



## REVIEW

## Social influences on foraging in vertebrates: causal mechanisms and adaptive functions

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We summarize 20 years of empirical and theoretical research on causes and functions of social influences on foraging by animals. We consider separately studies of social influence on when, where, what and how to eat. Implicit in discussion of the majority of studies is our assumption that social influences on foraging reflect a biasing of individual learning processes by social stimuli rather than action of independent social-learning mechanisms. Our review of theoretical approaches suggests that the majority of formally derived hypotheses concerning functions of social influence on foraging have not yet been tested adequately and many models are in need of further refinement. We also consider the importance to the future of the field of integrating 'top-down' and 'bottom-up' approaches to the study of social learning.

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The last two decades have seen a virtual explosion in research on social influences on the foraging behaviour of nonhuman animals. The wealth of information now available reflects the work of scientists from many disciplines: experimental and developmental psychology, economics, artificial intelligence, anthropology and primatology, as well as biological fields from ethology and behavioural ecology to population and evolutionary biology.

For those working on problems of social foraging, the fundamentally interdisciplinary nature of the field has been and is a source of both excitement and frustration. The excitement results from constant exposure to new perspectives on familiar problems, the frustration from an ever-expanding literature with which to deal.

Our review is organized in terms of causal and functional analyses (Tinbergen 1963), although such division of the field is arbitrary in that many investigators concerned primarily with analysis either of causal mechanism or function have considered the phenomena they study from the alternative perspective. Nevertheless, the dichotomy between causation and function reflects a

fundamental division in biological studies (Mayr 1974) and is as useful an organizational device as any.

## BEHAVIOURAL PROCESSES IN SOCIAL FORAGING

## Signals, Cues and Signs

Classical ethologists were particularly interested in signals 'ritualized' to promote intraspecific communication (Tinbergen 1952). Behavioural ecologists have focused their attention on communication between coevolved signal senders and receivers competing in an arms race of manipulation and 'mind reading' (Krebs & Dawkins 1984). However, social foraging by vertebrates depends most often not on specialized or coevolved signals, but on information-bearing 'cues' (Markl 1985; Seeley 1989) or 'signs' (Hauser 1996) that do not appear to have been shaped by natural selection for intraspecific communication.

As animals engage in routine daily activities, they coincidentally provide information of use to others. For example, the rasping sound an agouti, *Dasyprocta punctata*, makes when gnawing on a nut attracts other agoutis, as well as the occasional predator, to rich, but patchy and ephemeral, feeding sites (Smythe 1970). Similarly, as members of a colony of Norway rats, *Rattus norvegicus*, travel from their burrows to food or water,

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they create trails through the undergrowth that influence the movements of those that come after (Calhoun 1962; Telle 1966).

It is unlikely that agoutis eating nuts or rats leaving their burrows to forage are emitting signals specialized to guide the behaviour of others (Williams 1966). Nevertheless, the feeding behaviour of one agouti or disturbance of the substrate caused by passage of many rats provides unambiguous messages to those sufficiently alert and behaviourally flexible to detect and exploit them. 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 (for exceptions, see Elgar 1986; Wrangham 1986; Brown et al. 1991). Consequently, causal analysis of social influences on animal foraging will generally involve investigations of how the foraging behaviour of an individual is biased by the behaviour (cues) or residual consequences of behaviour (signs) produced by others seeking nutrients.

Similarly, the use of signs and signals produced by foraging conspecifics does not appear to depend on learning processes specific to social situations. Effects on the usual operant and respondent conditioning of such behavioural processes as local and stimulus enhancement (Heyes et al. 2000) are sufficient to explain essentially all known instances of social influence on foraging. Demonstrations of a role for imitation, a type of learning specialized for exploitation of public information, remain both tentative and largely restricted to apes (e.g. Tomasello 1996; Whiten & Custance 1996; Zentall 1996; Custance et al. 1999).

### When, Where, What and How to Forage

For animals that forage actively, finding and ingesting food is a complex process requiring a sequence of choices: (1) when to undertake foraging expeditions; (2) where to look for food; (3) which potential food items to ingest and which to avoid eating; (4) which motor patterns to use to overcome protective devices (e.g. shells, spines or chemical defences); and (5) when to leave one patch for another, etc. At each step, information acquired from conspecifics can increase the efficiency of those able to use such 'public' information (Valone 1989) effectively.

### Empirical Studies of Social Influences on When, Where, What and How to Eat

#### *When to eat*

Somewhat surprisingly, given the importance of decisions as to when to eat in the exploitation of ephemeral sources of food, there are relatively few studies of how vertebrates use observation of the behaviour of others to determine when to seek food. Brown (1986), who studied social foraging by cliff swallows, *Hirundo pyrrhonota*, feeding on localized concentrations of insects seldom lasting more than 20 or 30 min, was interested in social influences on where colony members foraged, not in social influences on latencies to seek ephemeral foods.

Observations of feeding behaviour of free-living primates indicate that infant baboons tend to feed at the same time as their mothers (King 1994). However, the plants baboons exploit are not ephemeral, so temporal contiguity in feeding by mothers and dependent young probably serves some function other than informing young when to forage.

In the only instance of which we know where it has been demonstrated that a vertebrate can use socially acquired information to decide when to look for food, Galef & White (1997) introduced naïve laboratory rats into established colonies that were either trained or not trained to come to a feeding site at a specific hour. Naïve animals placed in trained colonies found food introduced at the usual hour an average of 5 min after trained colony members returned to the colony harbourage site after feeding. Naïve animals placed into untrained colonies took 40 min to reach the feeding site after food was placed there. This difference in latencies of experimental and control subjects to find food was sustained even when the possibility of local enhancement was precluded (Galef & White 1997).

#### *Where to eat*

*Information centres and local enhancement.* The literature describing both field and laboratory studies of social influences on where to eat is massive. One major stream of field research reflects attempts to determine whether, as Ward & Zahavi (1973) first proposed, birds' roosts serve as information centres from which unsuccessful foragers can follow successful foragers to patchy, rich, but ephemeral feeding sites. The results of such studies provide unequivocal evidence that birds tend to travel to and feed in locations where they can see other birds feeding (e.g. Krebs et al. 1972; Krebs 1973; Capretta 1977; de Groot 1980; Brown 1986; Waite & Grubb 1988; Gotmark 1990; Avery 1994, 1996). In such cases of local enhancement (Thorpe 1963) social information is acquired at a feeding site (e.g. in bats see Barclay 1982; Balcombe & Fenton 1988; Wilkinson & Boughman 1998), not at a roost, as the information centre hypothesis requires (but see Wilkinson & Boughman 1999). No truly convincing evidence that birds' roosts or nesting areas serve as information centres in Ward & Zahavi's (1973) sense of the term has yet been provided (Wittenberger & Hunt 1985; Mock et al. 1988; Richner & Heeb 1995), although promising, possible instances of vertebrate information centres continue to be explored (e.g. Rabenold 1987; Wilkinson 1992; Marzluff et al. 1996).

*Rodents.* Influences of local enhancement on feeding site selection by rodents has received considerable attention (for reviews, see Galef 1977, 1982, 1996a, b). The simple presence of an adult Norway rat, even an anaesthetized one, at a feeding site causes conspecific juveniles to approach from a distance and to eat. Juvenile rats prefer sites where adults are feeding to those where pups are feeding, and this difference is a result of age-related differences in body size (Gerrish & Alberts 1995).

Adult rats also deposit persistent chemicals on both feeding sites and foods they exploit (Galef & Beck 1985; Laland & Plotkin 1993), and leave scent trails as they move from feeding site to harbourage site (Galef & Buckley 1996). Such residual signs cause juveniles to explore and feed at marked sites in preference to unmarked alternatives.

*Other mammals, birds and primates.* Local enhancement effects on feeding site selection have been demonstrated in a variety of mammals from domestic pigs, *Sus scrofa* (Nicol & Pope 1994) to naked mole-rats, *Heterocephalus glaber* (Judd & Sherman 1996), as well as in birds (e.g. Krebs et al. 1972; Krebs 1973; Capretta 1977; de Groot 1980; Avery 1994, 1996). Local enhancement is particularly salient in juvenile primates (Watts 1985; King 1991, 1994) especially when they are either eating foods that are difficult to process (King 1994) or exposed to potentially noxious items (Whitehead 1986; but see Boinski & Fragaszy 1989).

*A special case (African buffalo).* Prins's (1996, pp. 219–236) observations of African buffalo, *Syncerus caffer*, suggest that, before moving towards a selected grazing ground, buffalo cows make communal decisions about where to forage. Although a single study indicating a behavioural process that requires so unexpected a level of communication in a nonprimate mammal requires confirmation, verification of Prins's observations would open a new chapter in studies of animal social foraging. Kummer (1995) discussed evidence of similar communal decision making by hamadryas baboons, *Papio cynocephalus*, although such decision making by baboons did not directly affect choice of foraging sites.

#### *What to eat*

Because different foods are not randomly distributed in space, animals feeding together are likely to consume the same foods. Consequently, local enhancement can lead groups of animals to exploit similar foods as well as similar feeding sites (Galef 1985; Gerrish & Alberts 1995). There are, however, a number of ways in which animals can directly bias one another's food choices.

*Learning while nursing.* The milk of lactating rats contains flavours of foods that nursing mothers are eating. Suckling pups detect these food flavours in their mother's milk, and at weaning, prefer foods with these flavours (Galef & Sherry 1973).

Rabbits, *Oryctolagus cuniculus*, affect the food choices of their young via their milk, via maternal fecal pellets that nestlings ingest, and prenatally, as a result of an as yet unexplored process (Bilko et al. 1994; Hudson & Altbacker 1994; Altbacker et al. 1995; Hudson et al. 1999; see also Hepper 1988). Woodrats, *Neotoma floridana*, prefer to cache, but not to eat, foods their dam ate while rearing them (Post et al. 1998).

*Communication via breath.* The breath of rats (Galef & Stein 1985), and probably of mice, *Mus domesticus*

(Valsecchi & Galef 1989), Mongolian gerbils, *Meriones unguiculatus* (Valsecchi et al. 1996; Galef et al. 1998) and spiny mice, *Acomys cahirinus* (McFadyen-Ketchum & Porter 1989) that have recently eaten carries food odours allowing conspecifics to identify, and causing them to prefer, foods detected on the breath of others. Such socially induced food preferences are surprisingly robust, lasting for weeks (Galef 1989), and can even reverse learned aversions to foods (Galef 1986; Provenza & Burritt 1991; Yoerg 1991; Provenza 1994) or preferences based on inherent palatabilities of foods (Galef 1986, 1989). The duration of such social effects on food preference are such as to permit development in the laboratory of traditions of food preference that persist over 'generations' (Laland & Plotkin 1990; Galef & Allen 1995; Laland 1999).

*Learning via visual cues.* In many avian species visual cues mediate socially induced food selection. For example, day-old domesticated chicks, *Gallus gallus domesticus*, observing a motor-driven arrow making 'pecking' movements directed towards a distinctively coloured plastic pinhead subsequently peck disproportionately at pinheads of the same colour (Suboski & Bartashunas 1984). Red-winged blackbirds, *Agelaius phoeniceus*, that see conspecifics eating a coloured food prefer food of that colour for days after (Mason & Reidinger 1981; Mason et al. 1984; Fryday & Greig-Smith 1994). Similarly, 48 h after seeing video images of conspecifics feeding from a visually distinct bowl, Burmese fowl, *Gallus gallus spadiceus*, preferred to feed from similar bowls (McQuoid & Galef 1992, 1993).

*Active teaching of food choices.* At some point during the year or more that many monkeys and apes depend on their mothers for nutriment, young begin to feed independently, and mothers might be expected to guide food choices of offspring actively. However, although marmosets (*Callithrix* spp.), tamarins (*Leontocebus* spp.) and capuchin monkeys, *Cebus apella* (de Waal 1997) share food with their offspring (Ferrari 1987), true food sharing (i.e. 'voluntary donation of food by one animal to another' King 1991, page 103; Feistner & McGrew 1989) seems to be rare among primates (Altmann 1980; Visalberghi & Fragaszy 1995, but see Nishida et al. 1983; Watts 1985). Solicitation or scrounging of food items from adults by juveniles is, however, common (King 1994; Fragaszy et al. 1997; for further references, see Galef 1996a).

Although it seems likely that eating food scraps taken from adults has an effect on development of food preferences in young primates, there is currently no direct evidence that scrounged food biases juveniles' food preferences (Fragaszy & Visalberghi 1996), and events that seem likely to result in social learning do not always do so (Galef 1996b). Consistency in food selection from generation to generation in free-living primates in itself does not provide convincing evidence of social influences on food choice (Milton 1993).

#### *What not to eat*

Unexpectedly, Norway rats that interact with a conspecific that has eaten an unfamiliar food and become

sick or unconscious show an enhanced preference for, rather than aversion to, that food (Galef 1985; Galef et al. 1990; but see Kuan & Colwill 1997; and Galef & Whiskin, *in press*). However, rats may be unusual in lacking a means of communicating avoidance of foods or feeding sites. Least chipmunks, *Tamias minimus*, communicate avoidance of depleted caches (Devenport et al. 1999) as may red foxes, *Vulpes vulpes* (Henry 1977), coyotes, *Canis latrans* (Harrington 1982), and wolves, *Canis lupus* (Harrington 1981). Birds of various species readily learn by observation to avoid eating foods they see conspecifics eat and become ill (Mason et al. 1984; Fryday & Greig-Smith 1994; Johnston et al. 1998).

Reports of adults actively preventing young from ingesting items that the adults have learned to avoid eating are surprisingly rare even in primates (see, for an example, Fletemeyer 1978).

#### How to eat

**Rodents.** Black rats, *Rattus rattus*, inhabiting otherwise sterile pine forests in Israel feed on pine seeds they extract from pine cones. Rats from elsewhere in Israel were unable to learn to extract seeds from pine cones either by trial and error or by observing proficient conspecifics extract seeds. However, rats born to dams unable to open cones and foster reared by proficient seed extractors became proficient exploiters of pine cones as did individuals that had experience of completing the removal of scales from cones that had been partially opened by either another rat or a human experimenter (Terkel 1994, 1995).

Weigl & Hanson (1980) reported facilitation of learning to open hickory nuts by naïve captive red squirrels, *Tamiasciurus hudsonicus*, that had seen conspecifics open them. Previde & Poli (1996) found that young golden hamsters, *Mesocricetus auratus*, can learn socially to use their teeth and forepaws to retrieve food dangling at the end of a small chain, and Laland & Plotkin (1990) have shown that Norway rats learn to dig for buried pieces of food by observing conspecifics engage in digging behaviour.

**Birds.** Sherry & Galef (1984, 1990) examined a laboratory analogue of the classic observation of social transmission of the habit of milk-bottle opening by European parids (Fisher & Hinde 1949). Milk-bottle opening is often attributed to learning by imitation. However, Sherry & Galef (1984, 1990) found that feeding from containers opened by others was as effective in increasing the frequency with which naïve individuals opened containers as was watching a conspecific open containers.

Palameta & Lefebvre (1985) found that naïve birds that saw a trained bird both pierce a cover and eat learned to do so more rapidly than naïve birds that saw the model piercing the paper but not eating. Dawson & Foss (1965), Galef et al. (1986), Lefebvre et al. (1997a), Fritz & Kotschal (1999) and Campbell et al. (1999) have each provided evidence that learning of simple motor patterns used by conspecific models to obtain food facilitates acquisition of those motor patterns by naïve individuals,

although the precise mechanism underlying such social learning remains to be determined.

In an interesting survey of the notes sections of ornithology journals, Lefebvre et al. (1997b) found a positive correlation across avian orders between forebrain size and frequency of feeding innovations, suggesting that the tendency to innovate when feeding has a physiological basis.

**Primates.** Evidence consistent with the hypothesis that primates learn socially how to process foods is now fairly extensive (Lefebvre 1995). In chimpanzees, *Pan troglodytes*, in particular, field studies have revealed that many social groups comprising the species use idiosyncratic methods to process difficult foods (for a review, see Boesch & Tomasello 1998; Whiten et al. 1999). However, because essentially nothing is known about how such population-specific patterns of feeding behaviour develop in the wild (but see Boesch & Boesch 1990; Boesch 1991; Boesch et al. 1994) or why a given pattern is habitual in one population, rare in another, and totally absent in yet others (but see Nishida & Uehara 1980; Nishida 1987, 1991; Chapman & Fedigan 1990; McGrew 1992), it is only probable rather than demonstrated that social learning of some kind plays an important role in the development and diffusion of primate 'traditions'.

Observations by Hauser (1988) of vervet monkeys, *Cercopithecus aethiops*, in Amboseli National Park in Kenya that, like chimpanzees at Bossou and Gombe (Goodall 1986), use plants as sponges may provide some hint as to how such behaviours might originate and spread (but see Kitahara-Frisch & Norikoshi 1982). Details of the conditions under which diffusion of the sponge-using behaviour occurred are consistent with the hypothesis that most vervets learned to use sponges by observing the behaviour of conspecifics. Boesch (1991) has proposed that adult chimpanzees at Tai actively teach their young to use hammers and anvils to break open nuts, but it is difficult to know how this or any other idiosyncratic behaviour observed in the wild develops (Galef 1984, 1996b).

Byrne & Byrne (1993) have shown that when the feeding behaviours that free-living gorillas, *Gorilla gorilla*, use to eat each of four major food types are analysed by human observers as a series of subgoals carried out in logical order, essentially all gorillas use the same basic techniques, although with variations. For example, when eating nettles gorillas: (1) accumulate a bundle of leaves; (2) detach stinging petioles from the leaf blades; (3) fold the leaves so that the least noxious surfaces face the lips; and (4) ingest the leaves. Byrne (1996) has suggested that such food-handling procedures are learned socially by imitation at the level of the logical structure of the task. However, as Whiten (1996) has pointed out, there is as yet no reason to believe that each gorilla does not learn the logical pattern of feeding on various foods by either trial and error or some social learning process other than 'program-level' imitation.

That apes may learn to process food by imitating a sequence of actions used by others is suggested by recent studies showing that chimpanzees may learn by



observation not only what actions to use but also in what order those actions should be performed (Whiten et al. 1996; Whiten 1998). Whether such copying of motor patterns represents 'true' imitation remains open to debate, as does the definition of 'true imitation' itself. In any case, in chimpanzees observation of others penetrating the mechanical defences of some edible object can facilitate penetration of those defences by the observer.

### Summary

Evidence of an important role for social learning of various kinds in development of efficient patterns of foraging is overwhelming. While in the womb (Hudson & Altbacker 1994), suckling (Galef & Sherry 1973), weaning (Galef 1977) or foraging as an adult (Galef 1988), information extracted from conspecifics provides individuals with at least partial answers to the questions of when, where, what and how to eat. Although in many cases we do not yet know precisely how such social information is acquired or how socially acquired information is integrated with individually acquired information, there can be no question that public information of various kinds influences the ways in which individuals acquire food.

## FUNCTIONS OF SOCIAL FORAGING

In the second part of this review, we explore the consequences of using public information (i.e. information resulting from exposure to the behaviour of others) while foraging as well as information acquired privately. We also discuss methods used to determine under what ecological circumstances use of public information should be most beneficial to foragers.

### When to Eat

The problem of when to eat has two facets: 'tracking' and 'assessment'. In situations involving tracking, a previously depleted resource recovers unpredictably, and foragers must engage in sampling to determine if and when a resource has recovered. In assessment, a forager determines when it is best to abandon a depleting patch and search for a new one. We discuss each in turn.

#### Tracking

Economic models of tracking (Stephens 1987; Tamm 1987; Shettleworth et al. 1988) predict that the optimal frequency at which an unpredictably fluctuating patch should be sampled depends on the amount of food available when the patch is in the 'good' state and the frequency of alternation between states. Although economic models are qualitatively successful at predicting sampling by solitary foragers, a game-theoretic approach is required to predict tracking by animals using socially acquired information to determine the current state of a patch (Krebs & Inman 1992).

In the social tracking game proposed by Krebs & Inman (1992), sampling a fluctuating patch is assumed to be costly, whereas information acquired from observing the

behaviour of a sampling companion is not. Analysis of Krebs & Inman's two-person game leads to the prediction that each of two outcomes is equally likely: either 'player A' samples a variable patch at the optimal rate for a solitary forager, and 'player B' never samples, instead relying solely on public information acquired from player B, or the reverse.

There is empirical support for the Krebs & Inman (1992) model. Starlings, *Sturnus vulgaris*, foraged individually in an experimental arena containing two operant devices (Inman 1990, cited in Krebs & Inman 1992). One device acted as an unpredictably fluctuating patch; the other provided an unchanging, but low, level of reward. When starlings were placed in pairs in the apparatus, one sampled the fluctuating alternative just as it did when alone and the other ceased to sample, relying entirely on its companion's sampling just as predicted by models based on game theory. When a light signalled the state of the fluctuating patch so that no sampling was required to assess it, both birds ceased sampling and went to the fluctuating patch only when the light signalled that it had recovered. The results of these experiments provide preliminary evidence that starlings will use social sampling strategies to enhance their foraging efficiency.

If, as the results of Inman's model and experiment suggest, a few members of foraging groups actually sample a fluctuating patch, then groups of foragers may often have access to little more information than solitary foragers. If so, the conclusion that public information usually provides a substantial advantage to social foragers (e.g. Clark & Mangel 1984; Valone 1989) needs to be re-evaluated.

In an alternative model developed by economists, public information can be copious but lead to incorrect decisions by generating 'informational cascades' (Hirshleifer 1995; Bikhchandani et al. 1998). In an informational cascade, personal sampling of a fluctuating patch is very costly, so imitating the choices of others faced with a choice between patches is more profitable than sampling for oneself. When one of two alternative patches is equally likely to be in rich and poor states, observing the successive patch choices of just two others who have chosen independently to exploit the variable patch can induce all subsequent observers to forage there, even if the observers' subsequent personal sampling indicates that the variable patch is in its poor state (Hirshleifer 1995; Bikhchandani et al. 1998). In this particular instance, public information can override personal information completely, inducing long series of incorrect decisions. It is important to explore the applicability of informational cascades to social-foraging systems to estimate the extent to which the short-term profitability of social learning can also lead to long-lived, potentially costly errors.

#### Assessment

An individual can forage more effectively if its decision to leave one patch to search for another is based on information as to the current quality of the patch it is exploiting (Oaten 1977; Green 1980, 1984; McNamara & Houston 1980; Iwasa 1981; McNamara 1982).

Foragers should, therefore, continuously assess the quality of a patch as they exploit it. In fact, solitary downy woodpeckers, *Picoides viridens*, have been shown experimentally to discriminate empty artificial patches from those filled with hidden food. The woodpeckers increased their foraging efficiency by staying longer in patches recognized as containing food than in patches personal sampling indicated were empty (Lima 1984).

Animals foraging in groups can increase their foraging efficiency by using the sampling behaviour of other group members to estimate the quality of the shared patch. Assuming that all group members sampled, Clark & Mangel (1984), and more recently Valone (1989), have proposed that group exploitation of a patch would allow individuals to use information generated by the success or failure of companions to assess the current residual value of a patch with greater speed or accuracy than could be achieved by solitary foragers.

Indeed, there is some experimental evidence that social foragers use public information to assess the value of a depreciating food patch (Templeton & Giraldeau 1996). Using the approach developed by Lima (1984) mentioned briefly above, Templeton & Giraldeau (1996) presented starlings with two patch types: empty patches each of which contained 30 probe sites that were devoid of food, or full patches where three of 30 probe sites contained food. The finding that birds tested individually probed more extensively before leaving a full patch than an empty one suggests that the birds assessed the quality of patches they were exploiting.

The number of probes a subject made before leaving a patch was influenced by the presence of a foraging companion. Starlings probed more holes when a companion probed only a few, and probed fewer holes when a companion probed many. It can be inferred from such a response to public information that the starling's decision to leave a patch was based on a mixture of personal information, acquired as a result of its own probings, and public information, acquired by watching a companion probe.

Further evidence of use of public information was obtained in a field experiment, again with starlings as subjects (Templeton & Giraldeau 1995). Starlings observed outside the laboratory used public information only when they could do so while they themselves were sampling. When the birds foraged in an environment where opaque barriers prevented subjects from simultaneously probing themselves and seeing others probe, they behaved as if they used only personal information to assess patch quality. However, when the barriers were lowered, allowing the starlings to see one another while probing, they behaved as if they used both public and personal information to assess patch quality.

Although use of public information has been documented in starlings, investigations on budgerigars, *Melopsittacus undulatus*, suggested that, although they assessed patch quality, they may not use public information to do so (Valone & Giraldeau 1993). The markedly different outcome of studies of the use of public information for patch assessment by starlings and budgerigars, although preliminary, suggests that investigations to

determine both which species use public information in assessment and which ecological conditions promote use of public information will be of value. How public and private information is integrated when making decisions about patch desertion remains to be determined.

## What to Eat

Public information can be used to increase efficiency of exploitation of either familiar or novel prey. Below, we discuss each in turn.

### Novel prey

Public information could be especially useful when foragers are confronted with novel prey, especially in circumstances where errors in prey selection can have important negative consequences (e.g. ingestion of toxins; Mason 1988). Presumably, animals that learn to recognize their food, especially those that forage on a wide range of food types, should be most likely to commit costly errors and, therefore, should be most likely to benefit from using public information. There has, however, been no systematic survey of the literature to test the hypothesis that dietary generalists are more likely than dietary specialists to use public information when selecting among unfamiliar foods.

Klopfer (1961) proposed that although both conservative and opportunistic foragers might benefit from using public information, the two types of foragers would use socially acquired information differently; opportunistic species would use public information to avoid ingesting noxious foods, whereas conservative species would use such information primarily to include novel items in their feeding repertoires. Klopfer's preliminary support for the hypothesis, obtained with greenfinches, *Carduelis chloris*, as subjects, was deemed inconclusive in a recent reanalysis (Lefebvre & Giraldeau 1996). Mason and colleagues (reviewed in Mason 1988) have shown that red-winged blackbirds, an opportunistic species, learn both to avoid and to include prey by observing feeding responses of conspecifics and that public information led to longer-lasting avoidance than preference learning. Although a number of other studies have provided evidence consistent with the hypothesis that dietary opportunism and gregarious lifestyles are associated with social learning (reviewed in Lefebvre & Giraldeau 1996), a critical reappraisal of the evidence did not find a reliable association among variables (Lefebvre & Giraldeau 1996).

Galef and colleagues have accumulated considerable experimental evidence regarding behavioural mechanisms that support the use of public information by rats when selecting a novel food to eat. Unfortunately, no amount of exploration of behavioural mechanisms supporting social learning in a single species can tell us whether use of public information in acceptance of novel foods is adaptive. To answer such functional questions, comparative analyses are needed, and no systematic comparative analysis of public information use by mammals has yet been undertaken, although preliminary results suggest that a number of rodent species may use similar

behavioural mechanisms in learning socially to ingest unfamiliar foods (Valsecchi & Galef 1989; Valsecchi et al. 1996).

### *Familiar prey*

Formal models of diet selection by individuals have considered the consequences of having to learn both which prey types were available and their relative abundances (Getty & Krebs 1985; Getty et al. 1987). However, no model of social diet selection has yet included public information, although a few empirical studies have documented apparent social effects on diet choice. Inman et al. (1987) reported that pigeons, *Columba livia*, in the presence of a conspecific feeding from an assortment of seeds, tend to shift their seed preferences so as to reduce dietary overlap. Robichaud et al. (1996) have both confirmed this result and demonstrated that the effect is influenced by dominance relations. Murton (1971) reported the opposite for wood pigeons, *Columba palumbus*; new flock members tended to choose to forage on the type of prey selected by other flock members. Unfortunately, neither study provided strong evidence that the social effects were a consequence of use of public information rather than of relative availability of alternative food items. Stronger evidence would require experiments demonstrating social effects while controlling for resource availability.

### **Where to Eat**

Food is often difficult to find, and public information about food location can be beneficial, allowing its users to feed from patches with little investment in searching. Useful public information can be obtained at a feeding site, or more rarely, at a roost or breeding site that serves as an 'information centre' (Ward & Zahavi 1973). We first consider information transfer that occurs at a feeding site and then explore the issue of information centres.

#### *Information transfer at a feeding site*

Animals are often attracted to areas where conspecifics are active. For instance, McQuoid & Galef (1992, 1993) have shown that Burmese fowl are attracted to a place where another bird was seen feeding for as long as 48 h after observation. More generally, feeding individuals are often joined by companions attempting to gain a share of the resources others have uncovered (for reviews see Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000).

The question we ask here is what ecological circumstances promote the use of information concerning where to forage that is provided by feeding conspecifics. One commonly invoked benefit of joining successful foragers at a feeding site is that joining allows a forager to partake in a companion's discovery, increasing the number of food clumps an individual can exploit and, perhaps, increasing its foraging rate, while also decreasing its chances of not encountering any food at all (Krebs et al. 1972; Caraco 1981; Caraco & Giraldeau 1991; Wilkinson & Boughman 1999; Giraldeau & Caraco 2000). Individuals could look for foraging companions while

searching for their own food. Alternatively, searching for one's own food and searching for feeding conspecifics could be behaviourally incompatible activities.

It has been proposed that the latter case would give rise to a 'producer-scrounger' game where 'producer' searches for food and 'scrounger' searches for others who are feeding (Barnard & Sibly 1981; Caraco & Giraldeau 1991; Vickery et al. 1991). In formal models of the producer-scrounger game, individuals can alternate between the two search strategies, but always play one at the expense of the other. Optimal solutions are frequency dependent; the greater the proportion of the population scrounging, the less profitable scrounging is as a strategy. The stable equilibrium frequency of the two strategies (Mottley & Giraldeau 2000) changes with different foraging conditions and group sizes. Looking for feeding conspecifics to join may not, therefore, be a fixed, universally employed behaviour, but a strategic behavioural decision designed to maximize foraging efficiency.

In small, captive flocks of spice finches, *Lonchura punctulata*, the observed frequency of joining a group at a food patch changed with seed distribution in a way that was qualitatively consistent with predictions of formal models of the producer-scrounger game (Giraldeau & Livoreil 1998). Similar qualitative support of flexible joining has been obtained with small flocks of starlings (Koops & Giraldeau 1996).

Such effects provide only indirect support for the hypothesis that individuals adjust the intensity with which they search for feeding companions in response to changes in the payoffs for adopting this strategy. Birds could, for instance, maintain a constant investment in searching for opportunities to join others, but respond to changes in joining opportunities caused by changes in patch richness or interpatch distances. Direct evidence of strategic searching for companions requires measurement of searching effort directed at companions. A recent study of captive flocks of spice finches provides such evidence.

Coolen et al. (in press) report that the probability of an individual joining a feeding flock is predicted by the frequency with which it hops with its head pointed either at or above the horizon. Conversely, the frequency with which an individual discovers its own food is predicted by the frequency with which it hops with its head pointed below the horizon. When seed distribution is changed, there are changes not only in frequency of flock joining, but also in head position while hopping. Hopping with the head pointed at or above the horizon is not seen when foraging conditions call for no joining at all. So at least in spice finches, the behaviour of 'looking for companions' responds to foraging conditions, and acquisition of public information is used strategically to increase foraging efficiency.

#### *Transfer at an 'information centre'*

A breeding colony or roost serves as an 'information centre' when individuals that have been unsuccessful at finding food return to such a centre and follow successful foragers on subsequent trips from the centre to a food patch. Until very recently, the information centre

hypothesis had not been formally modelled (Mesterton-Gibbons & Dugatkin 1999; Barta & Giraldeau, *in press*; but see Wilkinson & Boughman 1999). Consequently, it has frequently been tested and rejected on the basis of deductions that are less than rigorous (Barta & Giraldeau, *in press*).

In a formal model, applying only to breeding colonies, information transfer at a colony site was analysed as a producer–scrounger game (Barta & Giraldeau, *in press*). Birds could search for food (play producer) or return to the colony and wait for a successful forager to return to feed its young (play scrounger). The model predicted that the evolutionarily stable solution (ESS) has very few individuals in a colony playing producer. One would, therefore, predict that instances of information transfer will be relatively rare in an information centre operating at the ESS. Consequently, the information centre hypothesis cannot be refuted on the basis of infrequent observation of information transfer at a colony site. The model leads to the further conclusion that observed frequencies of information transfer lower than the frequencies with which colony members produce information would convincingly refute the information centre hypothesis (Barta & Giraldeau, *in press*).

### Learning How to Eat

Little effort has been devoted to exploring the ecological circumstances that promote learning how to forage (Dukas 1998). It is unfortunate that learning of motor skills used in foraging, the most studied component of social learning from a psychological perspective, is also the least studied component of social learning from an ecological perspective. Attempts to develop an ecology of learning are recent (Shettleworth 1984, 1999; Dukas 1998). Although specific models diverge, they generally predict that learning should be selectively advantageous only when environmental change is slower than the learning rate (Bernstein *et al.* 1988; Dukas 1998). Such qualitative predictions concern conditions promoting learned rather than instinctive responses, but are not informative as to the conditions that promote social rather than nonsocial learning. The latter are still a subject of some debate.

Boyd & Richerson (1985, 1988) have modelled the evolution of social versus nonsocial learning as a function of rates of environmental change. When environments change very slowly, genetic transmission is optimal and no learning is favoured (Laland *et al.* 1997). When the rate of environmental change is slow, only social learning is optimal. However, when the environment changes rapidly, dependence on social learning prevents effective tracking of environmental change, so only individual learning is optimal. A mixture of social and individual learning is expected at intermediate rates of environmental change.

Assuming that the majority of environments change at intermediate rates, an assumption difficult to verify, models like Boyd & Richerson's (1985, 1988) predict that social learning should be widespread. On the basis of such models, the scant instances of social learning of motor

skills used in feeding observed in free-living animals is unexpected. Either there are hidden costs to social learning of motor skills, possibly involving the development and maintenance of cognitive structures to support such activities (Laland *et al.* 1997), the speed with which environments change for most animals is relatively high, or social learning may be necessary only when social circumstances make the usual mechanisms of individual learning ineffective (Giraldeau *et al.* 1994). For example, scramble competition for divisible foods reduces each individual's likelihood of discovery and hence the evolution of learned patch discovery skills (Giraldeau 1984). Social learning can evolve despite such reduced opportunity to discover patches for one's self because information generated by companions can be used instead (Giraldeau *et al.* 1994). Sibly (1999) has proposed an alternative approach to modelling the evolution of social learning as a coevolutionary process involving 'receivers' (observers) and 'transmitters' (tutors). He explored a number of factors such as relatedness that promote social learning and predicted that, in many circumstances, evolution should produce polymorphic receivers.

Testing adaptive hypotheses concerning social learning of motor skills can be conducted in either of two ways. First, identification of a small number of species able to learn motor skills socially would permit exploration of conditions under which individuals do and do not show social learning of motor skills. Unfortunately, at the moment too few species have been studied in sufficient detail to allow such studies to be conducted. Alternatively, an extensive sample of species that can and cannot acquire motor skills socially would allow us to compare the ecological niches of species of each type. Again, no such sample is currently available, and obtaining the requisite data would be a colossal task that would yield results only in the long term.

A possible alternative approach to determining which species can and cannot acquire motor skills socially is to use records of feeding innovations, such as that compiled by Lefebvre *et al.* (1997b) for birds. Innovation in feeding technique is a necessary first step in social transmission of new foraging skills (Laland & Reader 1999). A comparative survey of ecological characteristics of bird species reported to innovate could provide an important clue as to circumstances that favour rapid acquisition of new foraging techniques.

### Summary

We know little about the ecological circumstances that promote learning over nonlearning, and even less about ecological circumstances promoting social over nonsocial learning. A single formal model of social tracking of food resources has been tested once with some qualitative success, suggesting that public information about when to eat is used more frequently when private information is costly than when it is cheap. Complementary conclusions have been reached concerning assessment of patch leaving: use public information in patch-leaving decisions only if acquiring public information about



patch quality does not prevent acquisition of private information. Verbal models of what to eat exist, but there are no formal hypotheses about relative advantages of public and private information in diet selection.

Game-theoretical models predict when foragers ought to use public information in deciding what to eat, and these models are supported by a few recent experiments with feeding flocks. However, little support has yet been provided in natural settings for information centres, where individuals obtain information from others at a distance from a feeding place. There are some formal hypotheses about when public information should play a role in learning how to eat, but available data are insufficient and predictions from the models are difficult to test.

The emerging behavioural–ecological approach to social learning highlights the negative frequency dependence of pay-offs resulting from use of public information. This negative frequency dependence, evident in both producer–scrounger and information centre games, but possibly common to most instances of social learning, carries the implication that the initial advantage of social over individual learning causes the trait to spread. However, once social learning has reached ESS levels, the resulting frequency dependencies may result in social learning being no more useful than individual learning. Consequently, animals using social learning today may be doing so not because net benefits of social learning are greater than those of individual learning, but because using social information is an ESS. Such frequency dependence should result either in only a subset of a population being able to learn socially or a population all of whose members are capable of social learning, but only some of which do so at any given time.

## CONCLUSIONS

In the study of social learning, as in contemporary study of many other aspects of animal behaviour, there is a tension between causal and functional approaches. In studies of causation, the approach is generally ‘bottom-up’. An investigator begins by discovering a potentially interesting behavioural characteristic of some animal then analyses the behavioural or physiological processes that initiate, direct and maintain it. The direction an investigation takes is driven primarily by the behaviour itself, although theoretical considerations often play an important role in determining which aspects of the behaviour are explored.

Studies of function, on the other hand, tend to be ‘top-down’. An investigator becomes interested in an adaptive characteristic of some behaviour, constructs a formal model to determine the conditions under which the proposed functional pattern of behaviour should be observed, and then looks to see whether animals behave as predicted by the model, using feedback from empirical investigations to improve the model itself. In such cases, empirical investigation is driven by the model, although studies of behaviour shape the model’s development.

Practitioners of the bottom-up approach are often wary of the top-down method, suggesting that history

shows that models are frequently superseded by improved variants, and experiments designed to test discarded models are rarely of interest. On the other hand, a fact of interest is of interest forever (e.g. the dance of honeybees (Lindauer 1961; Gould & Gould 1988) is fascinating, whatever the current state of models or theories of central-place foraging).

Those using a top-down approach are concerned that without organizing theory and formal quantitative predictions, empiricism produces a mass of facts lacking coherence or generality. Researchers using top-down approaches propose that only that approach can produce a systematic, cohesive body of knowledge. For example, as pointed out above, even 30 years of investigation of social foraging in Norway rats cannot provide the type of data that would be of greatest interest to modellers of the ecology of social learning.

The current lack of integration between top-down and bottom-up approaches to the study of social learning may appear to be a potential source of conflict and confusion. We view the existing tension more positively. As practitioners of bottom-up analyses sharpen their abilities to test hypotheses and proponents of top-down approaches produce formal models that are increasingly amenable to empirical test, the possibility of creative syntheses can only increase. Construction of an enduring scientific edifice requires the contribution of both ‘architects’ and ‘bricklayers’.

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