ANIMAL BEHAVIOUR, 2006, 72, 1451–1456
doi:10.1016/j.anbehav.2006.05.006

Social foraging in *Bufo americanus* tadpoles

CHARLES SONTAG, DAVID SLOAN WILSON & R. STIMSON WILCOX
Department of Biological Sciences, Binghamton University

*(Received 27 May 2004; initial acceptance 31 July 2004;
final acceptance 20 May 2006; published online 16 October 2006; MS. number: A9900R)*

Animals can find food using information from the food itself or from conspecifics that are also looking for food. Social information can be actively communicated or based on unavoidable by-products of feeding activities. We present three experiments that explore the relative importance of odour gradients and social information as *Bufo americanus* tadpoles locate food sources. In the first experiment, tadpoles rapidly aggregated at food patches and discriminated between the qualities of two food patches spaced 15 cm apart in the field. In a second experiment, the initial presence of tadpoles at one food patch enhanced aggregation for 1 h, compared to an identical food patch without tadpoles spaced 114 cm apart. In a third experiment, the time required to initial contact with a single food patch did not change over a 16-fold range of food concentration, suggesting that *B. americanus* tadpoles have a limited ability to locate food from a distance using information from the food itself. Finding food and discriminating food patch quality from a distance is probably a major adaptive advantage of sociality in *B. americanus* tadpoles, although the presence or absence of active signalling remains to be determined.

It is common to suppose that animals evolve to live in groups primarily to avoid predators, despite the disadvantages of competing for food (Alexander 1975; Alcock 1998; Giraldeau & Caraco 2000). However, foraging provides another potential advantage for living in groups, when conspecifics provide a source of information for finding food that outweighs the disadvantages of competition once food is found. Social foraging need not be cooperative. Rather, it can span the range from extreme cooperation to extreme exploitation (Hamilton & Dill 2003). The social insects represent the cooperative extreme, in which individuals actively signal the location and quality of resources, sometimes over an area of several square kilometres (Seeley 1995; Anderson & Franks 2003). Producer–scrounger systems represent the exploitative extreme, in which dominant individuals monitor the foraging activity of subordinates and displace them when food patches have been found (Vickery et al. 1991; Beauchamp et al. 1997; Bikhchandani et al. 1998; Giraldeau & Caraco 2000; Galef & Giraldeau 2001; Hamilton & Dill 2003). This kind of parasitism can easily be dysfunctional for the group as a whole and presumably persists only because subordinates gain other advantages from staying in the group (Bikhchandani et al. 1992, 1998; Giraldeau et al. 2002).

This article examines the use of social information to find food in American toad *Bufo americanus* tadpoles. The gregarious nature of these tadpoles has been interpreted primarily as a defence against predators (Wassersug 1973; Petranka 1989; Skelly & Werner 1990; Anholt et. al. 1996; Petranka & Hayes 1998), although a number of other advantages have also been proposed (Bragg & King 1960; Licht 1967; Beiswenger & Test 1966; Beiswenger 1977; Hoff et al. 1999), including feeding facilitation after food is found (Bragg 1968; Beiswenger 1972; Test & McCann 1976). Our inquiry begins with a field experiment that demonstrates the ability of *B. americanus* tadpoles to aggregate at food patches and distinguish among patches of different quality. Circumstantial evidence from this experiment suggests that the tadpoles rely primarily upon social information rather than information emanating directly from the food. Two laboratory experiments demonstrate the importance of social information and an inability of *B. americanus* tadpoles to sense food directly from a distance based on odour cues. Our research suggests that using conspecifics to find food is a major advantage of sociality in *B. americanus*, although the cooperative versus exploitative nature of social foraging remains to be determined. We end by discussing the theoretical plausibility of cooperative social foraging in this species.

Correspondence: C. Sontag, Department of Biological Sciences, Binghamton University, Binghamton, NY 13902-6000, U.S.A. (email: bg23338@binghamton.edu).

0003–3472/06/$30.00/0

MATERIALS AND METHODS

Experiment 1

Do tadpoles locate food patches and discriminate patch quality in the field?

We prepared food patches of known quality by adding different amounts of flake fish food (Tetra Fin goldfish flakes, Tetra Sales, Blacksburg, Virginia, U.S.A.) that we ground into a powder to a mixture of agar and gelatine (20 g of granular agar, 14 g of gelatine, 1000 ml of water). We then poured the mixture into plastic 33-mm-slide casings on a glass plate and allowed it to harden, providing a substrate suitable for tadpole feeding. When removed from the glass and plastic casing, each rectangular patch measured $2.2 \times 3.4 \times 0.2$ cm and comprised approximately 2 ml of the food/agar/gelatine matrix.

We placed two patches that differed in food concentration by a factor of four (0.1 g/ml versus 0.025 g/ml) 15 cm apart, in 3–5 cm of water, and equidistant from shore in a shallow pond inhabited by *B. americanus* tadpoles. The light colour of the pond bottom provided good contrast with the tadpoles and food patches, enabling recruitment to be videotaped from the shore by a camera on a tripod. The location was taped for 2 min before adding the patches and for 30 min after adding the patches, during which we retreated at least 10 m from the shore to avoid disturbing the tadpoles. Analysis of the tapes consisted of superimposing an acetate sheet on the video screen with a circle corresponding to a radius of 25 cm in the field and divided into 12 sectors. The circle was centred on the point equidistant between the two patches and tadpoles were counted as they crossed the periphery of the circle or between sectors inside the circle. In this fashion, an exact count of the tadpoles could be obtained as they converged upon the two patches. Twenty trials were run between 18 June and 29 June 2001, during which the tadpoles were between Gosner stages 25 and 37 (Gosner 1960).

Experiment 2

Does the presence of conspecifics influence patch choice of tadpoles?

For this experiment, we placed approximately 400 tadpoles in a 3-m-diameter wading pool that was filled with water to a depth of 35 cm and placed in a room with a 14:10 h light:dark cycle and a constant temperature of 18°C. We placed two 7.5-cm-diameter cylinders, each filled with 50 g of chopped canned spinach, upright in the pool, 114 cm apart and equidistant from the edge, and placed 10 randomly selected tadpoles inside one of the cylinders. After a 6-min acclimation period, we gently removed the two cylinders, leaving two food patches identical except for the initial presence of 10 tadpoles on one of them. The number of tadpoles on each patch was counted at 4-min intervals by an observer sitting quietly at the edge of the pool. The average amount of time spent on a patch was measured for a subset of 20 tadpoles. We conducted 16 trials between 23 August and 17 September 1999. The tadpoles for this experiment were collected from a single egg mass from the field on 12 June 1999, and maintained at a low temperature and on a restricted diet to delay their development. Tadpoles were between Gosner stages 25 and 38 (Gosner 1960) at the time of the experiment. In the analysis, we subtracted the 10 tadpoles that we initially used to 'seed the patch' when comparing the numbers of tadpoles at the two patches.

Experiment 3

Does the number of tadpoles or the quality of food reduce searching time for a food resource?

For this experiment, we placed a single food patch similar to those used in the field experiment, in the centre of a 41×74-cm Plexiglas tray that was filled with water to a depth of 2 cm. We tested three concentrations of food varying over a 16-fold range (low = 0.00625 g/ml; medium = 0.025 g/ml; high = 0.1 g/ml) and three densities of tadpoles (1, 3, 10) with five replicates per treatment in a 3×3 factorial design (a total of 45 trials). In each trial, we placed the food patch in the centre of the tray and placed the tadpoles 20 cm away from the food in a 5-cm cylinder, which was gently withdrawn after a 4-min acclimation period. The trials were videotaped from above to determine the time required for tadpoles to first contact the food patch. These trials were completed between 14 and 29 September 2002, using tadpoles collected from four egg masses collected on 28 May 2002, and maintained at a low temperature and restricted diet to delay their development. Tadpoles were between Gosner stages 25 and 38 (Gosner 1960) at the time of the experiment. For each trial, we used tadpoles from a single egg mass.

RESULTS

Experiment 1 examined whether tadpoles discriminate between food patches of different quality. Tadpoles started to aggregate at both food patches within minutes. However, within 15 min, the mean ± SD number of tadpoles at the high-quality patch (154.25×140.74, $N = 20$) was significantly greater than that at the low-quality patch (66.65 ± 39.92, $N = 20$). More tadpoles also aggregated at the high-quality patch in 15 of the 20 trials (paired t test: $t_{19} = 3.047$, $P = 0.007$). Fifteen minutes was chosen as the period for measurement because, by the end of the 30-min trial, the high-quality patch was often nearly completely fragmented and consumed.

Although it is possible that the tadpoles were relying entirely upon information from the food patches themselves, the following observations indicate the use of social information. (1) Movement towards the patches occurred from well over a metre away. (2) The tadpoles did not move directly towards the patches from all directions, but instead tended to form columns that looked intriguingly like ant columns, especially when the videotapes were played in fast motion (see Supplementary Material). (3) Tadpoles would move to join columns that moved towards the patches rather than

moving directly towards the patches. (4) The absence of recruitment to areas without food patches was not because of an absence of tadpoles in these areas. (5) In some cases the movement of a column appeared to become disorganized, resulting in the diffusion of the column or a reversal of direction, indicating the disruption of social information. (6) Feeding on the patches sometimes created turbulence and a plume of silt that enabled us to see the direction of (very slow) water movement. There was no correspondence between the columns of tadpoles and the direction of the plumes, which would have been the case if tadpoles were responding directly to odour gradients.

Experiment 2 was designed to detect the use of social information by providing two identical food patches that differed only in the initial presence of 10 tadpoles. Recruitment to the patch seeded with tadpoles was greater than that to the unseeded patch (Fig. 1). Four minutes after the start of the experiment, significantly more tadpoles recruited to the high-quality patch (paired t test: $t_{15} = -3.143$, $P = 0.004$), and this difference remained significant at 52 min ($t_{15} = -2.153$, $P = 0.048$); the second test was not independent of the first. Individual tadpoles ($N = 20$) spent a mean $\overline{X} \pm \mathrm{SD}$ of $6.46 \text{ min} \pm 5.09$ on a patch, which suggests that the 'seed tadpoles' had left long before the trial was completed. Nevertheless, their effect continued through the tadpoles that were attracted by their initial presence.

Experiment 3 was designed to detect the use of information emanating directly from a food patch, presumably in the form of an odour gradient. The time required for tadpoles to first contact a single patch declined with the number of tadpoles in the tray (ANOVA: $F_{2,42} = 5.509$, $P = 0.008$; Fig. 2), but was not influenced by the concentration of food over a 16-fold range ($F_{2,42} = 0.166$, $P = 0.847$; Fig. 3). If the tadpoles were capable of detecting food at a distance by following an odour gradient, they should have found the concentrated food patch more quickly.

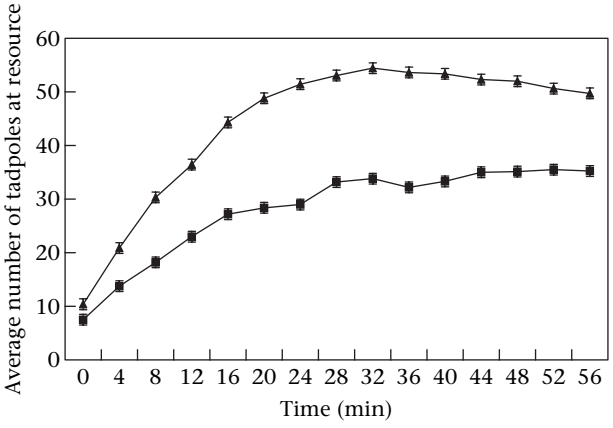

Figure 1. Relation between the number of tadpoles present during the original colonization and the number of tadpoles at a resource during a 56-min period. Mean + SE number of tadpoles counted at the control (■) and the seeded (▲; minus 10 to account for the original additions) resource every 4 min for 56 min.

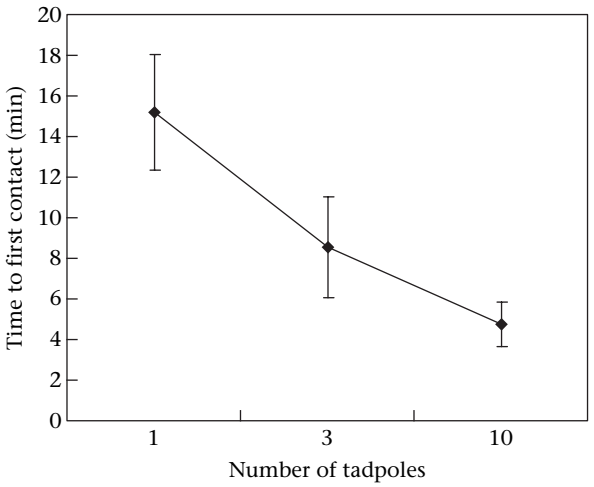

Figure 2. Relation between group size and time to first contact in minutes. Mean + SE time to first contact determined for each group size.

DISCUSSION

The results of our experiments show that *Bufo americanus* tadpoles use social information to locate food patches and to discriminate between food patches of different quality. *Bufo americanus* tadpoles are opportunistic feeders on detritus, epiphytes, suspended matter, and even carrion (Beiswenger 1972; Test & McCann 1976). Their resource environment is patchy at a variety of temporal and spatial scales. Nevertheless, apart from early natural history observations in a *Scaphiopus* species (Bragg & King 1960; Bragg 1968), using conspecifics to find food is a hitherto unrecognized advantage of sociality in toad tadpoles. Aggregations are usually explained as a defence against predators (Petranka 1989; Skelly & Werner 1990; Anholt et al. 1996; Watt et al. 1997; Petranka & Hayes 1998). The tadpoles of *Bufo* species are unpalatable to many predator

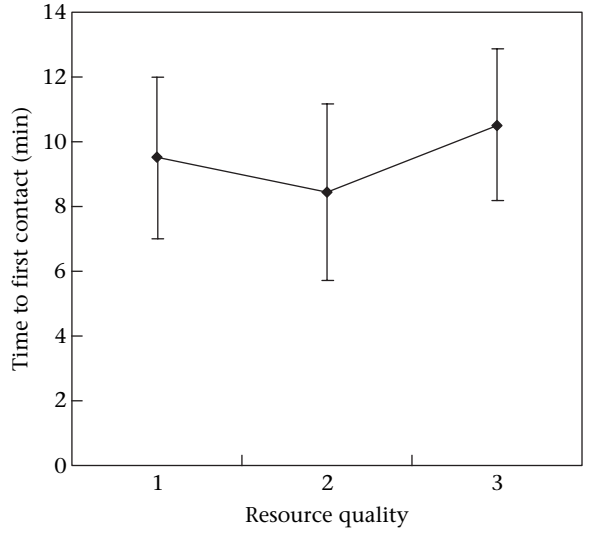

Figure 3. Relation between resource quality and the time to first contact in minutes. Mean + SE time to first contact determined for resources of high (1), medium (2) and low (3) quality.

species and aggregation is a common strategy of toxic prey (Brodie et al. 1978; Kruse & Stone 1984). Nevertheless, there is little direct evidence for a defensive advantage of grouping in *B. americanus* tadpoles and several studies report dispersal in response to chemical cues from predators (Petranka et al. 1987; Petranka 1989; Petranka & Hayes 1998). *Bufo americanus* tadpoles are usually abundant and conspicuous within their habitats, but not necessarily tightly grouped; instead, there is usually a continuum from scattered individuals to dense aggregations. It is possible that their unpalatability enables them to forage without regard to most predators rather than having to form tight groups to avoid predators. In any case, the two potential advantages of sociality need not be mutually exclusive and can even reinforce each other, as discussed below.

The results of experiment 3 also suggest that *B. americanus* tadpoles do not use odour cues emanating directly from the food to locate food from a distance. The diffusion of molecules in perfectly still water is very gradual (Dittmer et al. 1996; Grasso 2001), but turbulence created while placing the food patches in the trays and by the animals themselves should have created odour gradients that varied over the 16-fold range of food concentrations. In addition, the quantitative result of this experiment based on the time required for tadpoles to first contact each patch is supported by qualitative observations in the laboratory and field. We frequently observed tadpoles failing to move directly towards a food patch even from a distance of a few millimetres, so physical contact may be required to detect the presence of a food patch. Given this limited ability to detect food directly, it is remarkable that recruitment to food patches from distances of a metre of more took place within minutes in the field trials. Perhaps the reliable presence of conspecifics as a source of information about food has made the ability to detect food directly from a distance unnecessary. It would be interesting to compare the sensory abilities of *B. americanus* with more solitary species of tadpoles in this regard.

The sensory mode(s) of information transmission remains to be determined. Vision is unlikely to be the exclusive mode because *B. americanus* tadpoles are nearsighted (-30 dioptre), focusing primarily at a distance of a few centimetres (Mathis et al. 1988). The detection of surface waves is probably an important sensory mode for this species, because individuals respond to each other's movements even when they are not on food patches, and groups but not individuals can discriminate patch quality in laboratory experiments (C. Sontag, R. S. Wilcox & D. S. Wilson, unpublished data).

Cooperation or Exploitation?

Social foraging has been studied from a number of theoretical perspectives. Some models are based on the maximization of individual fitness, such as the ideal free distribution (Kennedy & Gray 1993; Jackson et al. 2004; Jonzen et al. 2004) and producer–scrounger models (Vickery et al. 1991; Beauchamp et al. 1997; Bikhchandani et al. 1998; Giraldeau & Caraco 2000; Galef & Giraldeau 2001; Hamilton & Dill 2003). These do not necessarily lead to cooperative outcomes and in many cases individuals are predicted to conceal information as much as possible. The only reason that social foraging persists is because the information cannot be entirely concealed. Other models, especially those developed for social insect colonies, assume that the group is a cooperative foraging unit with evolved signals for communicating the location and quality of food (e.g. Seeley 1995; Camazine et al. 2001; Anderson & Franks 2003).

Our experiments establish the existence of social foraging in *B. americanus*, but more research is required to distinguish among the various theoretical possibilities. For example, the mere fact that more tadpoles aggregated at the higher-quality patch does not indicate that social foraging in this species follows an ideal free distribution, which would require measuring the degree to which fitness declines as a function of density on each patch. Since we are only in the process of discovering the sensory mode(s) of transmission, we do not know whether information about food location and quality is actively signalled or is an unavoidable cue. Nevertheless, it is important to evaluate the theoretical likelihood of cooperative versus exploitative social foraging in *B. americanus* and other social vertebrates to guide future research.

In a review article, Galef & Giraldeau (2001) interpret virtually all examples of vertebrate social foraging as noncooperative and based on inadvertent cues, such as the rasping sound of an agouti gnawing nuts: 'Such cues and signs, by-products of engaging in life-sustaining activities, are the basis of almost all known instances of vertebrate social learning about when, where, what and how to eat' (page 4). This is in stark contrast to literature on social insects, which unequivocally demonstrates cooperative foraging, including highly adapted communication systems for locating patches and discriminating patch quality. Theoretically, the only reason that foraging might be more cooperative in social insects than in social vertebrates is because genetic relatedness tends to be higher in social insects. However, this is only a trend; genetic relatedness can be quite low in social insect colonies (because of multiple queens or multiple mating by single queens) and quite high in social vertebrate groups (e.g. $r = 0.5$ for full siblings). Moreover, even though cooperative foraging inherently involves behaviours that benefit others at some individual cost, the benefit/cost ratio can be very high, as when a patch contains much more food than a single individual can consume. Factors such as predation can augment the benefit/cost ratio if recruiting others to a patch dilutes the morality rate along with the feeding rate (Giraldeau & Caraco 2000). In these cases, cooperative social foraging can evolve given a very modest coefficient of relatedness or even random groupings (Wilson 2000, 2004a).

A growing literature indicates that Galef & Giraldeau's (2001) assessment of cooperative social foraging in vertebrates is too pessimistic (Wilson 2000, 2004b; Anderson & Franks 2003; Conradt & Roper 2003). In the case of *B. americanus*, their natural population structure (large clutches often deposited in small bodies of water) and kin recognition abilities (Waldman & Adler 1979; Blaustein & O'Hara 1980; Waldman 1981, 1982, 1985; Hoff

et al. 1999) are likely to create at least a modest degree of genetic relatedness among interacting individuals. Furthermore, the food patches that they exploit are likely to be large compared to individual needs, and their defensive advantages of being surrounded by conspecifics probably compensate for the disadvantages of competition. In short, even though more research is required, it is fully plausible that social foraging in *B. americanus* will prove to be at least partially cooperative.

Acknowledgments

We thank Anne Clark for her input, John Titus for his support, Dale Madison for his early input, and our student helpers Marco Aiello, Aaron Miller, Leah Miller, Joe DePietrio, Ki Kim, Celeste Li, Deepak Sandeep, Samah Mohiuddin, 'Omar', Sarah Latif and Stacey Latif, among others.

Supplementary Material

Supplementary Material for this article may be found, in the online version, at doi:10.1016/j.anbehav.2006.05.006.

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