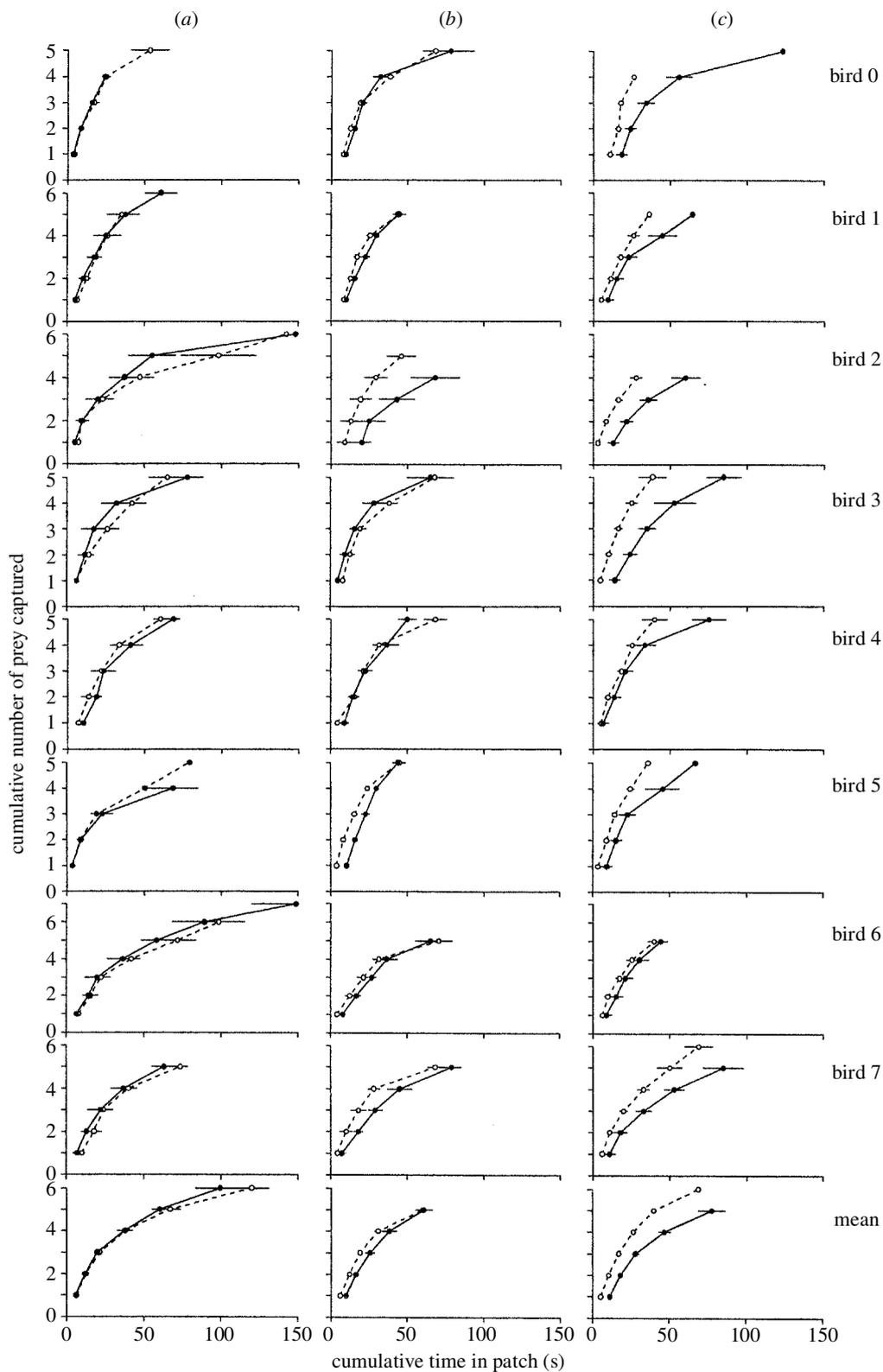


Figure 3. Gain functions for each experimental subject under different conditions in the solitary (segmented line) and social (solid line) patch. Values are the mean cumulative time in patch ( $\pm$ s.e.) for successive prey captured. The bottom row shows the mean gain functions. (a) No flock; (b) control flock; and (c) flock.

lower gain functions in the social patch when zebra finches were nearby (e.g. subject 2; figure 3b). This effect is more pronounced, and applies to all subjects, under the flock condition. A repeated measures ANOVA using prey capture time as the response variable, and including only

the first four prey so as to homogenize prey numbers across subjects and treatments shows that this effect was significant (patch  $\times$  prey interaction,  $F_{3,28} = 7.945$ ,  $p < 0.0005$ ). The gain functions also show that birds did not capture the first prey as quickly as in the solitary

patch, and hence the first prey appears shifted to the right.

#### 4. DISCUSSION

The presence of conspecifics next to a feeding patch caused starlings to behave as if the attractiveness of that patch had increased. This was expressed in a higher rate of work and reduced time in the alternative (solitary) patch, and a slower rate accompanied by longer patch times in the social patch, so that overall a greater proportion of the time was spent under social conditions. The additional time devoted to the social patch was most likely due to the occurrence of behaviours addressed to the social companions rather than to the feeding task, as shown by the fact that they took longer to start working for food, they accumulated responses (hence rewards) at a slower rate, and they then took longer to switch patches after the last reward had been collected. The best description of the changes observed is that it looks as if when a flock is present near the social patch the subjects are aroused to get back there as soon as possible. To this effect they hurry their foraging when they are away from the flock and slow it down when close to it. This finding fits the broadest definitions of interference, because the presence of others causes a decline in the subject's intake rate (Sutherland 1996). Such an all-encompassing definition, however, may obscure the interpretation in this case, because previous studies considered interference mechanisms such as fighting, kleptoparasitism, resource depression, physical obstruction (visual field) or in general any situation where the 'competitors' alter physically the circumstances of the forager (e.g. Ranta *et al.* 1993; Sutherland 1996). Here we show a decline in intake rate even though the presence of conspecifics does not modify feeding opportunities. When aware of the option of being near to conspecifics, our animals also changed their foraging behaviour when foraging elsewhere, by foraging at a higher intake rate, as if, to put it anthropomorphically, they were in a hurry to solve their foraging needs quickly to be able to return to where their conspecifics were. Our results make it obvious that the gain function (cumulative rewards versus patch time) and consequently the pattern of patch depletion were not rigid constraints but were partly caused by the deployment of behavioural options available to the subjects, such as working at a slower or faster rate. This result poses interpretation problems to the conventional foraging theory attitude of treating the gain function as an ecological constraint. It is impossible to establish on the basis of these laboratory data whether under natural ecological circumstances the tendency to forage close to conspecifics evolved as an adaptation to obtain extra food through alternative routes, for example if groups of nearby foragers offer the opportunity for kleptoparasitism or for more precise location of high prey density spots, or because conspecifics' proximity is adaptive for non-foraging purposes, such as shared predator detection. The findings, however, illustrate the complexity of developing optimality models of decision-making and testing them experimentally.

For instance, in a recent study of social foraging in spice finches (*Lonchura punctulata*), Livoreil & Giraldeau

(1997) found that the gain function of individuals foraging singly appeared to be steeper than that of individuals foraging in a trio. They then used these empirical gain functions to predict patch departures on the basis of rate maximization. Because their subjects shared the patches but did not show overt aggression, the slower gain functions under social conditions could have been mediated by pseudointerference (food exploitation competition by other flock members) or by modified individual behaviour such as that shown by our starlings. Livoreil and Giraldeau's analysis implicitly assumes the former, treating the gain function as a constraint. This is also manifested in that to compute gain functions these authors pool data collected under both short and long travel times. If experimental treatment modified working rate as social companions do in our experiments, the gain functions obtained by pooling would not be representative of the foraging problem faced by the finches under either condition.

If we accept the limitation imposed by the fact that the animals build their own foraging circumstances (and we must do so at least for our experiment) it is pertinent to ask for the justification of using a rate-maximizing predictive model of behaviour for individual components of the behavioural cycle. Put directly: since the birds are not rigidly limited in working rate, but 'choose' to work at a slower rate when in company and speed up when they forage away from the flock, they are obviously not rate maximizing all of the time. Otherwise they would be working at an optimal rate under all circumstances. Is it reasonable, then, to use rate maximizing as a currency to predict patch departures?

It may seem paradoxical, but we feel that the rate-maximizing modelling approach is justified even when taking self-defined constraints into account. We recognize that the choices of the animal in one behavioural dimension (sociality) create the problems they face in another dimension (foraging). It would appear that, given that social conditions induce the subject to work at a given rate (a phenomenon that we do not yet understand functionally), decisions about patch exploitation can be quantitatively predicted by rate maximization under the constraint imposed by a self-imposed rate of working.

We believe that this approach is more justified the more precise the predictions being tested. Hence, we next use the empirically obtained gain functions to examine if patch exploitation can be predicted by assuming that the birds were maximizing gain rate. This is effectively what Killeen *et al.* (1981) did when they found that rats worked more slowly when travel time was longer and slowed down close to the time of patch departure. These authors used these self-imposed nonlinear gain functions to predict patch behaviour (see discussion in Kacelnik & Houston 1984). Similarly, Giraldeau *et al.* (1994), using chipmunks, noticed that gain functions were shallower when they (the experimenters) detected the presence of other chipmunks in the vicinity. They attributed the shallowing of the gain function to resource defence, which would not have been an appropriate assumption for our experiment, but whatever the justification, these authors used the self-generated modification of the gain function to predict changes in patch departure time under rate maximization (see also Ydenberg *et al.* 1986; Ranta *et al.* 1995).

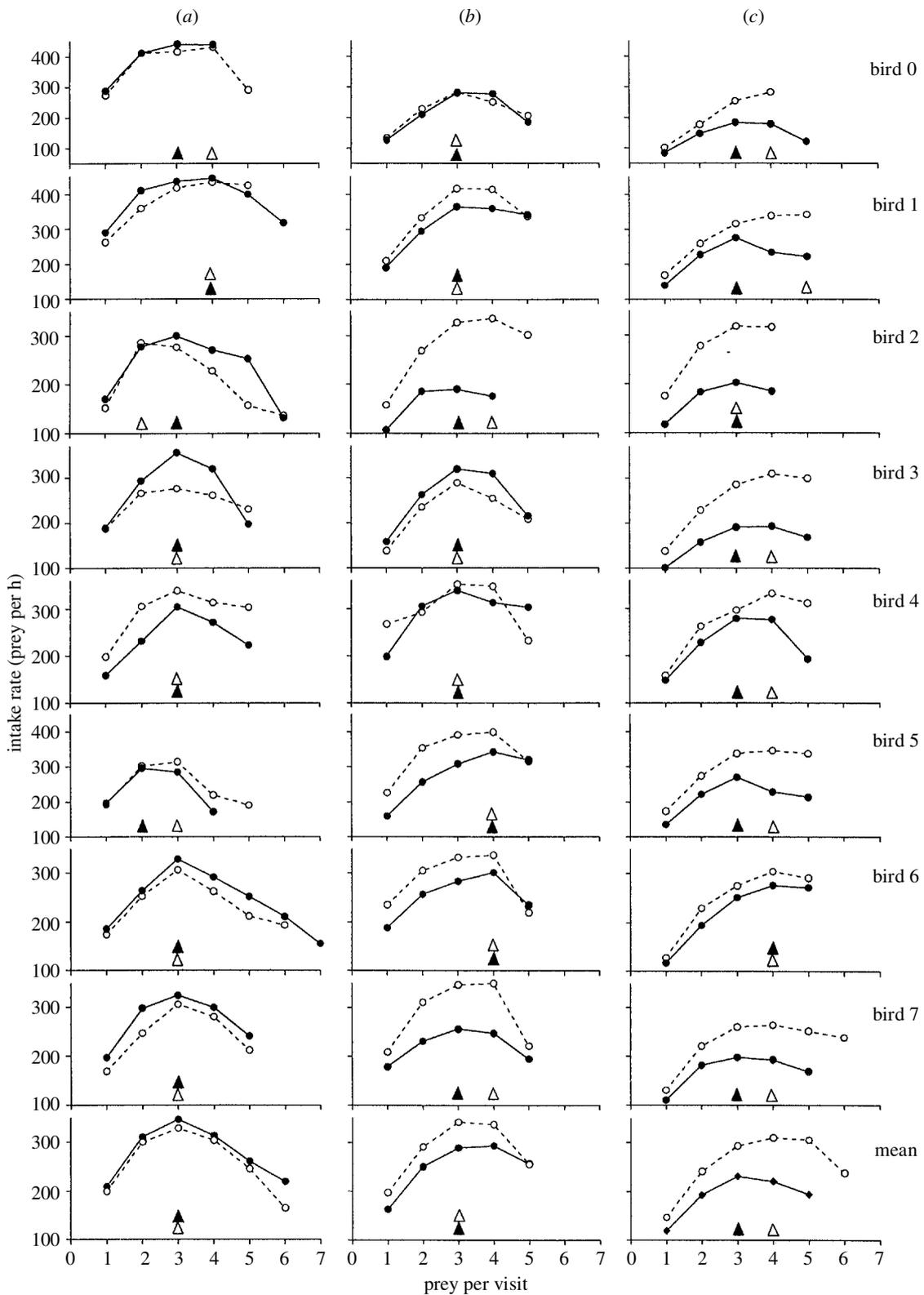


Figure 4. Expected prey intake rate as a function of the number of prey captured per visit in the solitary (segmented line) and social (solid line) patch. The bottom row shows the mean across subjects (mean  $\pm$  s.e.). Triangles indicate the optimal number of prey captured per visit for the solitary (open) and social (solid) patch. (a) No flock; (b) control flock; and (c) flock.

Ignoring the discreteness of the gain function for the sake of simplicity, we can calculate the long-term intake rate ( $R(t_i)$ ) corresponding to different patch times by using the ratio of number of prey captured ( $n_i$ ) in patch  $i$  as a function of time in that patch to the total time spent foraging (travel time ( $\tau_i$ ) plus feeding-pecking time ( $t_i$ ),

$$R_i(t_i) = \frac{n_i(t_i)}{\tau_i + t_i}.$$

We computed the travel time as the total time that subjects spent switching from one patch to the other, adding together the time between the last pecking

response and entering the 'travel' patch, the time in the travel patch, and the time between entering a patch and the first response. We differentiated both directions of travelling since birds, in the flock condition, moved more quickly from the solitary to social patch than in the return way. This difference creates yet another problem for our quantitative test. The starlings were experiencing a regular sequence of the form:

long  $\rightarrow$  steep  $\rightarrow$  short  $\rightarrow$  shallow  $\rightarrow$  etc...

where 'long' or 'short' are travel times and 'steep' or 'shallow' are gain functions. Using these values to compute the optimal giving-up policy poses a new difficulty: Should we predict patch exploitation using the travel time that precedes a visit or that that follows it? In theory, this may be an unnecessary question, because a rate-maximizing subject should use average travel time, but on the basis of previous empirical evidence this is not to be expected. Starlings experiencing a random sequence of short and long travels have been found to tune into the preceding travel time (Cuthill *et al.* 1990), while the same species when exposed to a strict alternation of short and long travels initially, tune into the last travel, and after some training (when they learn about the alternation) switch to pay attention to the forthcoming one (Cuthill *et al.* 1994). Similar tracking trends were found in pigeons by Kacelnik & Todd (1992) and Todd & Kacelnik (1993). If subjects were minimizing the time to the next capture they should use the forthcoming travel time, but if they predict average travel times using the last remembered instance encountered they might use the preceding one. The implication is that it would be possible to justify any of the three combinations of travel and gain functions.

Since there is no clear solution to this problem, we conducted the analysis of rate maximization using all three options. Fortunately for our present purposes, there were no major quantitative differences in the conclusions to be drawn: rate-maximizing visit lengths were almost unaffected by the choice of travel combination. We decided to use the theoretically more defensible use of average travel times. Figure 4 shows expected feeding rate as a function of prey per visit using individual gain functions and averaging travel in both directions for each subject. The figure shows that in most conditions the highest intake rate would be achieved by taking three prey per visit, with the exception of the solitary patch in the flock condition, when four prey per visit is optimal. By reference to figure 2*b* we see that the starlings took the predicted three prey per visit in virtually all cases. The rate curves in figure 4 show that one might expect a shift towards greater number of prey per visit in the solitary patch under the flock condition. Figure 2*b* shows that there was indeed a trend in this direction, but since the expected change was less than one whole integer it is not surprising that the change was not statistically significant.

The estimated maximum mean intake rates during non-social conditions were 328.8 prey per hour and 347.2 prey per hour in the solitary and social patch, respectively. In social conditions, maximum mean intake rates dropped to 311.9 prey per hour and 231.3 prey per hour in the solitary and social patch, respectively. Therefore, even theoretical birds that followed the policy of always

taking three prey per visit would lose as a consequence of the changes imposed by responding to conspecifics.

Since birds did not capture three prey in each visit, the actual rates experienced were not those calculated assuming exclusive use of the highest-yielding visit length, but depended on the proportion of visits in which different prey numbers were taken. As an approximation we can use the values in figure 2, showing that visit length in the social patch were 63 s and 3.1 prey, respectively, when there were starlings nearby, and 51 s and 3.3 prey when there were not (figures 1*a,b*). This corresponds to yields of 177 prey per hour in social conditions and 233 prey per hour in non-social conditions. Thus, intake rate decreased in the order of 24% for being social.

From a functional perspective, our results are consistent with (but do not prove) a 'non-foraging' hypothesis for starling social foraging. Under laboratory conditions, starlings compromise feeding returns in exchange for gregariousness. The data do not support accounts of group leaving and/or joining decisions based on increasing feeding returns (see, for example, Kacelnik *et al.* 1992; Pulliam & Caraco 1984; Clark & Mangel 1986; Ranta *et al.* 1995; Beauchamp 1998; Giraldeau & Beauchamp 1999). It is possible, and indeed likely, that gregariousness under different scenarios would actually result in increased profitability, but it is highly unlikely that increased profitability acts as the main proximate factor influencing the decision to join or leave a group. The adaptive significance of the behavioural responses uncovered here may become apparent when similar experiments are repeated under field conditions. This, we feel, ought to be the next step.

We thank M. Dawkins and M. Evans for discussion and suggestions during the initial stage of this study and L.-A. Giraldeau for very useful commentaries on a previous version of the manuscript. The research was partly funded by the Wellcome Trust (Research Grant 046101 to A.K.). R.A.V. was supported by a Presidente de la República Fellowship (Mideplan, Chile) and an ORS award scheme (UK), and during final writing, by Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT) 3950023 (Chile), and a Departamento de Investigación y Desarrollo (DID) travel grant (University of Chile).

## REFERENCES

- Barnard, C. J. & Sibly, R. M. 1981 Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543–550.
- Beauchamp, G. 1998 The effect of group size on mean food intake rate in birds. *Biol. Rev.* **73**, 449–472.
- Bernstein, C., Kacelnik, A. & Krebs, J. R. 1988 Individual decisions and the distribution of predators in a patchy environment. *J. Anim. Ecol.* **57**, 1007–1026.
- Caraco, T. 1981 Risk-sensitivity and foraging groups. *Ecology* **62**, 527–531.
- Charnov, E. L. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Clark, C. W. & Mangel, M. 1984 Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* **123**, 626–641.
- Clark, C. W. & Mangel, M. 1986 The evolutionary advantages of groups foraging. *Theor. Popul. Biol.* **30**, 45–75.
- Cuthill, I. C., Kacelnik, A., Krebs, J. R., Haccou, P. & Iwasa, Y. 1990 Starlings exploiting patches: the effect of recent experience on foraging decisions. *Anim. Behav.* **40**, 625–640.

- Cuthill, I. C., Haccou, P. & Kacelnik, A. 1994 Starlings (*Sturnus vulgaris*) exploiting patches: response to long-term changes in travel time. *Behav. Ecol.* **5**, 81–90.
- Elgar, M. A. 1987 Food intake rate and resource availability: flocking decisions in house sparrows. *Anim. Behav.* **35**, 1168–1176.
- Fretwell, S. D. & Lucas, H. J. 1969 On territorial behavior and other factors influencing habitat distributions in birds. *Acta Biotheor.* **19**, 16–36.
- Giraldeau, L.-A. & Beauchamp, G. 1999 Food exploitation: searching for the optimal joining policy. *Trends Ecol. Evol.* **14**, 102–106.
- Giraldeau, L.-A. & Caraco, T. 1999 *Social foraging theory. Monographs in behavior and ecology*. Princeton University Press. (In the press.)
- Giraldeau, L.-A., Kramer, D. L., Deslandes, I. & Lair, H. 1994 The effect of competitors and distance on central place foraging eastern chipmunks, *Tamias striatus*. *Anim. Behav.* **47**, 621–632.
- Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour. An approach based on state*. Cambridge University Press.
- Kacelnik, A. 1984 Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *J. Anim. Ecol.* **53**, 283–299.
- Kacelnik, A. & Houston, A. I. 1984 Some effects of energy costs on foraging strategies. *Anim. Behav.* **32**, 609–614.
- Kacelnik, A. & Todd, I. A. 1992 Psychological mechanisms and the marginal value theorem: effect of variance in travel time on patch exploitation. *Anim. Behav.* **43**, 313–322.
- Kacelnik, A., Krebs, J. R. & Bernstein, C. 1992 The ideal free distribution and predator–prey populations. *Trends. Ecol. Evol.* **7**, 50–55.
- Killeen, P. R., Phillip, J. & Hanson, S. J. 1981 Central place foraging in *Rattus norvegicus*. *Anim. Behav.* **29**, 64–70.
- Koops, M. A. & Giraldeau, L.-A. 1996 Producer–scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models. *Anim. Behav.* **51**, 773–783.
- Lima, S. L. 1987 Vigilance while feeding and its relation to the risk of predation. *J. Theor. Biol.* **124**, 303–316.
- Livoreil, B. & Giraldeau, L.-A. 1997 Patch departure decisions by spice finches foraging singly or in groups. *Anim. Behav.* **54**, 967–977.
- McNamara, J. M. & Houston, A. I. 1990 State-dependent ideal free distributions. *Evol. Ecol.* **4**, 298–311.
- Pulliam, H. R. & Caraco, T. 1984 Living in groups: is there an optimal group size? In *Behavioural ecology: an evolutionary approach*, 2nd edn (ed. J. R. Krebs & N. B. Davies), pp. 127–147. Oxford, UK: Blackwell.
- Ranta, E., Rita, H. & Lindström, K. 1993 Competition versus cooperation: success of individuals foraging alone and in groups. *Am. Nat.* **142**, 42–58.
- Ranta, E., Rita, H. & Peuhkuri, N. 1995 Patch exploitation, group foraging, and unequal competitors. *Behav. Ecol.* **6**, 1–5.
- Rita, H. & Ranta, E. 1998 Competition in a group of equal foragers. *Am. Nat.* **152**, 71–81.
- Sutherland, W. J. 1996 *From individual behaviour to population ecology*. Oxford University Press.
- Templeton, J. J. & Giraldeau, L.-A. 1995 Patch assessment in foraging flocks of European starlings: evidence for the use of public information. *Behav. Ecol.* **6**, 65–72.
- Todd, I. A. & Kacelnik, A. 1993 Psychological mechanisms and the marginal value theorem: dynamics of scalar memory for travel time. *Anim. Behav.* **46**, 765–775.
- Valone, T. J. 1993 Patch information and estimation: a cost of group foraging. *Oikos* **68**, 258–266.
- Vásquez, R. A. 1995 Decision making in variable environments: individuals, groups, and populations. DPhil thesis, University of Oxford, UK.
- Ydenberg, R. C., Giraldeau, L.-A. & Kramer, D. L. 1986 Interference competition, payoff asymmetries, and the social relationships of central place foragers. *Theor. Popul. Biol.* **30**, 26–44.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.