

# Information and its use by animals in evolutionary ecology

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**Information is a crucial currency for animals from both a behavioural and evolutionary perspective. Adaptive behaviour relies upon accurate estimation of relevant ecological parameters; the better informed an individual, the better it can develop and adjust its behaviour to meet the demands of a variable world. Here, we focus on the burgeoning interest in the impact of ecological uncertainty on adaptation, and the means by which it can be reduced by gathering information, from both 'passive' and 'responsive' sources. Our overview demonstrates the value of adopting an explicitly informational approach, and highlights the components that one needs to develop useful approaches to studying information use by animals. We propose a quantitative framework, based on statistical decision theory, for analysing animal information use in evolutionary ecology. Our purpose is to promote an integrative approach to studying information use by animals, which is itself integral to adaptive animal behaviour and organismal biology.**

## Introduction

Uncertainty poses significant problems in life. For an animal to best exploit potential opportunities and avoid danger, anticipating its environment is crucial. This includes assessing the range of options available to it, the probable consequences of pursuing each option, and the probable behaviour and states of other animals, and so on. However, these key ecological features will seldom be wholly predictable owing to changeable weather conditions, the behaviour of other organisms, or other factors that are out of the direct control and experience of the animal. Therefore, to adjust to changing ecological circumstances, most animals must continuously attempt to reduce uncertainty by gathering information when it is available [1]. Doing so might entail costs however, because animals must redirect valuable resources, including energy and time, to information gathering at the expense of basic biological demands, such as growth and reproduction. Nevertheless, information use is a key feature of

adaptive behaviour and, as so, is central to organismal biology [2].

Explicitly informational approaches are adopted widely and consistently in molecular, developmental and neurobiology (e.g. [3–5]), and draw mainly on communication theory concepts of information (e.g. [6]). Here, information is specified as a numerical measure of the uncertainty of an outcome (Shannon–Weaver entropy; see Glossary), focussing exclusively on its ambiguity-reducing properties. For example, neurobiologists typically measure the productivity of neuronal networks in terms of the signal:noise ratio that those networks transmit [7]. By contrast, work in behavioural and evolutionary ecology has been rather piecemeal, with analyses restricted to different biological contexts, such as foraging, mate choice, navigation and communication in isolation. Moreover, informal use of the term 'information' is the norm, because ambiguity reduction by itself rarely encapsulates all of the

## Glossary

**Credible threat or promise:** a reliable indicator (signal) of what an animal will do in the future.

**Inadvertent social information:** expression coined by Danchin *et al.* [2] to refer to a class of cues that are produced inadvertently by individuals engaged in some activity, such as foraging, fighting, mating, and so on.

**Personal information:** information that an individual acquires from interacting directly with its environment.

**The posterior:** the revised estimate by an animal of local environmental quality; the posterior is derived by incorporating the sampling information into the prior distribution, using Bayes' theorem (Box 1) [54].

**Prior distribution:** the expectation of an animal about environmental quality, which is assumed to have a previously experienced or 'known' (genetically determined) distribution.

**Public information:** expression coined by Valone [27]. A type of inadvertent social information conveying continuous, graded information about a feature that enables the observer to obtain an estimate of the quality of the feature (e.g. the richness of a food patch, the aggressiveness of an opponent, the dangerousness of a predator, the quality of a mate, etc.).

**Sampling information:** information derived from the experience of an animal.

**Signals:** sources of socially acquired information that are elicited to influence the behaviour of others. They are generally studied as 'communication' [42,43].

**Social cues:** a type of inadvertent social information that conveys discrete information about the presence or absence of some feature (e.g. presence or absence of predators or the spatial location of a food patch [19]).

**Socially acquired information:** any information that is generated by the behaviour of another organism.

**Shannon–Weaver entropy:** a numerical measure of the uncertainty (ambiguity) of an outcome [6].

important qualities of information from a whole-organism perspective [8]. Nevertheless, information use by animals attracts a wide range of ecological research effort, with much of this work implying that, for ambiguity reduction to be informative, it must be ‘useful’ to animals. However, such utility is rarely considered directly by researchers, let alone specified quantitatively and unambiguously. Following a brief overview of the potential sources of information available to animals and some consequences of their use, we sketch an explicit informational framework for analysing animal behaviour, which enables the ‘usefulness’ of uncertainty reduction to be specified from an evolutionarily functional perspective. In doing so, we hope to begin to unify our understanding of the evolutionary ecology of information use by animals.

There is a range of information sources available to animals. Direct interactions with the environment generate ‘personal information’, the sources of which often do not respond directly to the behaviour of the information gatherer. Alternatively, ‘socially acquired information’ [2] can be obtained by observing the behaviour of other animals, which might respond actively to the behaviour of the receiver (Figure 1).

### Personal information

Personal information use is common when animals attempt to navigate within a habitat (e.g. to and from a burrow or nest) or while migrating between habitats. Animals can navigate using a wide variety of reliable environmental cues of location, such as local landmarks, the sun, the stars, the geomagnetic field, and so on [9]. However, studies of animal navigation typically focus on elucidating mechanisms that enable accurate orientation to such cues without explicitly considering their informational qualities from an evolutionarily functional perspective. Nevertheless, this significant body of work has been crucial in identifying a range of sensory modalities in non-human animals, including sensitivity to UV light, infrared light, polarized light, special odours (pheromones), magnetic fields, electric fields, ultrasonic sounds and infrasonic sounds [10]. Such work has also generated insights into how information is processed in animal brains and

strengthened the case for cognitive processing by non-human animals [10].

A wide range of research effort has directly addressed the adaptive use of personal information by animals in non-navigational contexts. Much of this work has explored the consequences of uncertainty regarding food-item type and environmental quality on foraging decisions, and examined optimal sampling strategies [11,12]. Here, animals can use estimates of the amount of food eaten and the time taken to find it in different places to update their expectations about the location and quality of food, which they then use to make decisions about where to forage and for how long (Box 1), as well as what to eat [11]. Furthermore, animals can estimate their risk of mortality from predators from cues of predator activity or by the mere fact that they remain alive: the longer an animal lives, the lower its estimate of danger [13]. When deciding whether to mate, who to mate with or how much reproductive effort to invest in a particular breeding attempt, animals can also reduce their uncertainty by gathering personal information. Studies of female mating tactics suggest that inspecting males can improve estimates of local male availability and quality distribution, and the value of individual partners, enhancing the choices available to a female [14–17]. Similarly, males can improve their sperm allocation tactics by gathering information about the distribution and quality of local females [18]. Such research effort has established information as a crucial currency in animal decision-making and elucidated much adaptive behaviour [11,12].

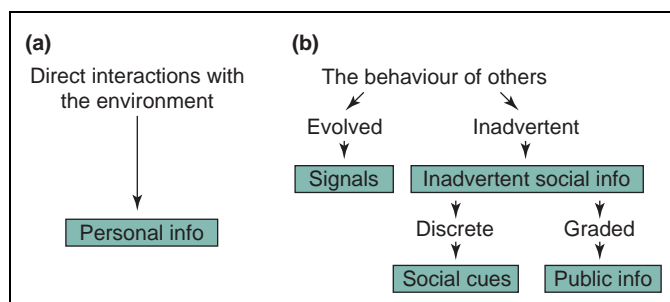
### Socially acquired information

In groups, animals can access socially acquired information [19] (Figure 1), sometimes in the form of evolved ‘signals’ but often as ‘inadvertent social information’ generated by the activities of their companions, such as foraging or breeding [2]. However, although using such information often avoids the acquisition costs and ‘sampling bias’ associated with individual trial-and-error-based personal information, it is not always worth attempting to use it [20]. This is because it might not always be available if sources are misinformative or out date rapidly, or if the available socially acquired information is costly to utilize. Indeed, a growing body of evidence suggests that animals use specific strategies for allocating effort between socially acquired and personal information, particularly when they cannot be used simultaneously [21].

#### *Inadvertent social information*

Inadvertent social information encompasses ‘social cues’, which convey discrete information, often about the spatial location or presence or absence of features, and ‘public information’, which conveys graded information about the quality of features. Animals seem to use public information less frequently than they do social cues, but the literature reports an increasing number of cases of public information use in foraging, habitat and mate choice [22].

Examples of social cues include the eating, fleeing and mating activities of other organisms. Eating reveals the location of food, fleeing suggests impending danger,



**Figure 1.** The classification of potential sources of information available to an animal according to whether information is obtained via direct interactions with its environment [personal information (a)] or from observing the behaviour of others [socially acquired information (b)]. Personal information can be ‘deliberately’ (evolved signals) or inadvertently provided. If other animals inadvertently produce the socially acquired information, it can be further differentiated according to whether it provides discrete (social cues: e.g. presence or absence of a predator) or graded information (public information: e.g. amount of food available in a patch) to the information gatherer. Redrawn, with permission, from [2].

### Box 1. Bayesian foraging

When analysing the optimal exploitation of a patch of food, the prior distribution is the distribution of patch qualities 'known' to the foraging animal in the environment, and the posterior is a revised patch quality distribution from which we can calculate the expected gains to the animal from continuing to forage in the patch. Furthermore, keeping track of the total time spent searching a patch and the total number of food items found during that time is often sufficient for a forager to estimate its current expected (instantaneous) intake rate [59]. Such sampling information should be straightforward to process for most animals; simple neural networks can utilize time and number information to produce outcomes that qualitatively match that of a Bayesian model [64].

We can estimate the remaining number of prey items in a patch from sampling information if the frequency distribution of patch qualities is 'known' (Equation I):

$$r(x, z) = \sum_{N=x}^{\infty} R(N|x, z)(N-x). \quad [\text{Eqn I}]$$

$R$  is the posterior probability that the patch initially contained  $N$  items, given that  $x$  items were found in the  $z$  time units spent searching [59,61]. When this probability is multiplied by the possible number of food items remaining ( $N-x$ ), and summed over all possibilities ( $x$  to  $\infty$ ), it results in the expected number of food items remaining,  $r$ . The instantaneous rate of intake can be calculated from the number of items remaining.

Furthermore, we can use  $x$  and  $z$  to estimate the potential intake rate, which is the expected number of prey to be found divided by the expected time until forager leaves the patch [57,61]. We must find this rate numerically: we pick some large final time by which the forager must leave the patch; then we work backwards to find the time,  $t_n$ , that the forager should remain in the patch if it has discovered  $n$  food items. Once we know the future stopping points, we can find the potential intake rate as follows.

The posterior probability that the patch will be left at the stopping point  $(n, t_n)$ , if  $x$  items were found at time  $z$ , is (Equation II):

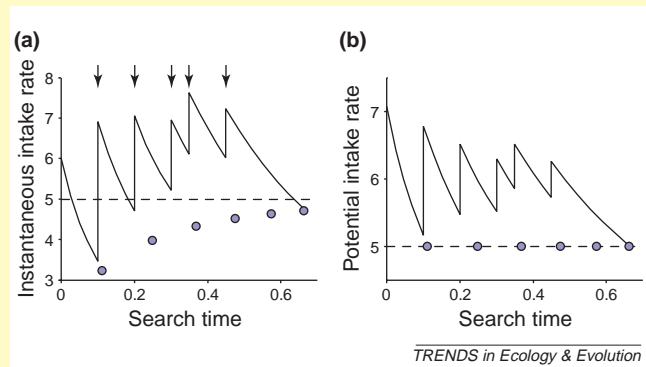
$$Po(n, t_n|x, z) = \sum_{N=x}^{\infty} L(n, t_n|N, x, z)R(N|x, z) \quad [\text{Eqn II}]$$

Here,  $L(n, t_n|N, x, z)$  is the probability of leaving the patch at  $(n, t_n)$ , given that it initially contained  $N$  items [65]. The expected number of prey left to catch is hence (Equation III):

$$\hat{n} = \sum_{n=x}^{\infty} (n-x)Po(n, t_n|x, z), \quad [\text{Eqn III}]$$

whereas mating indicates an acceptable sexual partner. Animals can benefit from such social cues [2], especially when discriminating between alternatives is costly or difficult. It can also result in informational cascades [23]: sequential social cue use within a group can initiate a cascade in which the socially acquired information overrides personal information. Once initiated, individuals copy decisions blindly, usually leading to correct choices (e.g. [24]), but sometimes also to errors with important population-level consequences [25]. Using the flight behaviour of flock mates to signify impending danger, for instance, creates valuable informational cascades when the first birds in a flock to flee an approaching predator trigger an explosive sequence of departures. Random flock departures by birds can, however, also trigger such flight cascades in the absence of any threat. Informational cascades might also occur in mate copying, and choosing roosts or colony locations [26].

Public information favours group cohesion because collective information about resource quality synchronizes



**Figure 1.** 'Bayesian foraging' on food patches among which the numbers of food items are 'clumped' in their distribution. (a) The expected instantaneous intake rate of an animal in a patch (solid curve) declines while no food is found, but jumps up every time an item is encountered (arrows). The solid circles specify the optimal stopping points: leaving a patch when the instantaneous intake rate drops to one of these maximizes the long-term intake rate, which is shown as the dashed line. (b) The expected potential intake rate (solid curve) is the expected intake rate for the remainder of the patch visit, if the forager decides to stay. To maximize the long-term intake rate (dashed line), the patches should be left when the potential intake rate drops to the long-term rate – at the stopping points (solid circles). Thus, the instantaneous intake rate is always less than the long-term rate at the stopping points (when the potential intake rate equals the long-term rate). The distribution of prey among patches used here is a negative binomial with a mean of 6 and variance of 42.

and the expected remaining search time is (Equation IV):

$$\hat{t} = \sum_{n=x}^{\infty} (t_n - z)Po(n, t_n|x, z). \quad [\text{Eqn IV}]$$

The potential intake rate at point  $(x, z)$  is thus (Equation V):

$$\Pi(x, z) = \frac{\hat{n}}{\hat{t}}. \quad [\text{Eqn V}]$$

Interestingly, if the food distribution among patches follows a clumped distribution (Figure 1), the instantaneous intake rate is not constant at optimal patch departure, but increases with search time. This result might appear to contradict simpler patch use models [11,59], but is explained by the correct analysis of information use using statistical decision theory; it is the potential intake rate of an animal that determines optimal patch departure when it forages in a Bayesian manner [61].

patch departures [27], enables rapid learning of local habitat depletion [28,29] and estimation of habitat or breeding colony quality [30]. Observing the number of offspring fledged from various colonies, for instance, can inform the settlement decision made the following year. For mate choice, public information is valuable when discriminating between mates is costly or difficult [31]. Nevertheless, the informational advantage of joining a group hinges on whether its members simultaneously collect socially acquired and personal information [26]. However, because processing graded information is relatively demanding [22,32], sensory or cognitive constraints are likely to limit the concurrent collection of public and personal information [33] and individuals might specialize on either type of information use [34]. This would produce negative frequency dependence in the value of public information; the more individuals collect it, the fewer produce exploitable information [27,35] (i.e. a producer-scrounger game [36]). With incompatibility of information type collected, therefore, we expect an equilibrium

combination of public information producers and users (scroungers) at which neither does better than the other: a mixed evolutionarily stable strategy (ESS) [37]. So, simply documenting public information use in groups does not mean that there are informational advantages to group membership; one also needs to demonstrate that animals can collect personal and public information concurrently. Nevertheless, public information use can also give rise to behavioural traditions with important evolutionary consequences, for instance establishing breeding colonies or mating preferences [2]. Furthermore, group foraging in social insects is attracting considerable attention, focussed on how individual foragers can pool public information so that the colony can exploit resources more efficiently [38–41].

### Signals

Many studies address the active exchange of information between animals. Two contrasting bodies of work have developed, one emphasizing the requirements for efficient communication in the presence of noise [42], the other the incentive for deceit (misinformation) and the strategic requirements for the maintenance of reliable information transfer [43]. Furthermore, when a system is at a signalling equilibrium, where neither signaller nor receiver can gain by changing their behaviour unilaterally, information is always advantageous to both provide and receive on average; nevertheless, receivers can be disadvantaged by responding to signals under some of the conditions at which the equilibrium persists [44]. This offers animals interesting possibilities for the strategic manipulation of social partners using information.

Consider two parents caring for their dependent offspring. Each would prefer that its partner care for the young, to avoid the costs of parental care and gain remating opportunities with other partners. If the male chooses whether to care before the female can, he can force the female to care by deserting. The female is disadvantaged here because she must respond to the action of the male, whereas the male is not so constrained. But, it is not the temporal order that is crucial to the outcome of parental conflict; rather it is the fact that the male has been able to inform the female reliably about what he will do. This puts her at a disadvantage because, once she knows the male will desert, it is in her best interests to care [45].

This example shows that it might benefit an individual to indicate its actions reliably [46,47]; the male can do this by deserting first. The female could attempt to force the male to care by threatening to desert whatever he does. But, because it would not be in her best interests to desert if he has already done so, her threat is not credible [45]. So how can an individual produce a credible threat or promise? One idea [45] is that an individual can do so by limiting its feasible choices and handicapping itself. For example, our female could handicap herself by lowering her energy reserves so that she risks starvation if she cares alone. Then, even if the male chooses first, his knowledge (that the best action of the female is to desert if he deserts) forces him to care [48]. Indeed, it has been

suggested that females sometimes force males to care by producing more young than they can care for alone [49].

Our example assumes that the female will always take the best action given her circumstances. To always behave optimally, however, requires unlimited behavioural flexibility. Instead, many organisms follow rules, based on neural and hormonal mechanisms, which limit their flexibility. For example, an angry person might retaliate when provoked, even if it is not in their best interests to do so. Thus, emotional states can act as credible threats or promises [47]. Of course, it would be beneficial to fake emotions persuasively, convincing an opponent of commitment to a particular action, while being able to take another action if necessary. But, such deception might be difficult to achieve, or it might not be in the long-term interests of the individual. With rules based on mechanisms, animals also have consistent ways of behaving (i.e. personalities or behavioural syndromes [45,50–52]). Consistency enables interacting individuals to infer future behaviour from the past, so that animals are able to make credible threats or promises, and altering how researchers must think about solutions to evolutionary games [45].

### Information use from an evolutionary perspective

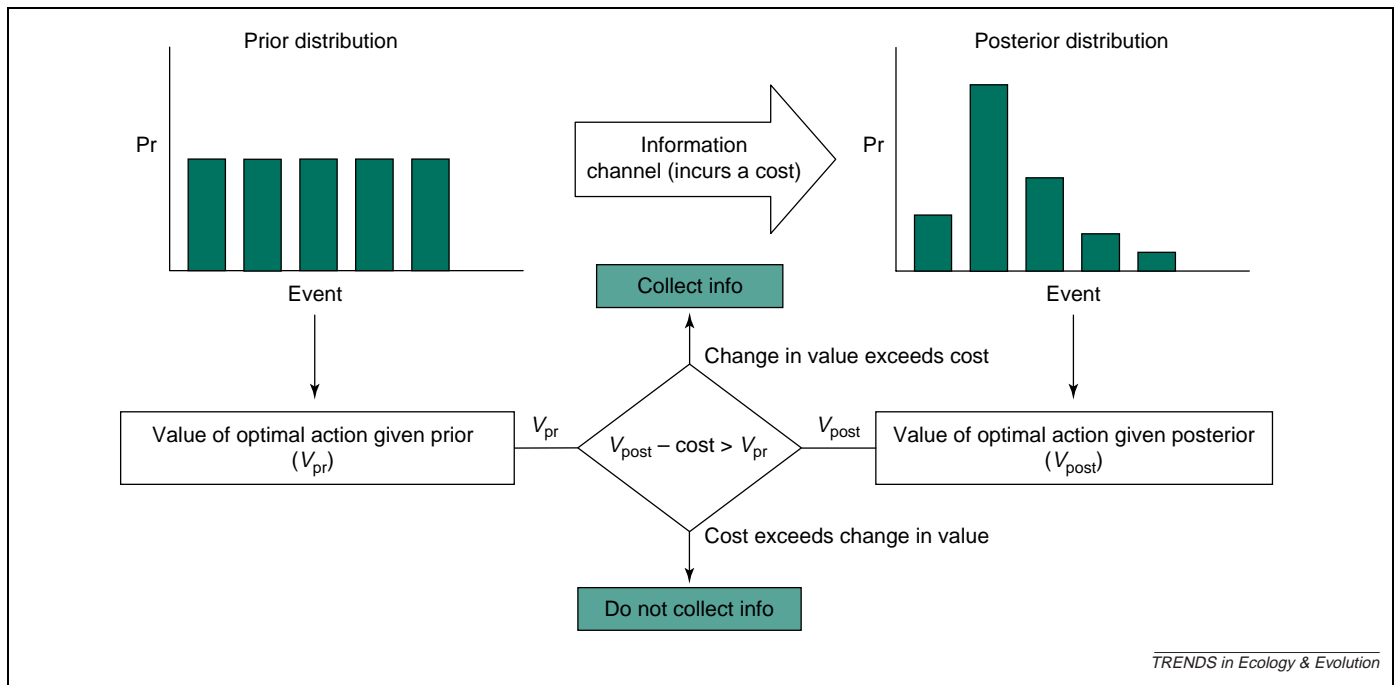
Our brief overview illustrates that information implies utility as well as uncertainty reduction when its use by animals is analysed [53]. In other words, Shannon–Weaver entropy [6] and other ideas that focus on the simple reduction of ambiguity do not suffice in organismal biology. Instead, we advocate an explicit framework based on statistical decision theory [54], within which biologists can explore information and its use by animals rigorously to generate quantitative predictions about adaptive behaviour.

#### *A statistical decision theory framework*

The statistical decision theory approach (Figure 2) involves three main elements [54]:

- *Priors and posteriors* The prior distribution represents what is knowable about the world to an animal without specific experience. A prior might be genetically determined or based on acquired experience; and static or updated during the lifetime of the animal (continuously or at ‘sensitive’ periods during development). In fact, we can think of genomes as priors set by the ‘experience’ of a lineage of ecologically important factors over its evolutionary history [55]. If the animal discovers something about a particular aspect of its environment, this discovery transforms the prior distribution into a posterior distribution via Bayes’ theorem [54].

- *Sampling information (via information channels)* For an information problem to exist, an animal needs some way of discovering things that will update the prior to a posterior. Most combinations of sensory, cognitive and physiological processes can be involved; any environmental change that induces a change in a receiver (e.g. consuming prey, observing a neighbour fleeing, mating, etc.) can generate a posterior. Indeed, such changes need not result from sensory stimulation nor involve cognition; determining alternative traits genetically can be regarded as using local gene frequencies



**Figure 2.** The statistical decision theory approach for analysing animal information use via a single information channel. The prior distribution of an animal represents its ‘knowledge’ about the probabilities of potential outcomes. This can come from previous experience or be genetically determined. For an information problem to exist the animal must have some way of reducing its uncertainty about outcomes by gathering information, usually at a cost. If it gathers information, its prior can be transformed into a posterior distribution using Bayes’ theorem [54]. An animal should gather information via the channel in question if the value of its optimal actions once it has reduced its uncertainty about potential outcomes, accounting for the cost of gathering the information, exceeds the value of its optimal actions without the information. Many real information problems will have multiple posteriors because there should be multiple potential outcomes of one’s information gathering efforts.

as information about prevailing conditions (O. Leimar, unpublished data).

• **Information and action** The information represented by the posterior distribution is valuable because it influences the actions of the animal. In a well formulated model, we can calculate the optimal action and the fitness consequences of any given posterior distribution; ultimately, for environmentally induced changes to have informational value, the posterior must change the functioning of an organism in an evolutionarily relevant manner [8].

When we have clearly specified these three pieces of the problem, we can ask several sorts of question. If the animal can obtain or provide information via two possible sources (channels), which is better? How much would the decision maker pay for information? Is there an optimal strategy for information acquisition? And so on. In this approach, information is not valuable merely as an academic abstraction, but also because it changes actions and improves performance. Although the ideas of prior and posterior distributions are general, the problems of how animals obtain information and the connection between information and action can be quite parochial. An animal might obtain information about mates differently from the way in which it obtains information about foraging patches. Statistical decision theory is a framework for thinking about information problems, rather than a body of cut-and-dried results. But even this simple framework can become complicated. For example, prior distributions can change over time (e.g. seasonally), so that remembered information is no longer valid and the prior must be updated continuously [56]. Furthermore, statistical

decision theory illustrates how the ‘worldview’ of an animal can restrict its ability to respond to local conditions. For instance, if the ancestors of an animal never encountered aerial predators (e.g. its prior expectation of danger from above is zero), it might never learn to be wary of ‘open sky; if its prior is zero then its posterior will always be zero no matter how compelling the evidence to the contrary.

**Box 1** illustrates how statistical decision theory can be used to analyse animal foraging behaviour. Indeed, we can readily apply statistical decision theory to analysing the use of information by animals in any context. In addition to its extensive application in foraging contexts [57–62], this approach has been applied to understanding information use in mating tactics, signalling and antipredator behaviour [13–17,44]. Furthermore, it should be possible to analyse the relative informational value of different cues of location used to navigate by. For example, we could specify the prior expectation of animal about the distance ‘home’ in the absence of the use of a particular landmark array (e.g. based on ‘dead reckoning’ or path integration [9]). The change in expected travel distance as a result of attending to the landmarks would then offer a measure of the navigational value of their use. Similar applications are also possible when analysing the provision and gathering of socially acquired information. For information provision, individuals might actively provide sampling information (e.g. be consistent) if it induces favourable changes in the behaviour of others (the posterior). **Box 2** lists some outstanding research questions suggested by an informational approach based on statistical decision theory.

### Box 2. Outstanding informational questions

- What is the scope for self-assessment during mate choice?
- How do females integrate multiple sources of information (e.g. their own assessments of mate value and the choices made by others; i.e. mate choice copying)?
- What is the impact of uncertainty on the strength of sexual selection?
- How do insights from the study of communication integrate into discussions of information acquisition and use?
- Can we predict which cues animals should attend to if they are maximizing their fitness?
- When are posteriors produced by inadvertent social information more valuable than those produced by personal information and signals?
- To what extent is the concurrent collection of inadvertent social information and personal information constrained (sensory versus cognitive versus strategic incompatibilities)?
- To what extent does culture arising from public information constrain evolution?
- When does self-handicapping offer net advantages in social interactions and how often do animals do this?
- Given that insuring against uncertainty is always an option, how does this affect the costs and value of information use?

### Concluding remarks

Information use by animals is key to their adaptive behaviour. Thus, its analysis is central to organismal biology. Nevertheless, evolutionary and behavioural ecologists do not adopt consistent, rigorous concepts of information, let alone apply explicit frameworks to generate informational hypotheses about adaptive animal behaviour. Statistical decision theory offers such a framework for specific naturally occurring decision problems, and fits nicely with the intellectual traditions of evolutionary and behavioural ecology. Its emphasis on how information is used contrasts sharply with ideas about information based on measures of ambiguity (e.g. Shannon–Weaver entropy [6]), which often give the impression that ambiguity reduction is valuable *per se*. Nevertheless, we can readily incorporate quantitative elements of such approaches within statistical decision theory (e.g. using ‘bits’ as units of sampling information). We feel, therefore, that statistical decision theory presents an ideal framework for generating testable hypotheses about the use of information by animals that are ‘explicit, quantitative and uncompromising’ [63], which is fundamental to any scientific enterprise.

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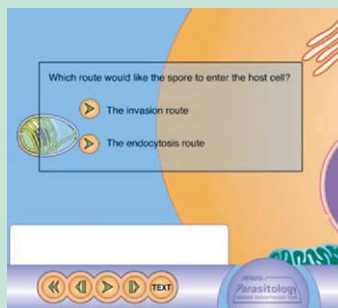
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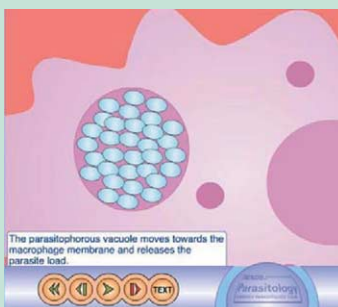
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