Public information for the assessment of quality: a widespread social phenomenon

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We propose that the use of public information about the quality of environmental resources, obtained by monitoring the sampling behaviour of others, may be a widespread social phenomenon allowing individuals to make faster, more accurate assessments of their environment. To demonstrate this: (i) we define public information and distinguish it from other kinds of social information; (ii) we review empirical work demonstrating the benefits and costs of using public information to estimate food patch quality; (iii) we examine recent work showing that individuals may also be using public information to improve their estimates of the quality of such disparate environmental parameters as breeding patches, opponents and mates; and finally (iv) we suggest avenues of future work to better understand the nature of public information use and when it might be used or ignored. Such work should lead to a more complete understanding of the behaviour of individuals in social aggregations.

Keywords: breeding patch assessment; eavesdropping; fighting; mate choice copying; sociality; vicarious sampling

1. INTRODUCTION

Animals make almost continuous, fitness-related decisions during their lives, such as where to live (habitat choice, migration), with whom to interact (territorial or resource contests, mate choice) and what to eat (diet choice, patch exploitation). Thus, understanding the behaviour of individuals requires an understanding of how animals make decisions. Much early theoretical work in behavioural ecology assumed individuals possessed perfect information about their environment (e.g. Charnov 1976). Subsequently, a growing trend has been to focus more directly on information acquisition and the decision-making process (e.g. Krebs & Davies 1997).

Within the field of foraging behaviour in particular, much work has been devoted to understanding how individuals make various types of foraging decisions (Stephens & Krebs 1986). Most of this work has focused on how individual foragers use information to estimate the quality of food patches. Solitary foragers can derive food patch estimates by obtaining personal sample information during patch search and exploitation (Valone 1991). Social foragers, however, have access to an additional source of information that is not available to solitary foragers: this information is known as 'public information' (Valone 1989). Specifically, public information is sampling information acquired vicariously by monitoring the sampling behaviour of others (Templeton & Giraldeau 1996; Giraldeau *et al.* 2002).

Although the notion of public information was orig-inally developed in the context of food-patch quality esti-mation and patch departure decisions, we propose that the concept is widespread: individuals in a variety of ecologi-cal contexts can obtain information from observing the sampling behaviour of other individuals, and thereby improve their estimates of the quality of numerous aspects of their physical and social environment. In this synthetic review, we first describe public information in more detail and distinguish it from other forms of social information. We then document the growing evidence that public infor-mation use may occur in a variety of contexts in addition to foraging, including estimation of the quality of breeding sites, opponents in contests and potential mates.

Public information can provide unique benefits to indi-viduals in social aggregations by providing information to reduce both estimation time and uncertainty about environmental quality. We demonstrate how an appreci-ation of the existence of public information can provide insight into poorly understood behaviours and show that public information is emerging as a key component in our understanding of how animals make decisions in numer-ous areas of behavioural ecology. As such, public infor-mation may provide a general, widespread benefit to individuals in social aggregations. Finally, we suggest potentially productive avenues for future research to better understand how individuals in a variety of social situations acquire information and make profitable decisions.

2. PUBLIC INFORMATION AND OTHER FORMS OF SOCIAL INFORMATION

(a) *Definition of public information*

Solitary foragers can derive their estimates of food patch quality from information or knowledge the forager has acquired prior to its arrival at the current patch ('pre-har-

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vest' or 'prior' information (Valone 1989)), and from directly sampling the patch. While patch estimates can be generated from either source of information, estimation accuracy tends to increase with the amount of information used and empirical work indicates that foragers can combine both sources of information to generate patch estimates while making patch departure decisions (e.g. Valone & Brown 1989; Valone 1992; Alonso *et al.* 1995; Olsson *et al.* 1999).

Social foragers can also use public information. By combining the prior and personal sample information with the public information obtained from observing the successful and unsuccessful sampling activities of others, an individual can estimate patch quality faster and more accurately. This results in more efficient resource exploitation and allows foragers to waste less time in unprofitable patches (Clark & Mangel 1986; Valone 1989, 1993; Templeton & Giraldeau 1995a, 1996; Smith *et al.* 1999).

(b) *Distinguishing public information from other forms of social information*

It has long been known that sociality can provide animals with access to a source of information about their environment that is unavailable to solitary individuals: the behaviour of other individuals. This social information can be used in a variety of ways (reviewed by Galef & Giraldeau 2001). For example, it can be used to enhance the recognition of novel prey types, as well as individual learning of novel behavioural traits involved in prey acquisition. The social learning of novel skills has been well documented in a variety of species in both the field and laboratory (e.g. Zentall & Galef 1988). Individuals can also learn about the location of food resources simply by being attracted to other foraging individuals, a process termed 'local enhancement' (e.g. Thorpe 1963; Poysa 1992).

Public information use, therefore, differs from social learning in that it provides information about the quality of an environmental resource, rather than how to obtain it. Public information also differs from local enhancement in two key respects: the point at which the information is obtained, and how the information is used. Unlike local enhancement (where social information is obtained before an individual arrives at a patch), public information is obtained after the forager has already entered the resource patch. Public information thus allows a forager to assess more accurately the quality of a resource patch and to decide whether to stay or depart; local enhancement, on the other hand, simply allows a forager to detect the presence or absence of a resource patch and thus to approach or not (but see Smith *et al.* 2001).

We suggest that the term 'public information' be restricted to vicarious sampling information obtained from others about the quality of an environmental resource. We believe it is important to emphasize this point because some researchers have recently expanded the use of the term to include any information obtained from others such that all forms of social learning involve the use of 'public information' (e.g. Giraldeau 1997; Giraldeau & Caraco 2000; Galef & Giraldeau 2001). However, this broader use of the term is not consistent with its original definition (Valone 1989) and, to us, obscures the unique aspect of public information as an extra source of sample information used both to increase the rate of assessment and to reduce uncertainty about the quality of an environmental resource. Instead, we propose that the more general term 'social information' be used to refer to any information obtained from observing the behaviour of others (Giraldeau *et al.* 2002).

3. EMPIRICAL EVIDENCE OF PUBLIC INFORMATION USE IN A FORAGING CONTEXT

Two predictions derived from models of public information use have been the focus of explicit empirical tests (Valone 1989). The first prediction involves how foraging success within a patch affects the order of patch departure by individuals when patch departure is determined only by an individuals' estimate of patch quality. In environments in which resources have a clumped distribution, the more successful a forager is within a patch, the higher its estimate of patch quality (e.g. Iwasa *et al.* 1981). When a group of foragers exploits a patch in such an environment and does not use public information, then the least successful foragers in a patch will have the lowest estimates of patch quality and therefore should depart from the patch before more successful foragers (Valone & Giraldeau 1993). If, however, all individuals in the group obtain public information from each other and weigh this equally with personal information, then all individuals will possess the same information about patch quality and thus possess identical patch estimates. When public information is used, therefore, individual foraging success of group members within a patch is not related to an individual's patch estimate and hence to the order of patch departure (Valone 1989). Thus, all individuals in the group are expected to depart from the patch at approximately the same time. The second prediction of public information use is that a group of foragers using public information should abandon an empty patch faster than a solitary forager, and faster than a group of individuals not using public information: a group of N individuals using public information collects information N times faster than a solitary forager or a group of individuals not using public information (Clark & Mangel 1986).

Templeton & Giraldeau (1995a) examined the predicted relationship between foraging success and order of patch departure for small flocks of free-living starlings (*Sturnus vulgaris*). In this field experiment, they manipulated directly the ability of birds to obtain public information by varying the location of food within cups: when food was deeply recessed, individuals could not observe the foraging success of others on the patch and so public information was not available; when food was not recessed, public information was available because foragers on the patch could observe when others found food. Templeton and Giraldeau found that when public information was not available, the least successful foragers departed first as expected. When public information was accessible, however, individual foraging success on the patch was no longer related to the order of patch departure, as predicted for the case of public information use.

In a second empirical test, Templeton & Giraldeau (1996) allowed captive starlings to forage on artificial 30-hole patches that were either completely empty or contained only a few food items hidden in the holes. This meant that a bird had to sample several empty holes before

deciding that the patch was empty. After solitary trials during which subjects acquired prior information about the distribution of food among patches, the birds were tested on a completely empty patch in each of three conditions: (i) alone (with a non-sampling partner); (ii) with a low information partner that sampled only a few holes; and (iii) with a high information partner that sampled all the holes in the patch. Subjects sampled fewer empty holes when with partner birds than when alone; but most importantly, they sampled fewer empty holes when with a high information partner than when with a low information partner. Thus, the starlings combined the unsuccessful public information from the partner birds with their own unsuccessful personal sampling information to recognize and depart from an unprofitable patch more quickly.

Smith *et al.* (1999) have conducted a similar set of experiments using captive red crossbills (*Loxia curvirostra*). They examined the sampling behaviour of focal crossbills exploiting empty patches (artificial trees containing pine cones with or without hidden seeds) paired with a non-foraging partner (i.e. 'solitary'), or paired with one or two other foragers. They found that focal birds in trios spent significantly less time and sampled fewer empty cones than birds exploiting patches as solitaires or in pairs. In other words, birds in groups of three apparently used public information about the lack of foraging success to reduce time spent on unprofitable patches.

Smith *et al.* (1999) also altered the type of public information available to the focal bird. Specifically, they manipulated the quality of the two halves of a patch so that the focal bird and the two partner birds could realize different levels of foraging success on the same patch. When the tree contained no food (information on the two sides of the patch was similar) focal birds in foraging groups departed from the tree faster than when they fed alone. But when the partner birds found food on their half of the tree, the focal bird would visit more cones on its half of the tree even though it never found food. In other words, the fact that individuals feeding on the same patch were finding food led the focal bird to continue unsuccessfully sampling the tree. Furthermore, when the focal bird was successfully finding food, but none of the partner birds was successful (because their half of the tree contained no food) the focal bird would leave the patch sooner than when its partners also found seeds. Thus, Smith *et al.* demonstrated how the performance of other group members (i.e. public information) affected the patch quality estimates of individuals.

The above experiments provide evidence that individuals use public information to generate estimates of the quality of food patches. We now demonstrate how public information has been, or can be, applied to other social settings in which individuals make assessments of environmental parameters such as breeding patches, potential mates and opponents.

4. EXTENSIONS OF PUBLIC INFORMATION USE

(a) *Estimating the quality of breeding habitat via prospecting for public information*

The quality of a breeding site can strongly influence fitness (e.g. Cody 1985) and therefore individuals can benefit by generating accurate estimates of the quality of a potential breeding site (Badyaev *et al.* 1996). The use of public information to assess breeding patch quality has been modelled for colonial nesting birds by Boulinier & Danchin (1997).

The model of Boulinier & Danchin (1997) (B&D model) envisions an environment that consists of breeding patches differing in quality. Breeding sites within a breeding patch are unlimited and equivalent in quality so that individuals only need to assess breeding patch quality. Boulinier and Danchin explore two ways in which individuals can assess breeding patch quality. Individuals can use their own past individual reproductive success or, they can assess patch quality by noting the reproductive success of other breeders in the patch. In other words, individuals can rely solely on personal sample information (their past efforts in the patch) or they can also use public information (the success of others in the patch) to estimate breeding patch quality. First-time breeders obviously cannot use their own past efforts and so they must either rely on public information to assess breeding patch quality or randomly select a breeding patch. Boulinier and Danchin show that when breeding patches differ in quality but exhibit positive temporal autocorrelation, individuals realize higher lifetime reproductive success by using public information to estimate breeding patch quality for future nesting decisions than if they did not use such information. This later assumption is critical: if breeding patch quality does not exhibit positive temporal autocorrelation, public information about patch reproductive success in one year would have no value for estimating breeding patch quality in the next year.

The B&D model makes several predictions about the use of public information to estimate breeding patch quality: (i) individuals should attempt to obtain public information about the reproductive success of different breeding patches at the end of a breeding season; (ii) individuals that obtain such information should breed next year in a patch that had higher than average success; and (iii) the decision to move to a new breeding patch or to re-nest in the same patch next year should be a function of the average reproductive success of individuals in different patches, i.e. the quality of all potential breeding patches should be assessed using public information. Thus, individuals that change their breeding patches from one year to the next should move to a patch that had a higher average patch reproductive success than the patch in which they bred this year.

Indirect empirical support for the model comes from a variety of sources. Prospecting behaviour occurs in many colonial nesting birds and prospecting individuals often visit many colonies (Reed & Oring 1992; Boulinier *et al.* 1996; Reed *et al.* 1999; Brown *et al.* 2000). This behaviour involves travelling over a colony and even sitting on the nests of other individuals (Cadiou *et al.* 1994). Prospecting tends to occur near the end of the breeding season when the most accurate information about average patch reproductive success is available (Boulinier *et al.* 1996). In addition, prospecting behaviour has been shown to be related to future breeding behaviour. Schjorring *et al.* (1999) showed both that new breeding cormorants (*Phalacrocorax carbo*) which had prospected actively in the previous year, had higher breeding success than individ-

uals which did not actively prospect, and that prospecting behaviour was concentrated at the end of the breeding season after eggs hatched but before chicks fledged. Thus, the function of prospecting behaviour may be to gain public information about average patch reproductive success of different locations to decide where to breed in the future (Danchin & Wagner 1997).

More direct support comes from three studies that have explicitly tested the B&D model. In the first, Danchin *et al.* (1998) examined year-to-year nesting decisions of colonial nesting kittiwakes (*Rissa tridactyla*). They first demonstrated that breeding habitat quality was fairly consistent from one year to the next, i.e. it exhibited positive temporal autocorrelation. They then focused on cases where personal and public information provided different information about sub-colony (breeding patch) quality. In particular, Danchin *et al.* examined the nesting decisions of birds that experienced a nest failure in one reproductive season. Typically, individuals that experience a nest failure (i.e. low individual reproductive success) are more likely to abandon their breeding site and nest elsewhere in future breeding attempts (e.g. Marzluff 1988; Switzer 1997). A colony nester that experiences a nest failure obtains personal information that indicates a breeding patch is of low quality. If such an individual only uses personal information to assess patch quality, it should move to a new patch for future breeding. However, nest failures can also occur for individuals that breed in high quality patches. Such individuals should not move to a new breeding patch because of the likelihood that they will move to a patch of lower quality (Boulinier & Danchin 1997). Thus, colony nesters that experience a nest failure but use public information to estimate patch quality should decide to re-nest in the same patch following a nest failure, when the overall reproductive success of their breeding patch is high. Danchin *et al.* (1998) found this to be true: individual kittiwakes that had low individual reproductive success tended to re-nest in the same patch when the reproductive success of others in the breeding patch was high. Such behaviour is consistent with the idea that individuals used public information about breeding patch quality to decide whether to remain at the same breeding site after an unsuccessful breeding attempt.

In a second test of the B&D model, Brown *et al.* (2000) examined the breeding decisions of colonial nesting cliff swallows (*Pterochelidon pyrrhonota*). After first documenting a positive temporal autocorrelation in breeding site (colony) quality they examined factors that affected the re-nesting decisions of individuals. Sites where individuals had the highest reproductive success showed the highest increase in colony growth, which was due in large part to immigrants. In addition, the probability of a site being re-used the following year was significantly influenced by colony-wide reproductive success: colony-wide reproductive success was higher at sites re-used the next season compared with sites not re-used (Brown *et al.* 2000).

The third explicit test found no evidence for public information use, but it too, lends support to the B&D model. Erwin *et al.* (1998) found no evidence that gull-billed terns (*Sterna nilotica*) used colony-wide reproductive success for breeding site selection. However, in their study, breeding sites did not exhibit positive temporal autocorrelation in quality and so individuals were not predicted to use public information.

While the B&D model was originally conceived for colony nesting species, its application need not be so restricted. For non-colonial breeders, a breeding patch is a nest location or territory. Provided that breeding sites are distributed in distinct patches that differ in quality, and such patches exhibit positive temporal autocorrelation in quality, individuals can benefit by acquiring and using information about patch reproductive success.

Two studies of non-colonial species document behaviour consistent with the idea that individuals prospect to obtain information about the quality of nest sites for future breeding. Zicus & Hennes (1989) showed that common goldeneyes (*Bucephala clangula*) investigate nest cavities of other individuals during the breeding season, and during the next breeding season preferentially used cavities from which young had fledged the previous year. In addition, Doligez *et al.* (1999) found that the behaviour of collared flycatchers (*Ficedula albicollis*), a non-colonial, cavity-nesting species, was consistent with the model. Here, patches consist of different woodlots, and these woodlots exhibited positive temporal autocorrelation in quality (patch-wide reproductive success). They showed that breeding dispersal (movement out of a woodlot) was strongly affected by patch-wide reproductive success: adult females tended to re-nest in woodlots with high patch reproductive success.

Thus, a growing literature supports the idea that individuals use, and benefit from, public information about breeding patch quality by observing the reproductive success of individuals in different breeding patches. While some of the above studies were specifically designed to test the hypothesis of public information use, others were not, and as such, can only provide data consistent with the idea that individuals use information from the activities of others to improve their estimates of the quality of environmental parameters. However, because public information *per se* was not manipulated directly, alternative explanations exist for the above observations and we explore one possible alternative theory: independent assessment of breeding habitat quality.

The independent assessment theory posits that all individuals independently estimate the quality of a resource and all evaluate the resource similarly. For example, recall that common goldeneyes preferentially nested in a subset of the cavities they visited the previous year—those that fledged young the previous year (Zicus & Hennes 1989). One explanation is that individuals prospected for information about cavity quality and the presence of fledglings indicated high quality cavities that were then used the next year. An alternative explanation is that the birds were independently assessing some other aspect of the nest site that exhibited temporal consistency, such as cavity size or location, to determine its quality rather than the presence of fledglings.

How could one distinguish public information use from independent assessment in this example? Manipulation of public information (fledgling success, in this case) makes predictions about how individuals will evaluate the quality of a cavity. Thus, in year 1, the quality of all cavities could be determined by recording fledgling success. Assuming temporal consistency in quality, one experimental protocol would be to artificially reduce fledgling success in 50%

of the high quality cavities before prospecting behaviour occurs. If prospecting birds use fledgling success to estimate cavity quality, the manipulated cavities should be avoided the following year, whereas if individuals are using other (abiotic) cavity properties to estimate cavity quality, they should not be avoided the following year. Future work on public information use in breeding habitat assessment should manipulate public information directly to test the B&D model.

(b) Opponent assessment and public information

A second application of the concept of public information involves the assessment of opponents. Individuals of many different species engage in contests with each other over resources such as territories, nest sites and mates. In such situations, individuals are not assessing the quality of an environmental resource *per se*, but rather must assess the quality of their opponent in order to determine how much time and effort to exert in a particular contest. Contests often take the form of an escalating sequence of ritualized displays and contact behaviours during which each competitor assesses the fighting ability of the other, a process referred to as sequential assessment (Enquist et al. 1990; Koops & Grant 1993). Each stage of sequential assessment provides an individual with information about the condition, size and strength of the opponent, and this personal sampling information can be acquired through visual, tactile or auditory cues (Clutton-Brock et al. 1979; Enquist et al. 1990).

Acquiring information about the fighting ability of a competitor is time consuming, energetically costly, and can entail a risk of injury (Huntingford & Turner 1987). One way in which individuals can obtain sampling information about the fighting ability of potential opponents is by observing contests between other individuals before becoming involved in an actual contest (Freeman 1987). In other words, individuals can benefit by collecting public information via 'eavesdropping' (Johnstone 2001; Peake et al. 2001).

Freeman (1987) examined this idea by staging contests between focal red-winged blackbirds (*Agelaius phoeniceus*) in the presence of neighbouring birds. Freeman measured both the behavioural response of a resident, and the subsequent changes in territory area to either a non-threatening intruder, an Eastern kingbird (*Tyrannus tyrannus*) model or a threatening intruder, a male red-winged blackbird model. He found that none of 12 males threatened by a kingbird lost territory area to neighbours while 8 out of 27 residents threatened by a red-winged blackbird subsequently lost territory area to neighbours. The key factor that correlated with the loss of territory area was the fighting intensity of the resident to the staged intruder: 6 out of 12 males that only weakly attacked the intruder lost area while only 2 out of 15 males that vigorously attacked the intruder lost territory area to neighbours. In addition, only 1 out of 29 control residents (no staged intruder) lost territory to neighbours. In total, these results suggest strongly that individuals can assess the fighting ability of neighbours by observing contests.

Two recent studies on fishes have tested this theory more directly. Johnsson & Akerman (1998) first allowed subjects (rainbow trout, *Oncorhynchus mykiss*) to observe contests between pairs of fishes (dyads). Dyads were allowed to interact for 48 h and the dominant individual was determined (dominant). Subjects were then paired either with a dominant that they had observed (familiar fish) or with a dominant that they had not observed (unfamiliar fish). In half of all resulting interactions, the subject fish was scored as being more dominant and thus there was no effect of familiarity on contest outcome. However, subjects paired with a familiar fish established a dominance hierarchy in significantly less time compared with subjects paired with an unfamiliar opponent. Thus, the benefit of the public information obtained by watching a dyad contest was that it reduced time spent in subsequent opponent assessment. Oliveira et al. (1998) reported similar findings with the Siamese fighting fish, *Betta splendens*. Subjects that viewed a contest took longer to approach and display to an observed winner than to an observed loser while no such differences were noted when subjects interacted with winners and losers that had not been observed previously. Thus, in these three examples, the benefit of public information is that individuals more rapidly and more accurately assessed the fighting ability of their opponents, and made profitable decisions based on this information.

Future work to determine the generality of these findings might focus on how often individuals acquire public information about potential opponents before engaging them in a contest. Such behaviour should be advantageous both because the initial stages of the contest should be shortened, thus reducing the cost of the contest, and because seeing the outcome of a contest may allow the observer to avoid a fight altogether. These predictions could be tested in a variety of species by manipulating the amount of time a naive individual spends observing a contest between two other individuals.

(c) Mate quality assessment and copying behaviour

Public information may also be used for mating decisions. A growing number of studies have reported that the mate-choice decisions of individuals may be influenced by viewing the mating decisions of others (Dugatkin 1992, 1998; Gibson & Hogland 1992). Such non-independent mate choice has been termed 'copying' behaviour (e.g., Losey et al. 1986; Pruett-Jones 1992).

In spite of much theoretical work, the costs and benefits of copying are poorly understood (Dugatkin 1996). Suggested costs include increased time to mating, sperm depletion and the possibility of copying a poor mate-choice decision (Gibson & Hoglund 1992••4••). The presumed benefits of copying have been more difficult to determine. Copying can reduce search costs for mates but this benefit may be offset by the additional waiting time to mate. Some workers have proposed that copying may also be beneficial when mate assessment is difficult or when individuals possess informational asymmetries (Gibson et al. 1991; Dugatkin & Godin 1992, 1993). These presumed informational benefits of copying, however, were not formalized to the degree that specific predictions about copying behaviour could be generated (Bikhchandi et al. 1992; Gibson & Hoglund 1992••4••; Stohr 1998).

Nordell & Valone (1998) formalized the informational benefit of mate-choice copying by showing how it may be

a form of public information use. They assumed that mate choice involves estimation of the quality of a resource, potential mates, and considered a single focal female that must simultaneously assess the quality of two potential mates that differ in quality. (This is the standard design of empirical tests of copying behaviour.) If the female can discriminate between their qualities, she should mate with the male of higher quality. If she cannot discriminate between their qualities, the best she can do is to select one male at random. Thus, the female would have a 50% probability of mating with the higher quality male.

If, however, the focal female observes another female assessing the two males, the focal female can benefit in two ways. First, the focal female can obtain public information about the relative quality of the two males by observing their courtship behaviour while they interact with the other female. Second, the focal female can obtain information about relative male quality by observing the mate-choice decision of the other female; that female's decision indicates her personal assessment that the chosen male was of higher quality. The public information obtained by observing the interactions may allow the focal female to discriminate between the two males more easily. If not, the focal female can still benefit by mate-choice copying when the second female can accurately discriminate between the two males (Nordell & Valone 1998).

The public information framework assumes that individuals rely first on their own assessment abilities and copy the mating decisions of others only when their discrimination ability is inadequate (Nordell & Valone 1998). Such a process reduces the possibility that individuals will enter a fitness-reducing, erroneous informational cascade in which individuals only rely on the information obtained from others (Giraldeau et al. 2002). Specifically, this framework predicts: (i) individuals that have poor discrimination ability should often copy the mate choice of others; (ii) individuals with superior discrimination ability should rarely copy; and (iii) copying behaviour should increase as the discrimination task becomes more difficult: when two potential males are very dissimilar, copying should rarely be observed; when two males are of similar quality, copying is more likely.

While specific empirical tests of the public information theory are lacking, other empirical work on mate-choice copying is consistent with these predictions. Most observations of copying behaviour occur when females are presented with experimentally matched (i.e. visually similar) males (Dugatkin 1992; Dugatkin & Godin 1992). When males are not matched, copying is rarely observed (e.g. Brooks 1996). For instance, Dugatkin (1996) demonstrated that the degree of similarity of two potential males affects copying behaviour as predicted by the public information framework: when two males differed by less than 25%, females frequently copied; when two males differed by 40%, females did not copy the mate-choice decision of other females. In addition, young female guppies tend to copy the mating decisions of older females but not vice versa (Dugatkin & Godin 1993). If discrimination ability improves with age and experience, such behaviour is consistent with the predictions of public information use outlined above.

Mate-choice copying has been observed in a growing number of species and, presumably, the behaviour confers some benefit to individuals (Dugatkin 1996). Numerous alternative hypotheses have been proposed to explain copying behaviour (reviewed by Westneat et al. 2000) and so public information use remains one of many possible explanations for non-independent mate choice. However, viewing this behaviour as potentially resulting from the acquisition of public information sheds new light on copying and generates novel predictions about when mate-choice copying should and should not be observed. Further empirical work is now needed to better evaluate this and other hypotheses involving non-independent mate choice (Westneat et al. 2000). For instance, empirical work should examine how the discrimination abilities of individuals influence the prevalence of non-independent mate choice. In addition, future work might examine whether individuals acquire information about the qualities of potential mates simply by observing the courtship behaviour of others rather than by observing both courtship and a mate-choice decision. Allowing females to observe various stages of courtship, but preventing them from observing the final mating decision of another female could test this idea (Giraldeau et al. 2002).

5. THE FUTURE OF PUBLIC INFORMATION

We envision several avenues of future inquiry. Additional studies are required to determine the generality of public information use in a variety of contexts, and to distinguish public information use from alternative hypotheses and other forms of social information (e.g. Smith et al. 2001; Giraldeau et al. 2002). Such work will probably require direct manipulation of the putative public information. Templeton & Giraldeau (1996) and Smith et al. (1999) provide two examples of how such manipulations can be conducted.

We also believe that the theory of public information use requires further sophistication. Public information use will probably be influenced by a variety of factors: if individuals observe each other to acquire information, visual context will affect the use of public information. For instance, individuals in a food patch may not be able to determine when another forager has found food if the handling time of food items is very small (Valone & Giraldeau 1993). Similarly, the value of public information may depend on the cost of acquiring sample information. If accurate personal sample information can be easily acquired, public information may be ignored, especially if the cost of its acquisition is high (Templeton & Giraldeau 1996). This proposal could be tested by manipulating both the cost of acquiring personal information, and the cost of acquiring public information, simultaneously (Templeton & Giraldeau 1995b).

At present, models of public information use assume that public information is simply additional sample information. This means that the sample information generated by an individual is given equal weighting with all public information it obtains. We suspect that this assumption is too simplistic. There may be many situations when a forager would benefit by weighting its own sample information more heavily than any public information it obtains. One case in which this might be true is when an adult obtains public information from a juvenile. Juveniles are often less adept at searching for food (e.g.

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