



Target article

Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet

John M.C. Hutchinson*, Gerd Gigerenzer

Max Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany

Abstract

The Centre for Adaptive Behaviour and Cognition (ABC) has hypothesised that much human decision-making can be described by simple algorithmic process models (heuristics). This paper explains this approach and relates it to research in biology on rules of thumb, which we also review. As an example of a simple heuristic, consider the lexicographic strategy of Take The Best for choosing between two alternatives: cues are searched in turn until one discriminates, then search stops and all other cues are ignored. Heuristics consist of building blocks, and building blocks exploit evolved or learned abilities such as recognition memory; it is the complexity of these abilities that allows the heuristics to be simple. Simple heuristics have an advantage in making decisions fast and with little information, and in avoiding overfitting. Furthermore, humans are observed to use simple heuristics. Simulations show that the statistical structures of different environments affect which heuristics perform better, a relationship referred to as ecological rationality. We contrast ecological rationality with the stronger claim of adaptation. Rules of thumb from biology provide clearer examples of adaptation because animals can be studied in the environments in which they evolved. The range of examples is also much more diverse. To investigate them, biologists have sometimes used similar simulation techniques to ABC, but many examples depend on empirically driven approaches. ABC's theoretical framework can be useful in connecting some of these examples, particularly the scattered literature on how information from different cues is integrated. Optimality modelling is usually used to explain less detailed aspects of behaviour but might more often be redirected to investigate rules of thumb.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Animal cognition; Cognitive ecology; Cue integration; Ecological rationality; Fast and frugal heuristic; Multiple cues; Optimality modelling; Rule of thumb; Take The Best

1. Introduction

We both work in a research group called the Centre for Adaptive Behaviour and Cognition (ABC). Its main research topic is the cognitive mechanisms by which humans make decisions. We call these mechanisms *heuristics* and our thesis is that rather simple heuristics both work surprisingly well and are what humans

* Corresponding author. Tel.: +49 30 82406352;

fax: +49 30 82406394.

E-mail address: hutch@mpib-berlin.mpg.de
(J.M.C. Hutchinson).

widely use. Simple heuristics correspond roughly to what behavioural biologists call rules of thumb. Our aim in this paper is to relate ABC's research to biological research on behaviour. One of us (GG) is the director and founder of ABC, and, like most of the group, is a psychologist by training; the other (JMCH) is a behavioural ecologist who has worked in ABC for the last four years.

For a more thorough review of ABC's results and outlook, read the book *Simple Heuristics that Make Us Smart* (Gigerenzer, Todd and the ABC Research Group, 1999). Another book *Bounded Rationality: The Adaptive Toolbox* (Gigerenzer and Selten, 2001) provides more of a discourse between ABC and other researchers. In the current paper, we seek to identify where behavioural biologists and ABC have used similar approaches or arrived at similar results, but also to clarify exactly where the two schools disagree or diverge on tactics. We thus hope to discover ways in which each discipline might learn from the other; we try to be open about potential limitations of ABC's approach. This paper is written to inform both biologists and psychologists.

Before making more general points we start by giving some examples of the simple heuristics that ABC has studied, and then some examples of rules of thumb from biology. These will convey better than any definition the range of phenomena to which these terms are applied. The succeeding sections will deal more systematically with the principles behind ABC's research, and contrast its techniques and findings with those from research on animal rules of thumb.

2. Examples of fast and frugal heuristics in humans

2.1. *Take The Best*

Consider the task of which of two alternatives to choose given several binary cues to some unobservable criterion. An example is deciding which of two cities is the bigger, given such cues as whether each has a university or has a football team in the premier league. Gigerenzer and Goldstein (1996) proposed the following decision mechanism: (1) consider one cue at a time, always looking up the cue values for

both alternatives; (2) if both cue values are identical examine the next cue, otherwise ignore all other cues and make a decision on the basis of this single cue; (3) if no cues are left to examine, guess. Such a process is called lexicographic because it resembles the obvious way to arrange two items into alphabetical order: first compare the first letters and only if they are identical consider the next letter. A hypothetical biological example might be a male bird that compares itself with a rival first on the basis of their songs; if the songs differ in quality the weaker rival leaves, and only otherwise do both remain to compare one another on further successive cues, such as plumage or display.

We have not yet specified the order in which cues are examined. Intuitively it makes sense to try to look up the more reliable cues first, and also those that are most likely to make a distinction. Gigerenzer and Goldstein (1996) proposed to rank cues by validity; validity is defined as the proportion of correct inferences among all inferences that this cue, if considered in isolation, allows (a tie does not allow inference). With this cue order, the heuristic has been named *Take The Best*. This order might have been individually estimated from a sample, or learned by instruction, or have evolved by natural selection.

Amazingly, the predictive accuracy of this heuristic, judged on a real-world dataset about German cities, was about equal to, or better than, that of multiple regression (Fig. 1; Gigerenzer and Goldstein, 1999, p. 93). Fig. 1 further compares the performance of *Take The Best* against two computationally sophisticated algorithms that also each construct a decision tree (H.J. Brighton, personal communication). Especially, when the "learning" sample of cities used to construct the trees is small, *Take The Best* nearly always outperforms these methods in accurately comparing sizes of the remaining cities (i.e. in cross-validation). Chater et al. (2003) have performed a slightly different analysis for other sophisticated algorithms, including a three-layer feedforward neural network, and observed a similar pattern. These are surprising and striking results, especially as at least the comparison against multiple regression holds in 19 other such real-world comparison tasks besides the original city-size example (Czerlinski et al., 1999).

Take The Best is fast to execute and frugal in the information used, since usually not all cues are exam-

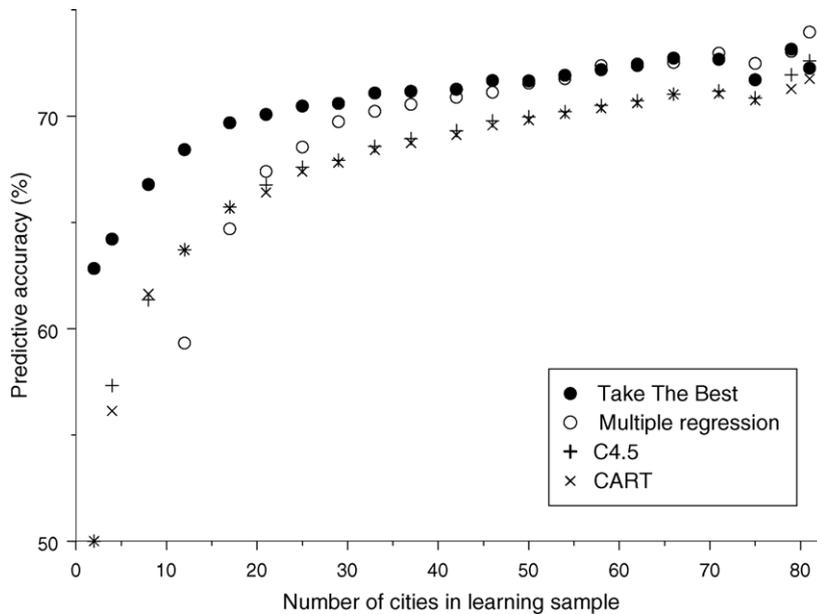


Fig. 1. Predictive accuracy of Take The Best (TTB) compared to multiple regression and to two computationally intensive algorithms designed to generalise well to new samples: C4.5 (Quinlan, 1993) and CART (classification and regression tree: Breiman et al., 1984). Another such algorithm, MML (Buntine and Caruana, 1992), performed similarly to CART and C4.5. The task is judging which of two German cities has the larger population, based on nine cues (same dataset as Gigerenzer and Goldstein, 1999; Chater et al., 2003). The abscissa specifies the number of cities in the learning sample to which the regression equation or decision tree is fitted, and the ordinate specifies the predictive accuracy achieved in the test set (remaining cities of the 83). Results are averaged over 1000 random selections of the learning set. Except for multiple regression, the strategies can each be expressed as decision trees. The intensive algorithms first grow a tree (for instance, in the case of C4.5, iteratively using reduction in entropy as a criterion for which cue to use for the next split), and then prune it so as to avoid overfitting. Results for multiple regression are not shown for learning sets involving fewer cities than the number of cues; the regression algorithm was not one that eliminated cues of low statistical significance. (Figure provided by H.J. Brighton.)

ined. It is simple in that it involves only comparisons of binary values, rather than the additions and multiplications that are involved in the standard statistical solutions to the task. This degree of frugality and simplicity applies to the execution of the procedure. If the prior ranking of cues by validities must be individually learned, this requires counting, and prior experience of the task with feedback. Nevertheless, it is still relatively much simpler to gauge the rank order of validities than the cue weights in a multiple regression equation, partly because validities ignore the correlations between cues. Note, however, that ordering by validities is not necessarily optimal; finding the optimal order requires exhaustively checking all possible orders (Martignon and Hoffrage, 2002). In natural biological examples, a good ordering of cues could have been achieved by natural selection or by individual learning

through trial and error; such an ordering might perform very well yet be neither ranked by validity nor optimal. Simulations show that performance remains high if the ordering of cues only roughly matches validity (Martignon and Hoffrage, 2002), or if the ordering is generated by a simple learning algorithm, itself a simple heuristic (Dieckmann and Todd, 2004; Todd and Dieckmann, in press).

Take The Best was originally envisaged as a heuristic that processed information already in memory. However, when subjects are presented with the binary cues in written form, a variety of experiments have identified situations under which Take The Best and similar decision heuristics accurately describe how people sample and process the information (Rieskamp and Hoffrage, 1999; Bröder, 2000, 2003; Bröder and Schiffer, 2003; Newell and Shanks, 2003).

2.2. Comparing heuristics in structure and performance

Take The Best can be viewed as a sequence of three building blocks.

Search rule: examine cues in order of validity, at each step comparing values between alternatives.

Stopping rule: stop search when a cue discriminates.

Decision rule: choose the alternative indicated by the discriminating cue.

This can be compared with a different class of heuristics based on tallying.

Search rule: examine cues in arbitrary order, checking values of both alternatives but not necessarily consecutively.

Stopping rule: stop search after m cues.

Decision rule: tally these m cue values for each alternative and choose the alternative with the higher tally.

The amount of information used by Take The Best (its frugality) varies from decision to decision; the frugality of tallying is always m pairs of cue values. If m is all the cues available, tallying is called Dawes' Rule (named after the pioneering work of Dawes, 1979). Tallying is also simple to execute in that it requires only counting. Unlike Take The Best, it does not require knowing an order of cues, just which direction each

points (although the accuracy and frugality of tallying can benefit from more complex prior calculations to set m and eliminate cues likely to be uninformative). Like Take The Best, the predictive accuracy of Dawes' Rule is as good as, or better than, multiple regression for the 20 real-world datasets (Czerlinski et al., 1999).

With some of these datasets Take The Best performed better than Dawes' Rule and with others worse. We now have some understanding of how the environment (i.e. the statistical structure of cues and criterion) determines this (Martignon and Hoffrage, 2002). Not surprisingly, in environments in which the weights from a multiple regression are roughly equal for all cues (Fig. 2), Dawes' Rule, which is equivalent to multiple regression with unit weights, performs better. Take The Best performs better when each cue weight is much greater than the next largest one. If each weight is greater than the sum of all smaller weights, and the order of weights matches that of validity, multiple regression must produce identical decisions to Take The Best. Such an environment is called non-compensatory because in the multiple regression an important cue cannot be outweighed by less important cues even if the latter all disagree with the former. It turns out that many of our 20 example environments tend towards having non-compensatory cue structures (Czerlinski et al., 1999): most cues add

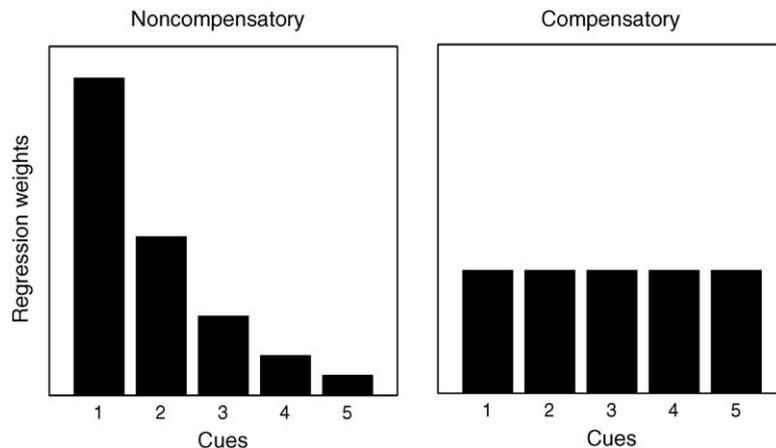


Fig. 2. Two environment structures shown by the cue weights from a multiple regression (cue values are 0 or 1). *Left:* a non-compensatory environmental structure where Take The Best is as accurate as any linear weighted combination of cues. The weights of the cues are 1, 1/2, 1/4, etc. *Right:* a compensatory environmental structure where Dawes' Rule is as accurate as any linear weighted combination. A cue weight reflects how much information the cue adds to that already provided by the better cues, not the independent correlation between the cue and the criterion. See Martignon and Hoffrage (2002).

little independent information to that provided by the most informative cues. Take The Best and Dawes' Rule can be viewed as each taking a bet on a different environment structure, whereas multiple regression tries to be a jack of all trades and computes its parameters to fit the structure (Martignon and Hoffrage, 2002).

It should now be clear that statements of the kind "This heuristic is good" are ill-conceived, or at least incomplete. A heuristic is neither good nor bad per se; rather, some are better than others in specified environments (e.g. compensatory or non-compensatory) on specified criteria (e.g. predictive accuracy or frugality). It follows that although ABC has an overall vision that simple heuristics are the solution that the brain uses for many tasks, we envisage that the heuristics used for different tasks will vary widely and not be special cases of one global all-inclusive model. This suggests a somewhat piecemeal research programme, which need not be a weakness: the same piecemeal approach has certainly not held behavioural ecology back (Krebs et al., 1983). Incidentally, ABC also puts no general restrictions on the extent to which heuristics are innate or learnt, or applied consciously or unconsciously. Nor has our research so far focussed on categorising specific instances of heuristic use along these dimensions. We expect that in different circumstances the same heuristic might fall into more than one category.

Formal models of heuristics like Take The Best and tallying have their roots in the work of Herbert Simon on satisficing and bounded rationality, but also in early models of heuristics for preferences, such as Tversky's (1972) Elimination by Aspects, and the work on the adaptive decision maker by Payne et al. (1993). Yet most recent work has abstained from formalising heuristics or considering the conditions when they work well (Kahneman and Tversky, 1996). ABC's work also differs from those parts of cognitive psychology that are typically strong in modelling, yet rely on versions of expected utility (no search or stopping rules; e.g. Prospect Theory: Kahneman and Tversky, 1979) or on Wald's sequential analysis (which has stopping rules, but relies on optimisation; Wald, 1947). Whereas ABC's research explores the benefits of simplicity, other schools of psychology try to explain complex behaviour by building equally complex cognitive models.

2.3. A heuristic in action

A different decision task is to classify an object into one of two or more classes, as in medical treatment allocation (Should a patient be in intensive care or the regular ward?). Fig. 3 shows a model of a heuristic that predicts a very high proportion of the decision outcomes made by London magistrates whether to grant unconditional bail or to make a punitive decision such as custody (Dhimi, 2003; 88% accuracy in cross-validation was representative). Just like Take The Best, this heuristic searches cues one at a time, can stop search after any cue, and the outcome depends on that cue alone. This is why both Take The Best and this decision tree are examples of what ABC calls one-reason decision-making. The decision tree is based on observations of court outcomes, whereas when magistrates were asked how they made their decisions they told a totally different story consistent with the official Bail Act; this specifies that they should consider many other cues such as the severity of the crime and whether the defendant has a home. It could be that the simpler heuristic was used unconsciously, but unfortunately data on outcomes alone provides no convincing evidence what information was considered or how it was processed (one alternative heuristic that does consider all cues also had a high predictive accuracy).

2.4. Clever cues

Some very simple heuristics perform well not because of the method of combining cues but because they utilise a single "clever" cue. Loosely speaking, the heuristic lets the environment do much of the work. One example is the Recognition Heuristic (Goldstein and Gigerenzer, 2002): if one alternative is recognised and the other not, the recognised alternative is chosen independent of further information. It predicts the conditions for counterintuitive less-is-more effects: Americans made better inferences about German city sizes than about American ones, because with American cities they too often recognised both alternatives and could not apply the Recognition Heuristic.

Another example of a heuristic relying on a clever cue is how players catch a ball. To a Martian it might look like we are solving complex algebraic equations of motion to compute the trajectory of the ball. Studies have concluded instead that players might utilise a

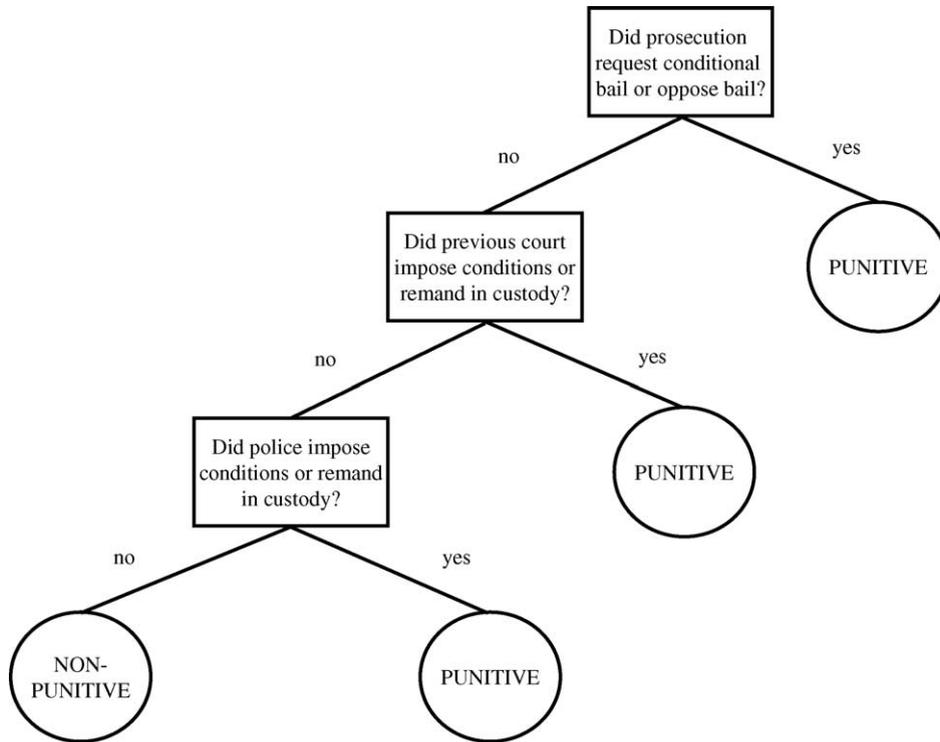


Fig. 3. Simple decision tree based on the bail decision outcomes of London magistrates (after [Dhmi, 2003](#)). The exact number and choice of cues depended on which randomly selected subset of judgements formed the learning sample (to which the tree was fitted), but the number of outcomes predicted in cross-validation was typically 85–92%, and this particular tree described 96% of outcomes in fitting.

number of simple heuristics (e.g. [McLeod and Dienes, 1996](#); [Oudejans et al., 1999](#)). The Gaze Heuristic is the simplest candidate and works if the ball is already high in the air and travelling directly in line with the player: the player fixates his gaze on the ball, starts running, and adjusts his speed to ensure that the angle of the ball above the horizon appears constant ([Gigerenzer, 2004](#)). Another heuristic better describes actual behaviour: it has the same first two building blocks (fixate and run) but the third one is modified to keep the image of the ball rising at a constant speed. If players manage to follow either heuristic, they and the ball will both arrive at the same location when the ball reaches head height; the prediction is not that players run to a pre-computed landing spot and wait for the ball. Neither heuristic is optimal, in the sense that they miss balls that would be catchable by running as fast as possible towards the point of impact (although the second heuristic would be optimal if the ball were not slowed by air resistance: see [Brancazio, 1985](#)). Note

that players are typically unaware of using this sort of heuristic even though this accurately accounts for their behaviour. Biologist readers will probably already be asking whether other animals might also use similar heuristics: indeed, maintenance of a constant optical angle between pursuer and target has been found in a variety of animals besides humans, including bats, birds, fish and insects ([Shaffer et al., 2004](#)). Surely, it is not the only heuristic that we share with animals.

3. Some simple rules of thumb from biology

We now consider examples of rules of thumb from biology; there are many more that we could have chosen. Our aim in this section is to give a broad flavour of this area of biological research, and so we deliberately leave most comparisons with ABC's approach until later. The diversity of the biological examples and the lack of theoretical connections between

many of them are parts of the picture that we wish to convey.

A recently described example is the method by which the ant *Leptothorax albipennis* estimates the size of a candidate nest cavity (Mallon and Franks, 2000; Mugford et al., 2001). Natural nest sites are narrow cracks in rocks, typically irregular in shape. The ants' solution is first to explore the cavity for a fixed period on an irregular path that covers the area fairly evenly. While doing this it lays down an individually distinct pheromone trail. It then leaves. When it returns it again moves around but on a different irregular path. The frequency of encountering its old trail is used to judge size ($\text{rate} \propto 1/\text{area}$). This "Buffon's needle algorithm" is remarkably accurate: nests half the area of others yielded reencounter frequencies 1.96 times greater.

Another example concerns how the wasp *Polistes dominulus* constructs its nest (Karsai and Péntzes, 2000). The nest is a tessellation of hexagonal cells that grows as each new cell is added. Up to the 15-cell stage only 18 arrangements of cells have been observed. These arrangements are all compact, which ensures that less new material is required and that the structure is strong. However, these optimality criteria are inadequate explanations of why just these 18 arrangements: economy of material predicts 155 optimal arrangements, whereas not all the observed structures maximise compactness. A better explanation is a construction rule in which the wasp places each cell at the site where the sum of the ages of the existing walls is greatest. Age of wall might plausibly be judged by the concentration of pheromone added at the time of construction or the state of the larva inside. This rule explains all observed arrangements, with one exception that plausibly follows from a small mistake in execution of the rule. Further unexpected forms appear as the nest grows beyond 15 cells, but then it is plausible that the wasp does not visit all potential building sites, or that small differences in wall age get harder to judge as the structure gets older.

Social insects provide the richest source of rule-of-thumb examples (e.g. Müller and Wehner, 1988; Seeley, 1995; Camazine et al., 2001; Detrain and Deneubourg, 2002; Sato et al., 2003). Some of these examples concern mechanisms that ensure that individual behaviour is well integrated, when perhaps

there is some particular advantage of each individual rigorously following simple rules. But other examples do not concern coordination. Perhaps it is just that social insects are small animals with small nervous systems. This might matter because they really can only follow simpler rules than higher animals, but it could be merely that biologists are readier to view them as robotically following simple rules than larger animals that more closely resemble ourselves. Instead our suspicion is that the plethora of good examples of rules of thumb in social insects is because this way of thinking about mechanisms happens to have become prevalent in this research community, each new nice example stimulating similar interpretations of other phenomena. Perhaps then, rules of thumb will grow in prominence when researchers on other organisms realise the concept's usefulness. A more pessimistic explanation is that because social insects are small, studying their behaviour is difficult, and our knowledge incomplete, which allows simple rules of thumb to be adequate explanations. According to this viewpoint (suggested to us by a social-insect worker responsible for some of the nicest examples of rules of thumb!), further research will lead to simple rules of thumb being rejected in favour of more complex mechanisms.

Some of the earliest analyses of rules of thumb came from considering the varied ways that simple animals locate stimuli (Fraenkel and Gunn, 1940). For instance, a copepod (a planktonic crustacean) faced with two light sources follows a trajectory as if it were pulled towards each source with a force proportional to source intensity/distance². Such apparently complex behaviour is explicable by the simple rule that the animal adjusts its orientation so as to maximise the amount of light falling on a flat eye. More recent research has examined how a female moth locates a pheromone-producing male (Kennedy, 1983). She applies the simple rule of heading upwind when the pheromone concentration lies above a particular threshold. This will not always get her to the male, because variation in wind direction creates a meandering plume of pheromone. When she breaks out of a plume, the lowered pheromone concentration triggers her to cast back and forth cross wind with increasing amplitude until she reencounters the plume. Analytic models have estimated the efficiency of different methods of

taxis depending on aspects of environmental structure such as turbulence (Balkovsky and Shraiman, 2002; Dusenbery, 2001).

The two other areas of behavioural biology that make most frequent reference to rules of thumb are mate choice and patch-leaving. A paper by Janetos (1980) seems responsible for a tradition in behavioural ecology of modelling mate choice as a process of sequential assessment of candidate males. The two most discussed rules are for a female to accept the first male above a preset threshold or for a female to view a preset number of N males and then return to the best (“best-of- N ” rule). Janetos argued that animals follow simple rules that can achieve good but not optimal performance (Janetos and Cole, 1981). Other behavioural ecologists agreed that information constraints would restrict what sort of rule could be used, but preferred to hypothesise that a rule’s parameters were optimised for the environment (Real, 1990a). However, neither of these two rules explains adequately the patterns of return typically observed nor effects of the quality of previously encountered males on acceptance decisions, so somewhat more complex rules may be necessary (Luttbeg, 1996; Wiegmann et al., 1996; Hutchinson and Halupka, 2004).

Patch-leaving rules represent more of a success for modelling. The idea is that food items occur in patches, and that they are depleted by the forager, which should thus at some stage move to another patch. The question is when. The number of food items remaining is unknown to the forager, but it is indicated by the rate at which it finds items. An elegant optimality model derives how the rule of thumb should depend on the environment (Iwasa et al., 1981). In an environment in which all patches are of similar quality, finding a food item should decrease the tendency to stay because the patch has been depleted. In an environment in which some patches are very poor and some very good, finding a food item should increase the tendency to stay, because the success suggests that it is a better patch. Later, it was realised that if an independent cue was available indicating initial patch quality, even in the second type of environment the decremental decision rule can be better (Driessen and Bernstein, 1999). This fits empirical research on the parasitoid wasp *Venturia canescens*, which lays its eggs in caterpillars: the concentration of host scent sets the tendency to stay, this

decreases through some sort of habituation response, but the effect of finding a host further decreases the tendency to stay (Driessen and Bernstein, 1999). Between similar parasitoid species there is much variation in whether finding a host increases or decreases the tendency to stay, but we do not yet know enough about the environmental structure in most of these examples to judge whether the theory explains these differences (van Alphen et al., 2003; Wajnberg et al., 2003).

Models of patch-leaving decision rules show a historical progression from unbounded rationality assuming omniscience towards more realistic assumptions of what information is available. At the omniscient end is the Marginal Value Theorem (Charnov, 1976) specifying that the optimal switching point is when the instantaneous rate of the reward falls to the mean rate in the environment under the optimal policy. But how should the animal know this mean rate without knowing the optimal policy already? McNamara and Houston (1985) proposed a simple iterative algorithm by which this might be learnt while foraging efficiently. Another problem is that when prey are discrete items turning up stochastically, the underlying rate (=probability) of reward is not directly observable. The optimality models of Iwasa et al. (1981) and others are one response to this situation, but another is the simpler rule, not derived from an optimality model, of giving up after a constant time without finding an item. If the giving-up time parameter is appropriate, the performance may come close to that of the optimum rule (Green, 1984). In the real world, in which environmental parameters are uncertain, it could be that the giving-up time rule works better than the optimum computed for a simple model of the environment. A more recent example concerns when a bee should leave one inflorescence for another; the problem is that bumblebees increasingly revisit flowers that they have just emptied because they can only remember the last few visited. Goulson (2000) proposed that a good solution that agreed with bumblebees’ observed behaviour is to leave once two empty flowers are found. Other workers have modified optimality models to incorporate characteristics of known or hypothesised psychological mechanisms, such as Weber’s Law, Scalar Expectancy Theory and rate-biased time perception (Kacelnik and Todd, 1992; Todd and Kacelnik, 1993; Hills and Adler, 2002).

4. Heuristics are precise testable models of proximal mechanism

Having used specific examples to give a flavour first of the ABC programme and then of biological research on rules of thumb, we now start to explain more about the principles and assumptions underlying the former. The ABC programme has two interrelated components: the first is to study the heuristics that people actually use, the second is to demonstrate in which environments a given heuristic performs well. We call the first the study of the “adaptive toolbox”, and the second the study of the “ecological rationality” of heuristics. The next two sections address how ABC models the adaptive toolbox.

ABC is concerned with the cognitive process of decision-making, and in particular with which sources of information are considered and how they are processed in combination. Our concern is with mechanism, not merely with how behaviour depends on cue values (what optimality modellers call the policy). Although observations of the policy can lead us to reject some candidate mechanisms, this is not a sufficient test because a variety of mechanisms can generate identical policies. For instance, Take The Best makes decisions indistinguishable from multiple regression if the cue weights are non-compensatory. They are, however, distinguishable if one can monitor how many cues are examined and in which order.

Much decision-making depends on information already present in memory. We cannot rely on self-reports to know how we access such memories, but some information is obtainable from timing. For instance, one might hypothesise that humans rank two-digit numbers using the lexicographic strategy of first comparing the first digits alone, and only in the case of a tie looking at the second digit. In this example, the lexicographic heuristic must be rejected because experiments have shown that the timing of the decision does depend on the second digit even if the first digits differ (Moyer and Landauer, 1967).

It is an open question whether the same heuristics are used when the information is external in the environment as when it is already in internal memory. The results of Bröder and Schiffer (2003) suggest a difference. But external search, besides being much more tractable to study, is of importance in its own right, and also of practical relevance in formulating advice about

how internet sites, for instance, should present information. Using the program Mouselab it is possible to present information on a computer screen but require subjects to click on a button to read a cue value, so that we at least know the order in which they seek information and when they stop information search (Payne et al., 1993). Another potential approach is eye tracking.

Combining sources of information is a feature of decision-making in not just animals but even bacteria and plants: for instance, for a seed to germinate in response to springtime warmth or photoperiod often requires weeks of winter chilling to remove dormancy (Bradbeer, 1988); this requirement prevents premature germination in autumn. Some insects show strikingly similar requirements before emerging (Tauber and Tauber, 1976). The mechanism in plants cannot be the same as what is known of the process in the insect brain (Williams, 1956), but in principle the same algorithm might describe how the cues interact. ABC’s level of analysis is algorithmic, in the sense of Marr (1982). One advantage of this approach is that conclusions might apply across different decisions and different organisms; indeed, they also have relevance for programming computers. Another advantage is that algorithmic explanations are often simple enough to be readily comprehensible. To understand how computers perform a sorting task, for instance, it is natural to seek explanations at the algorithmic level, ignoring the chip’s circuitry.

In some invertebrates remarkable progress has been made in explaining some aspects of cognition in terms of the underlying neurobiology, although gaps in our knowledge remain in even the best-known systems (e.g. olfactory learning in honeybees: Menzel, 2001; Menzel and Giurfa, 2001). There is no prospect in the near future of the kind of cognitive processes that ABC considers in humans becoming understandable in such terms. However, brain imaging does provide a window to test whether some of the hypothesised processes occur. Heuristics are assumed to exploit evolved abilities such as recognition memory (Recognition Heuristic), recollection memory (Take The Best), and object tracking (ball-catching heuristics). Therefore, one can test whether, in situations where people act as predicted by a given heuristic, brain areas that are known to specifically reflect the corresponding ability are activated. The first study of this kind has used functional Magnetic Resonance Imaging (fMRI) to test whether decisions

made when the Recognition Heuristic can be applied are indeed accompanied by activation of brain regions underlying recognition memory but not of those underlying guessing or recollection memory (Volz et al., *in press*).

A complementary approach to testing the physical reality of a proposed heuristic is to attempt to model it using a framework such as ACT-R (Anderson et al., 2004). This is based on a restricted set of processing modules the properties of which are constrained by numerous independent studies. Translating a heuristic into ACT-R both confirms that it is cognitively plausible and makes testable predictions about reaction times and fMRI results. ABC has made a start with using ACT-R, for a model of a version of the Recognition Heuristic (L. Schooler, R. Hertwig, personal communication).

The heuristics that ABC describes may rely on input variables that require complex calculations to compute. For instance, the ball-catching heuristics rely on the ability to track a moving object against a noisy background, which is developing in two- or three-month-old infants (Rosander and von Hofsten, 2002), but which is extremely difficult to program computers to do. ABC's heuristics exploit these abilities but do not attempt to explain their mechanisms. The underlying assumption is of a hierarchical organisation of cognitive processing: heuristics on top of evolved or learned abilities. There is good evidence of a hierarchy in insects, because much of the processing is peripheral and electrodes can monitor what information is passed on to the central nervous system. It is less clear how well the assumption holds in vertebrates. ABC does not claim that algorithmic models are necessarily the best level of analysis for all that goes on in brains. The peripheral processing in retinas, for instance, can involve clever neuronal circuitry that perhaps is better analysed with models of neural networks. The same argument may apply to some higher level capabilities in humans: face recognition and language processing are possible instances. A computing analogy might be some time-critical task that has been written in machine code (or perhaps even out-tasked to a special video chip) and thus remains opaque to another programmer who knows only higher level languages (cf. Todd, 1999).

Equally, ABC does not deny that humans can consciously perform highly complex calculations to compare options. The question is whether they trouble to do

so for routine decisions, and also whether it is adaptive for them to bother.

The heuristics that ABC has proposed are highly specified; they are readily convertible to computer code and they yield bold quantitative predictions that are amenable to testing. This contrasts with most models of heuristics in cognitive psychology, which are often specified only at a level of detail described by block diagrams and arrows indicating that one quantity has some unquantified influence on another. Such models are typically so vague in their predictions that they are impossible to test. In order to facilitate rigorous testing, ABC tries to avoid heuristics with free parameters that must be fitted anew to each dataset or to each individual, unless they can be estimated independently. This is not because we necessarily deny that, for instance, there are individual differences in personality that might affect how or which heuristics are applied.

Given that real heuristics have not been written by a programmer but have evolved by the messy process of natural selection, and given that they are enacted by neurones not silicon, ABC's precisely specified models seem likely to be simplifications capturing the broad principle but eventually requiring adjustments in the detail. Nevertheless, on the current evidence perhaps less adjustment will be necessary than one might suppose.

5. The attractions of simplicity

The heuristics studied by ABC are simple in comparison with standard statistical procedures applied to the same task. Proposals by other psychologists for how our minds tackle these tasks typically also involve more complex processes such as Bayesian probability updating. Part of the reason why ABC's heuristics can be simple is that as their input they can utilise evolved or highly trained abilities, such as recognition memory, that may involve complex data processing.

It is not just Occam's Razor that has made ABC favour simple models. But we will start off by mentioning the weakest reason. That is that with simple heuristics we can be more confident that our brains are capable of performing the necessary calculations. The weakness of this argument is that it is hard to judge what complexity of calculation or memory a brain might achieve. At the lower levels of processing, some hu-

man capabilities apparently involve calculations that seem surprisingly difficult (e.g. Bayesian estimation in a sensorimotor context: [Körding and Wolpert, 2004](#)). So, if we can perform these calculations at that level in the hierarchy (abilities), why should we not be able to evolve similar complex strategies to replace simple heuristics?

One answer is that simple heuristics often need access less information (i.e. they are frugal) and can thus make a decision faster, at least if information search is external. Another answer, and a more important argument for simple heuristics, is the high accuracy that they exhibit in our simulations (e.g. see [Fig. 1](#)). This accuracy may be because of, not just in spite of, their simplicity. In particular, because they have few parameters they avoid overfitting data in a learning sample, and consequently generalise better across other samples. The extra parameters of more complex models often fit the noise rather than the signal ([MacKay, 1992](#); [Hertwig and Todd, 2003](#)). Of course we are not saying that all simple heuristics are good: only some simple heuristics will perform well in any given environment.

Although we would argue strongly that ABC has made an important advance in demonstrating how well simple frugal heuristics can perform, we do not yet know how generally the claim of “simple is good” can be extended. In the hope of stimulating others to test our claims, we now play the devil’s advocate and question the generality of our results. For instance, we cannot claim to have evidence that simple heuristics perform better than more complex ones for every task. Moreover, even in the tasks that we have investigated, we have inevitably not considered all possible heuristics, and the set considered is biased towards simplicity, so we cannot be sure that there are not other more complex heuristics that achieve equally impressive performance. For instance, although one strength of simple heuristics is that they generalise well by avoiding overfitting, other much more complex statistical procedures have also been designed to avoid overfitting (e.g. classification and regression trees, CART in [Fig. 1](#); [Breiman et al., 1984](#)).

It is tempting to propose that since other animals have simpler brains than humans, they are more likely to have to use simple heuristics. But a contrary argument is that humans are much more generalist than most animals, and that animals may be able to devote more cognitive resources to tasks of particular impor-

tance. For instance, the memory capabilities of small food-storing birds seem astounding by the standards of how we expect ourselves to perform at the same task ([Balda and Kamil, 1992](#)). Some better examined biological examples suggest unexpected complexity: for instance, pigeons seem able to use a surprising diversity of methods to navigate, especially considering that they are not long-distance migrants ([Wiltschko and Wiltschko, 2003](#); but cf. [Wallraff, 2001](#)). The greater specialism of other animals may also mean that the environments that they deal with are more predictable, and thus that the robustness of simple heuristics may no longer be such an advantage (cf. the argument of [Arkes and Ayton, 1999](#), that animals in their natural environments do not commit various fallacies because they do not need to generalise their rules of thumb to novel circumstances).

A separate concern is that for morphological traits there are plenty of examples of evolution getting stuck on a local adaptive peak and not finding its way to the neatest solution. The classic example is the giraffe’s recurrent laryngeal nerve, which travels down and then back up the neck because in all mammals it loops round the aorta. Nobody knows how common such a situation might be with cognitive traits. It could be that humans’ ability to learn through experience makes them more readily adopt simple heuristics than other animals that are more rigidly programmed and where natural selection alone is responsible for the adaptation.

Another way to consider the recurrent laryngeal nerve is that it may be simple in terms of what is easy for existing embryological processes to engineer. We can only make plausibility arguments about what algorithms are difficult for an organism to build or evolve. Those that are simple to engineer need not be those that are simple to describe: a perfect linear response is simple to describe but perhaps often difficult to engineer physiologically. For instance, nectivorous insects judge meal volume with stretch receptors in their guts, but the way these receptors work results in a non-linear response ([Real, 1992](#)). Artificial neural networks may provide some guidance about what sorts of processing is easy or hard to engineer ([Real, 1992](#); [Webb and Reeve, 2003](#)). However, what is easy to hardwire need not be easy to calculate consciously. For humans acting consciously, a weighted-additive calculation is much harder than tallying (weights all unity), but for an insect specialised on a specific task, evolution can have

hardwired the weights (for instance, by controlling sensitivity of the receptors for different cues); then the insect need simply tally these ready-weighted cues, yet it achieves what to us looks like a harder weighted-additive calculation (Franks et al., 2003).

6. Adaptation and ecological rationality

The following sections deal with the fit of the heuristics to the environment, which ABC refers to as ecological rationality. In this section, we compare and contrast this with biologists' concern with adaptation. Adaptation is the assumption underlying optimality modelling, a technique that has dominated behavioural ecology, and the next section will consider how useful this might be in investigations of cognitive mechanism. We will then turn from mechanisms to the other blade of Simon's scissors (1990), the environment.

ABC's research programme is very much concerned with heuristics working well in the environment in which they perform. Biologists mostly deal with rules of thumb that are adapted through natural selection, but the human heuristics that ABC studies have also been honed by individual or cultural learning of what works well. A likely possibility is that natural selection has set humans up with a set of heuristics (the adaptive toolbox: Gigerenzer et al., 1999) each member of which we can readily learn to apply as appropriate to a specific environment. Or the building blocks of heuristics (such as when to stop search) might be readily recombined to create novel heuristics suitable for a novel task. These possibilities deal with the objection that humans have not had time to evolve heuristics to cope with today's environments. If two environments share a common statistical structure, the same heuristics will work well. We require only a mechanism for learning or reasoning which heuristic from our toolbox works best in a novel environment (Rieskamp and Otto, submitted for publication).

The idea of adaptation is, of course, old hat to most biologists; they see no reason to believe that cognition is not adapted like everything else—hence, the field of cognitive ecology (Dukas, 1998; Shettleworth, 1998). Nevertheless, biologists face the same problem as psychologists that much behaviour must be studied in the artificial environment of the laboratory where its adaptive significance need not be obvious. For instance, one

result that has worried behavioural biologists is that in operant “self-control” experiments animals tend to forgo the option with a higher long-term reward rate in favour of one in which less food is delivered but with less delay (Logue, 1988). Recently, Stephens and Anderson (2001) suggested that a rule of thumb based on maximising short-term gain rate makes adaptive sense when the same reward structure as in the self-control experiments is presented in a patch-leaving context. In that context the difference in short-term rates between staying a short time or a long time in a patch agrees with, and even amplifies, the difference in long-term rates (see also Real, 1992; Stephens, 2002; and cf. Kareev, 2000). The argument is that the operant self-control task in which the decision rule had first been recognised, and in which it appeared deleterious, is an artificial situation, which played no part in the rule's evolution or maintenance. Such a result mirrors some of ABC's work (and that of other psychologists) pointing out that what have been viewed as maladaptive biases in humans are the by-products of rules that make adaptive sense in an appropriate environment (e.g. Arkes and Ayton, 1999; Hoffrage et al., 2000; Gigerenzer, 2000, Chapter 12).

The biologists' evolutionary perspective at least made them hanker for an adaptive explanation for the self-control results. Biologist readers may be amazed that adaptation is not at all a universal consideration in psychology. In fact, human psychologists do have a plausible defence. Many argue that our brain has evolved as a general-purpose calculating machine and that most of its capabilities, such as a facility at chess, are mere by-products, which have not been subject to direct selection. Allied to the general-purpose-calculating-machine viewpoint is the normative assumptions of the heuristics-and-biases school of Kahnemann and Tversky, that heuristics should be judged by whether they follow the rules of logic (Gilovich et al., 2002). Philosophically, ABC argues instead that what matters is not logic but performance, and that in real environments many so-called biases are adaptive (Gigerenzer, 2000, Chapter 12). And empirically we have found it a highly illuminating research strategy to apply the working assumption that our decision-making heuristics fit the statistical structures in our environments.

By “adaptation” biologists imply not only that a trait fits the environment but that it has been shaped by the

environment for that task. Therefore, claims of adaptation of heuristics are vulnerable to the arguments of the biologists Gould and Lewontin (1979), who were concerned about many claims of adaptation in biology being mere “just-so stories”. Unfortunately, human psychologists are not able to utilise many of the lines of evidence that biologists apply to justify that a trait is adaptive. We can make only informed guesses about the environment in which the novel features of human brains evolved and, because most of us grow up in an environment very different to this, the cognitive traits that we exhibit might not even have been expressed when our brains were evolving (Dawkins, 1982, p. 38). Biologists use a more detailed fit of trait to environment as evidence for adaptation, but because simple heuristics have few characters (e.g. parameters), even this approach may be unavailable.

It thus would be a weak argument (which ABC avoids) to find a heuristic that humans use, then search for some environment in which that heuristic works well, and then claim on this basis alone that the heuristic is an adaptation to that environment. The heuristic may work well in that environment, but that need not be the reason why it evolved or even why it has survived. For instance, our colleagues L. Schooler and R. Hertwig (personal communication) have constructed a model demonstrating that for a type of Recognition Heuristic it can be beneficial that we forget out-of-date information at a certain rate; but memory is used for a diversity of other purposes, so they rightly avoid claiming that this model explains the length of our memories. To claim adaptation, it is at least necessary to check that the heuristic is generally used only in environments in which it works well and better than other heuristics that we use in other contexts. ABC’s empirical research programme has yet to develop this far, although there is no barrier to it doing so.

ABC avoids the difficult issue of demonstrating adaptation in humans by defining ecological rationality as the performance, in terms of a given currency, of a given heuristic in a given environment. We emphasise that currency and environment have to be specified before the ecological rationality of a heuristic can be determined; thus, Take The Best is more ecologically rational (both more accurate and frugal) than tallying in non-compensatory environments, but not more accurate in compensatory ones (Fig. 2). Unlike claiming that a heuristic is an adaptation, a claim that it is ecolog-

ically rational deliberately omits any implication that this is why the trait originally evolved, or has current value to the organism, or that either heuristic or environment occur for real in the present or past. Ecological rationality might then be useful as a term indicating a more attainable intermediate step on the path to a demonstration of adaptation. There is nevertheless a risk that a demonstration of ecological rationality of a given heuristic in a given environment will mislead someone who uses this evidence alone to infer adaptation. Think of the Victorian habit of noting the most fanciful resemblance of an animal to a part of its environment as an adaptation. This reached its apogee in such ridiculous illustrations as pink flamingos camouflaged against pink sunsets (Gould, 1991, Chapter 14; sexual selection is the real explanation for most bright plumage).

7. Why not use optimality modelling?

Optimality modelling is used in behavioural ecology mostly as a test of whether a particular adaptive argument explains a particular phenomenon. The model is constructed to include the components of the explanation (maximised currencies, constraints, trade-offs, etc.) and often a deliberate minimum of anything else. The next stage is to calculate the optimal behaviour given these assumptions. If these predictions match empirical data, one can claim to have a coherent explanation for why that behaviour occurs. Sometimes the match occurs only over a restricted range of a model parameter, in which case measuring or varying the corresponding characteristic in the real world offers a further empirical test. In the absence of a match, a new or modified explanation must be sought.

ABC’s concern with adaptation to the environment might seem to ally it with optimality modelling. Much of ABC’s research has involved finding what decision rules work *well* in a model environment; optimality modelling involves finding what decision rules work *best* in a model environment. In both instances good performance is the basis of predictions, or even expectations, about the rules actually used. Optimality modelling has the attractions that there is no arbitrariness in deciding whether a heuristic works well enough, and no uncertainty whether there might be another better heuristic that one had not thought of. Moreover, it has

proved its practical utility in dominating the successful fields of behavioural ecology and biomechanics, making testable predictions that have not only stimulated empirical research but also strikingly often been well supported by the data. So, why does ABC not take this road?

Typically one prediction of an optimality model is the policy, which describes what behaviour is performed given any specified value of an individual's external environment and internal state. Although the policy can itself be viewed as a decision rule, it is the mechanisms generating policies that interest ABC and other psychologists. Behavioural ecologists do believe that animals are using simple rules of thumb that achieve only an approximation of the optimal policy, but most often rules of thumb are not their interest. Nevertheless, it could be that the limitations of such rules of thumb would often constrain behaviour enough to interfere with the fit with predictions. The optimality modeller's gambit is that evolved rules of thumb can mimic optimal behaviour well enough not to disrupt the fit by much, so that they can be left as a black box. It turns out that the power of natural selection is such that the gambit usually works to the level of accuracy that satisfies behavioural ecologists. Given that their models are usually deliberately schematic, behavioural ecologists are usually satisfied that they understand the selective value of a behaviour if they successfully predict merely the rough qualitative form of the policy or of the resultant patterns of behaviour.

But ABC's focus on process means that it is concerned with a much more detailed prediction of behaviour. A good model of the process can lead to predictions of behaviour that differ from standard optimisation models or for which optimisation models are mute. For instance, the ball-catching heuristics mentioned in Section 2 predict that the player catches the ball while running, the precise running speeds, and when players will run in a slight arc. All these predictions concern observable behaviours. The example of *Polistes* nest construction (Section 3) also showed how much more specific process models can be.

Nevertheless, there are several ways in which optimality modelling can help to suggest what rules of thumb the animal uses.

(1) The optimal policy provides clues. It does at least indicate aspects of the environment to which de-

isions might usefully respond, although it may be indirect cues that are actually used. Conversely, optimality modelling is helpful in pointing out what aspects of the environment a decision heuristic should ignore. In certain cases the optimal policy may be so simple that it can be generated by a simple heuristic. For instance, if items are randomly (Poisson) distributed across patches, [Iwasa et al. \(1981\)](#) showed that the optimal leaving rule is to spend a constant time in each patch regardless of foraging success. In other cases an examination of the form of the optimal policy can suggest a heuristic that would come close to generating such a policy. Thus, for a different patch-leaving model, [Green \(1984\)](#) plotted against the time spent on the patch the critical number of prey items that must have been found to make it worthwhile to stay longer. The calculations required were computationally involved but the thresholds fell quite close to a straight line through the origin, suggesting a simple rule that would perform close to optimally.

(2) If enacting the optimal policy would require, say, unrealistically extensive knowledge or demanding memory requirements to be achievable, it is possible to introduce more realistic information constraints into an optimality model. Several optimality models examine the effects of a restricted memory on performance and behaviour (e.g. [Hutchinson et al., 1993](#); [Roitberg et al., 1993](#); [Bélisle and Cresswell, 1997](#)). More common, and differing only in degree of specification, is to constrain the rule of thumb to be of a particular non-optimal form but use optimality to specify the values of any parameters. The expectation is that an adapted heuristic lies on a local optimum. Such an approach has been used both by biologists and members of ABC for mate choice rules ([Real, 1990b](#); [Wiegmann and Mukhopadhyay, 1998](#); [Todd and Miller, 1999](#); [Hutchinson and Halupka, 2004](#)), and [Real \(1990a\)](#) points out that in the appendix to Simon's classic paper on satisficing, [Simon \(1956\)](#) also uses optimality to set the threshold. As we learn more about an organism's sensory and cognitive capacities, and so can add ever more realistic constraints to an optimality model, one might hope that the different approaches converge in their predictions.

(3) Optimality modelling can be applied to the processes of gathering information and stopping search. Thus [Fawcett and Johnstone \(2003\)](#) calculated the optimal order of cues to examine given cues that differed in costs and informativeness. [Luttbegg \(1996\)](#) calculated

how a female should concentrate sampling effort on those males that earlier had appeared the most promising.

(4) Optimality modelling may help us in providing a gold standard against which to compare performance of candidate heuristics. If a simple heuristic performs almost as well as the optimum, there is less need to search further for a better heuristic. An ABC paper in this spirit is [Martignon and Laskey \(1999\)](#), which computes a Bayesian network against which to compare the performance of Take The Best.

(5) Any fine-scale mismatch between optimality prediction and observation can be suggestive of what rule of thumb is being used (although there are other potential reasons for a lack of fit—errors in model specification, evolutionary time lags, etc.). Even if the nature of the mismatch does not itself suggest the rule of thumb, it at least highlights a problem to which the solution may be the mechanism used by the animal. Thus, [Müller and Wehner \(1988\)](#) were stimulated by the systematic errors that ants make in path integration (i.e. their deviation from the optimal solution of heading straight back to the nest) to suggest a rule of thumb that explains these errors. This rule is to average the angles of each outward step, weighted by the distance moved. Another example is that the classic optimality models of diet choice predict a sudden switch from complete unselectivity to complete specialisation as density increases. However, experiments typically find gradually increasing partial preferences instead (e.g. [Krebs et al., 1977](#)). This was the stimulus to suggest various refinements that would explain the difference, such as that the birds make discrimination errors, or that they have to estimate prey density or value with learning rules that are sensitive to runs of bad luck. Such constraints and mechanisms can be incorporated in a new generation of more realistic optimality models (e.g. [Rechten et al., 1983](#); [McNamara and Houston, 1987a](#); [Bélisle and Cresswell, 1997](#)). As long as the additional hypotheses are confirmed by testing further independent predictions, this process of successively improving models can progressively inform us about cognitive mechanisms ([Cheverton et al., 1985](#)).

Thus we would encourage optimality modellers to consider decision processes to be interesting topics that their technique might address. Indeed, the rational analysis school of psychology has had some success with that approach ([Anderson, 1990](#); [Chater and Oaksford,](#)

[1999](#)). However, there remains a more fundamental reason for ABC's objection to the routine use of the optimality approach. There are a number of situations where the optimal solution to a real-world problem cannot be determined. One problem is computational intractability, such as the notorious travelling salesman problem ([Lawler et al., 1985](#)). Another problem is if there are multiple criteria to optimise and we do not know the appropriate way to convert them into a common currency (such as fitness). Thirdly, in many real-world problems it is impossible to put probabilities on the various possible outcomes or even to recognise what all those outcomes might be. Think about optimising the choice of a partner who will bear you many children; it is uncertain what partners are available, whether each one would be faithful, how long each will live, etc. This is true about many animal decisions too, of course, and biologists do not imagine their animals even attempting such optimality calculations.

Instead, the behavioural ecologist's solution is to find optima in deliberately simplified model environments. We note that this introduces much scope for misunderstanding, inconsistency and loose thinking over whether "optimal policy" refers to a claim of optimality in the real world or just in a model. Calculating the optima even in the simplified model environments may still be beyond the capabilities of an animal, but the hope is that the optimal policy that emerges from the calculations may be generated instead, to a lesser level of accuracy, by a rule that is simple enough for an animal to follow. The animal might be hardwired with such a rule following its evolution through natural selection, or the animal might learn it through trial and error. There remains an interesting logical gap in the procedure: there is no guarantee that optimal solutions to simplified model environments will be good solutions to the original complex environments. The biologist might reply that often this does turn out to be the case, otherwise natural selection would not have allowed the good fit between the predictions and observations. Success with this approach undoubtedly depends on the modeller's skill in simplifying the environment in a way that fairly represents the information available to the animal. The unsatisfying uncertainty of how to simplify is often not appreciated. [Bookstaber and Langsam \(1985\)](#) argue that by choosing simple models with many of the uncertainties ignored, we introduce

a bias in the optimal behaviour predicted, favouring complex rules over coarser ones.

The same criticism about simplification of real environments can also be made of any simulation of a heuristic in a model environment, so much of ABC's research is as vulnerable to the argument as optimality modelling. ABC has tried to avoid the criticism by using data from a variety of real-world environments. (This technique is rare in biology, but an analogous example is Nakata et al.'s (2003) testing of web-relocation rules in spiders; rather than make assumptions about the temporal and spatial autocorrelations in prey capture rates, they used observed rates from sticky traps set out in the field.) ABC demonstrated the high performance of Take The Best on a diverse set of 20 real-world problems (Czerlinski et al., 1999). It was hoped that the environmental structures in these examples would be representative of problems in other domains. However, these supposedly real-world problems are still gross simplifications from the sorts of decisions that we really face. For instance, the performance criteria were just frugality and accuracy, it had already been determined which cues were available, and there were no search costs. Another limitation is that one can judge how far the performance results are general to other decision problems only by understanding what statistical structures in these environments influenced performance of the heuristics tested. The best way to prove that a statistical structure has the hypothesised effect on performance is to construct simple model environments.

8. Environment structure

It should already be clear that ABC has an interest in identifying what statistical properties of the environment allow particular heuristics to perform well. Their identification enables us to predict in which environments a heuristic is used. We might then go on to ask whether such statistical properties are easy to recognise, and hence how a heuristic for selecting appropriate heuristics might work.

When describing the example of Take The Best we have already mentioned two pertinent aspects of environment structure, whether the cues are non-compensatory (Fig. 2) and the size of the learning sample (Fig. 1). Another aspect is whether cues show many

negative correlations with each other (specifying that high values of a cue always indicate, other things being equal, a better option; Johnson et al., 1989; Shanteau and Thomas, 2000). Negative correlations might be typical of competing commercial products, because, for a product to survive in the market place, traits in which it is weak must be compensated by other desirable features (e.g. for cars, a low maximum speed may be associated with low price or high safety). This is a different environment structure from city sizes, and also perhaps from male traits used by females for mate choice, where quality variation might be expected to generate a positive correlation between all traits (which is observed in some examples, but others show no correlation: Candolin, 2003). Other aspects of environment structure that ABC has analysed are "scarcity" (the number of objects relative to the number of cues in the learning sample; Martignon and Hoffrage, 2002) and the skewness of frequency distributions (Hertwig et al., 1999).

Behavioural ecology has also considered what aspects of the environment favour different rules of thumb, but often by using analytic techniques in combination with the optimality approach. We have already mentioned Iwasa et al.'s (1981) derivation of optimal patch-leaving rules, showing that how evenly prey are spread amongst patches determines whether a prey capture should make the predator more or less likely to move. Another example is McNamara and Houston's (1987b) derivation of how the forgetting rate of a simple linear-operator memory rule should depend on the rate at which the environment changes.

Autocorrelation in food supply may be an important aspect of environment structure for animals. One would predict that nectar-feeders would avoid returning to a flower immediately after exploiting it, but return once it has had time to refill. Whereas bird species feeding on aggregated cryptic invertebrates remain in a good spot (win-stay), nectar-feeding birds indeed tend to "win-shift" in the short-term (Burke and Fulham, 2003). Even naive captive-reared honeyeaters *Xanthomyza phrygia* more easily learned to win-shift than win-stay with short delays between feeding sessions, but vice versa with long delays (Burke and Fulham, 2003). An easy rule to ensure returning at regular intervals to a resource is to follow the same route repeatedly; such traplining behaviour is shown by nectar-feeding birds and insects as well as birds feed-

ing on flotsam along stream edges (e.g. Davies and Houston, 1981; Thomson, 1996). Spatial, rather than temporal, autocorrelation may be the important statistical structure determining movement rules for species feeding on non-renewing hidden food (e.g. Benhamou, 1992; Fortin, 2003).

9. Social rationality

For both humans and animals, an important component of their environment is social; that is it is generated by other individuals. Even plants can be considered to show social heuristics: for instance, seeds may use cues such as daily temperature fluctuations to sense when competitors are absent (Thompson and Grime, 1983). A simple human example of an adaptive social heuristic is to copy the choice of meal of someone who is more familiar with the restaurant.

There has been much analysis in both the human and biological literature concerning when it pays to copy other individuals (e.g. Henrich and Boyd, 1998; Sirot, 2001). One specific example concerns escape flights in flocks of wading birds. Birds in a flock that see their neighbours flying up should immediately copy them if it was a predator that alarmed the first bird. But how to avoid numerous false alarms? Checking for the predator themselves may be unreliable and cause delay, so instead Lima (1994) suggested that they might use the simple rule of flying only if at least two other birds in the flock have flown up simultaneously. Modelling confirms that this is an efficient strategy except when flock size is small (Proctor et al., 2001), and there is also empirical evidence of its use (Cresswell et al., 2000).

Not all social heuristics involve copying, and interaction may be only indirect. For instance, Thuijsman et al. (1995) considered simple rules responding to nectar volume that bees might use to choose between alternative patches of flowers. Although these rules seemed maladaptive when applied to an individual foraging in isolation (they cause matching), they made good sense in an environment where there are competitors for the nectar (they then produce an ideal free distribution). With hummingbirds sometimes an individual has a flower to itself, and sometimes competitors also visit (Gill, 1988). If a flower's nectar supply declines because of competition, the bird should decrease intervals

between visits, but increase them if weaker production caused the decline.

In the case of many social situations, what heuristic is adaptive for one player depends on the heuristic used by another. If this is mutual, the obvious method of analysis is game theory, which is widely used in theoretical biology. Most biological game theory centres on finding the Evolutionary Stable State (Maynard Smith, 1982), where both players behave optimally given the strategy of their opponent. This takes us back to ABC's objections to routinely using an optimality approach, but many game-theoretic biological models are often so abstract that the lack of realism of strategies such as hawk and dove is not an issue. This does not mean that they need be useless in helping us understand rules of thumb; for instance, game-theoretic analysis of the handicap principle has transformed our expectations of what sorts of mate-quality cues are attended to (Grafen, 1990). Nevertheless, as game-theoretic models become tailored more closely to real situations, it can turn out to be critical how we model what information is available to each player, and thus how they can "negotiate" (e.g. Barta et al., 2002).

Indeed, it is up to the modeller to specify the strategy set, and there is no reason why this cannot be restricted to plausible rules of thumb. Ongoing research at ABC (J.M.C. Hutchinson, P.M. Todd, C. Fanselow, personal communication) considers adaptive car parking heuristics in this context: the best heuristic for deciding whether to accept a parking space now or try closer to the destination depends on the patterns of cars in the car park, which depend on the heuristics used by other drivers. We set up computer tournaments between different candidate heuristics, each of which could vary in at least one parameter. The car park layout was kept constant but the less successful heuristics were less likely to be reused by drivers. The frequencies of competing strategies and of their parameter values were then left to "evolve". The victorious heuristic required that two conditions be satisfied for a space to be accepted: one was that it lay within a fixed distance of the destination, and the other that the local density of spaces was low. Leaving aside the question of how representative our single car park is of the diversity of real parking situations, our model is unrealistic in how deterministically the rule frequencies adjust depending on average performance in the preceding generation. In reality, each person is likely to show lots of noise in the

strategies they use, which can considerably affect what strategies are favoured in response (McNamara et al., 2004). So, there is a long chain of uncertain reasoning involved in a fully game-theoretic analysis. An alternative approach would be simply to calculate which heuristics perform well in response to patterns of spaces observed on real streets.

Computer tournaments between simple strategies were also the original method of analysis of the Iterated Prisoner's Dilemma game (Axelrod and Hamilton, 1981) in which one of the simplest strategies, Tit for Tat, was the victor. Tit for Tat has stood up remarkably well to new challengers, although recently a more complex rule has been claimed as superior (Hauert and Stenull, 2002). More important is that this paradigm has been influential in getting both economists and biologists thinking in terms of simple algorithmic response strategies, with sometimes deliberately limited cognitive abilities (Hoffmann, 2000). Unfortunately, existing claims of animals using Tit for Tat are unconvincing (Hammerstein, 2003); part of the problem is that real biological situations are much more complex than the Iterated Prisoner's Dilemma game, so that other strategies become available.

Another aspect of social rationality that ABC has started to investigate is the mechanisms by which individuals in a group amalgamate their separate knowledge or judgements to make a group decision (Reimer and Katsikopoulos, 2004). Maybe there is something to be learnt in this regard from research on group decision-making in social insects. For instance, Seeley (2003) considers how honeybees use simple rules to compare the quality of different potential nest sites even though no individual need have visited more than one site. Scouts that have discovered an inferior nest site advertise it (dance) less vigorously and for less time. Recruits are consequently more likely to visit the better sites, and dancing for inferior sites dies out. Seeley and Visscher (2003, 2004) discuss why it is adaptive that the colony moves when a critical-sized quorum (10–15 individuals) agree on one site, rather than waiting for a consensus or majority. This sounds like satisficing in that the colony takes the first option exceeding a threshold, but it is not a case of ignoring all but the first acceptable site, because scouts may already have visited other sites and competed to recruit nestmates.

A similar quorum rule has evolved in ants (Pratt et al., 2002). Franks et al. (2003) argued that this and other

voting methods restrict the sorts of heuristics that an ant colony can use to choose between nest sites. They considered such models as satisficing, Elimination by Aspects and lexicographic strategies, but produced firm evidence both that ants consistently select the best site and that even the least important cue could affect a decision. Thus, a weighted-additive model fitted best. They argued that such a mechanism may be inevitable in a parallel-processing superorganism in which the method of decision is roughly counting votes of individual workers weighted by their individual enthusiasm for their single site. This mechanism makes it infeasible that the colony could consider attributes successively in turn even if a non-compensatory environment structure would favour this.

10. How biologists study rules of thumb

Having now explained the principles behind the ABC programme, we concentrate again on biological research on rules of thumb. In this section we contrast the techniques of the two disciplines.

Many behavioural ecologists are interested mostly in the ultimate function of behaviour. To them rules of thumb may mostly seem important in providing a possible excuse if their optimality models fit only approximately. Then there are rarer behavioural biologists who, very much like ABC, do have an interest in the adaptation of rules of thumb. They may use similar simulation techniques to compare the performance of different rules of thumb. For instance, Houston et al. (1982) considered how a forager should decide between two resources providing food items stochastically each with an unknown reward rate (a "two-armed bandit"). Candidate rules of thumb included "Win-stay, Lose-shift", probability matching, and sampling each resource equally until one had yielded d more successes than the other. Which was the best rule depended on the environment, although the first two examples were generally the worst.

The simulation approach has the limitation that there is no guarantee that there are not simpler or better rules. One test is to give a real animal exactly the same task as the simulated agents and compare performance: thus, Baum and Grant (2001) found that real hummingbirds did better in two of their three model environments than did any of the simulated simple rules of movement. An-

other check on the biological relevance of postulated rules of thumb is to compare behaviour of the simulated agents with that of real animals. Some papers use the same simulation model to predict both behaviour and performance (e.g. Wajnberg et al., 2000). In this example, the parameters of the patch-leaving rule were first estimated from experimental data, but then varied to examine which mattered for performance. Other papers use simulation only to check whether postulated decision rules can explain observed emergent behaviours (e.g. Ydenberg, 1982; Keasar et al., 2002; de Vries and Biesmeijer, 2002); ultimate function is not the main focus.

However, most biological research on rules of thumb has not involved computing but an experimental, bottom-up approach that starts by observing the animals and is usually not driven by anything but the most intuitive theoretical expectations of what rules would work well. The interest is in details of mechanism, maybe aiming down to the levels of neurones and molecules. ABC has emphatically not taken this approach, but much of human and animal psychology has this emphasis on discovering the details of the mechanism. Although research in this tradition usually starts by investigating the response to single cues, sometimes attention may later shift to examining how cues are integrated. With this approach, rules of thumb are not the testable hypotheses with which one starts an investigation but rather they emerge at the end of the process as broad summary descriptions of the more detailed patterns already discovered. The adaptive advantages of the observed mechanism over others may only appear as speculation in the discussion.

Some of the most elegant examples of this bottom-up approach come from the classic work of Tinbergen (1958), although for him ultimate function was certainly not always a peripheral issue. For instance, he was interested in how a digger wasp *Philanthus triagulum* finds its way back to its burrow. By building a circle of fir cones around the burrow and then moving them while it was away, he showed that wasps use such objects as landmarks. He went on to examine what sorts of objects are used as landmarks, at what point they are learnt, and how close landmarks interact with more distant ones. He also became interested in how the wasps found their prey. Using a variety of carefully presented models hanging from a thread he showed that what first alerted the wasps was the appearance of

a smallish and moving object; they then approached closely downwind to check its scent, jumped on it, and then could use tactile or taste cues to further check its suitability. Although the right scent was necessary as a second stage, and although they could retrieve lost prey items by scent alone, without the initial movement stimulus a correctly smelling dead bee attracted no interest. Tinbergen was also surprised that, although homing wasps showed great sophistication in recognising landmarks visually, hunting wasps were easily fooled into smelling a moving object that was visually very unlike their bee prey.

Some of this type of behavioural research has developed beyond the behaviour to examine the neurological processes responsible. This can sometimes be uniquely illuminating with regards to rules of thumb. For instance, Römer and Krusch (2000) have discovered a simple negative feedback loop in the ear of bushcrickets, which adjusts the sensitivity of the ear according to the loudness of the signal. The consequence is that the female's brain is totally unaware of all but the loudest male cricket in the vicinity (or possibly two, if a different male is loudest in each ear). The consequence behaviourally is a rule of thumb for mate choice of simply heading towards the male that appears loudest (usually the closest). Whether this is adaptive has not been considered. Unfortunately, results at this almost physiological level of analysis are still largely restricted to perception, learning and memory (e.g. Menzel et al., 1993; Shettleworth, 1998; Menzel and Giurfa, 2001), not yet revealing much about cue integration or decision-making.

Advances in molecular biology mean that other non-neural mechanisms of cue integration are also becoming accessible. For instance, recent work has established that there are three independent pathways influencing when an *Arabidopsis* plant flowers (one responds to photoperiod, one to chilling, and one is endogenous), and how these pathways interact is something molecular biologists now hope to answer (Simpson et al., 1999).

In summary, although some biologists study rules of thumb in the same way that ABC studies heuristics, most of the results derive from experiment that has not been driven by theory. Such work often throws up surprises in the particulars, which one hopes theory can explain. ABC relies on other schools of psychology, for instance the heuristics-and-biases school (Gilovich

et al., 2002), to provide some of the empirical surprises that its theories explain.

11. How animals combine information from multiple cues

Much of ABC's research has been on the integration of different cues, so a disappointment about the biological research is that most papers examine a single cue. Often all other cues are held constant. When the interactions between cues have been investigated, and lots of such studies exist, most often the results are not related to those of other such studies. Recently a few papers have reviewed how females integrate cues to male quality (Jennions and Petrie, 1997; Candolin, 2003; Fawcett, 2003, Chapter 3) but results from many other domains of decision-making could be connected (e.g. Partan and Marler, 1999). This is certainly somewhere that ABC can contribute to behavioural biology, by providing testable theory of what statistical structures of cues favour what methods of cue integration.

This is not the place for a thorough review of the empirical results, but a general conclusion is the diversity of methods used to combine cues. For instance, Shettleworth (1998, Chapter 7) reviews how animals combine cues used in navigation (local and distant landmarks, path integration, sun compass, etc.). Experiments indicate clear cases both of a sequential application of cues and of averaging the locations pointed to by conflicting cues. However, even in those species that average, if there is too much conflict between cues, they tend to fall back on large-scale spatial cues, which in nature are the most constant and reliable. An interesting comparison is the rules for dealing with conflicting temporal cues (Fairhurst et al., 2003).

We now focus in turn on sequential and non-sequential cue assessment, finding in each case that empirical results from biology might prompt new directions of research for ABC.

11.1. Sequential cue assessment

Most studies measure only how cue values and the availability of cues affect the outcome of choice, not the process, so we cannot readily tell whether assessment of cues is sequential. The exception is if there is an observable behavioural sequence in which different cues

are seen to be inspected at each stage before others are available, or where different cues predict breaking off the process at different stages. For instance, female sage grouse first assess males in a lek on the basis of their songs, and then visit only those passing this test for a closer visual inspection of display rate (Gibson, 1996). Such a "layered" process of sexual selection seems extremely widespread (Bonduriansky, 2003) and clear sequences of cue inspection are similarly well known in navigation and food choice. Note, however, that a sequential process need not necessarily imply a fixed cue order, nor that cues observed at one stage are ignored in decisions at later stages. Thus, either visual or olfactory cues in isolation are sufficient to attract hawkmoths to a flower, but both cues must be present to stimulate feeding (Raguso and Willis, 2002).

Even where the sequential aspect is not apparent, a clear ranking of importance of cues is at least compatible with a decision rule like Take The Best. For instance, honeybees trained to identify model flowers decide on the basis of colour only if the odours of two alternatives match, and on the basis of shape only if colour and odour match (Gould and Gould, 1988, Chapter 8). Gould and Gould explained this order on the basis of validity: odour was the most reliable cue to the species of flower, colour varied more from flower to flower, and shape varied depending on the angle of approach. They also are clear that by the time the bee gets close enough to sense flower odour, all three cues are available.

However, other examples suggest that ABC's sequential cue assessment models may need to be extended. One complication is that most cues are quantitative rather than the binary cues on which Take The Best operates. A threshold can convert quantitative into binary, which might be applicable for categorisation into species or sex (e.g. Vicario et al., 2001), but most tasks studied involve comparison of a continuous criterion such as quality. With quantitative characters the distinction between compensatory and non-compensatory becomes muddled. If two individuals differ considerably on one cue, there may be no useful information to be gained by looking at further cues; but if they differ only a little, it may be useful to consider further cues without necessarily discarding the information from the first cue. With quantitative cues we may find that which cues predict choices depends on which exhibit the most variation in that habitat and

that year (e.g. Lifjeld and Slagsvold, 1988). We might observe such a pattern even if the same method of cue integration were used in the different environments, but it would not be surprising if choosers learnt not to trouble to examine the less informative cues in that environment. Another complication with quantitative traits is that intermediate cue values may be more attractive than either extreme (e.g. Calkins and Burley, 2003).

Whereas for search in memory or search on a computer screen examining cues in order of decreasing validity may make good sense, in the biological examples other factors seem more important. In mate choice the more reliable cues to quality tend to be examined last. In locating resources the cue giving the most exact location tends to be examined last. One reason is likely to be the cost of sampling each cue in terms of risk, energetic expenditure or time. For instance, mock fighting another male may be the most reliable cue to which of you would win a real fight, but mock fighting has considerable dangers of damage, and consequently is not attempted unless other safer displays have failed to make the difference in quality apparent (Wells, 1988; Enquist et al., 1990). Morphological cues may be judged at a glance whereas behavioural traits may require time to assess. Fawcett and Johnstone (2003) consider the optimal order to assess cues differing in informativeness and cost. The other related reason for less valid cues to be assessed earlier is that some cues must necessarily appear before others. For instance, a deer stag cannot help but see the size of its rival before it starts fighting it, and the deepness of a roar may be available as a cue to size even before the animals get close enough to judge size visually.

Paradoxically, in these situations a more non-compensatory environment may lead to examining cues in increasing order of validity (the reverse of Take The Best), at least in cases where the quantitative nature of cues means that cue values are unlikely to tie. As the chooser gets progressively closer or more willing to take risks, more cues become available; it should be adapted to read those new cues whose validities outweigh those of earlier cues, but less valid new cues are unlikely to provide useful additional information and so might be ignored. An interesting question is to what extent the orders in which cues are examined are adaptations. With sexual selection, it could often be that particular traits evolve as signals because of the stage of the assessment process in which they can be examined,

rather than that the cue informativeness of pre-existing signals has favoured an order of inspection.

11.2. Non-sequential cue assessment

There are striking examples of an additive effect of different cues. By manipulating realistic computer animations of sticklebacks *Gasterosteus aculeatus*, Künzler and Bakker (2001) showed that the proportion of choices for one image over another was linearly related to the number of cues in which it was superior (cf. tallying). Similarly, Basolo and Trainor (2002) showed in the swordtail fish *Xiphophorus helleri* that the time for a female to respond was explicable as the sum of the effects of each component of the sword (cf. weighted-additive). However, Hankinson and Morris (2003) pointed out an alternative explanation for such additive results, which depend on averaging the responses of many fish. An additive pattern need not be due to an additive interaction of the cues in all individuals, but to each individual responding to different single cues—each extra cue persuades another subset of the population. We do know of cases of different individuals in the same population attending to different cues (e.g. Hill et al., 1999). The method of processing may differ between individuals too; older female garter snakes demand males that are good on two cues, whereas either cue alone satisfies younger females (Shine et al., 2003).

More complex interactions between cues are also observed. For instance, in the guppy *Poecilia reticulata* colour affected choice when both animations showed a low display rate, but not when they both showed a high rate; conversely display rates mattered when both animations displayed colour, but not an absence of colour (Kodric-Brown and Nicoletto, 2001). Another complex pattern is suggested in the work of both Zuk et al. (1992) and Marchetti (1998); female choice was unaffected by manipulations of single male traits that earlier observational studies had suggested females were utilising. One interpretation is that if one signal disagrees with all the other signals, it is ignored, which might be adaptive if accidental damage to single morphological characters is not indicative of quality. Some traits that we can measure independently may well be treated by the animal as composite traits, implying that complex integration of cues may happen at an almost perceptual level (Rowe, 1999; Calkins and Burley, 2003; Rowe

and Skelhorn, 2004). One cue may alert the receiver to the presence of another (e.g. Hebets, 2005), or one cue may act as an amplifier for another (Hasson, 1991; for instance, contrasting plumage coloration makes it easier for the receiver to judge display movements). The usual assumption is that amplifiers rely on constraints in the way perception works, but such multiplicative cue interactions arise through other mechanisms also (Patricelli et al., 2003) and so it might be an adaptation to some particular environment structures. A multiplicative interaction favours two traits both being well developed over either one in isolation. Perhaps this is ecologically rational in negatively correlated environments (cf. Johnson et al.'s (1989) finding of the benefits of including interaction terms in choice models in such environments).

12. Breaking down disciplinary boundaries

In the preceding section we showed how empirical results on rules of thumb and ABC's theoretical approach could mutually illuminate each other. This short section examines further ways to develop the interaction.

ABC has already published research on heuristics used by animals. For instance, Davis et al. (1999) simulated various rules that a parent bird might use to allocate food amongst its chicks (feed them in turn, or feed the largest, or hungriest, etc.). Other ABC papers have dealt with rules of thumb for mate choice, which relate to both animals and humans (Todd and Miller, 1999; Simão and Todd, 2002; Hutchinson and Halupka, 2004). The resulting papers fitted comfortably into the biological literature, emphasising the similarities in approaches of the two schools.

Another way to break down the interdisciplinary barriers is to test theory developed in one school on the organisms (human or animal) of the other. ABC is currently testing whether humans use the same patch-leaving rules known from animals (Wilke et al., 2004). One experimental context is a computer game modelled on a foraging task, but another consists of internal search in memory for solutions to a Scrabble-like word puzzle. It is known that different species use different patch-leaving rules, presumably in response to their environments (van Alphen et al., 2003; Wajnberg et al., 2003), but we will test whether, as a generalist

species, individual humans can rapidly change the rule according to the environment structure encountered.

Equally valid a research strategy would be to move in the opposite direction, testing whether animals use the heuristics that ABC has proposed that humans use. Demonstrating the parallel evolution of human heuristics in other lineages facing similar environmental structures would provide more stringent tests of their status as adaptations. Studying humans has some advantages, such as the possibility to use introspection to formulate plausible hypotheses about our heuristics, but animals provide many other advantages. In most non-human animals it is clearer what is their natural habitat and it is possible still to study the animal's behaviour and its consequences in that environment. Comparative studies can test whether the rules of thumb used by related species have adjusted to their differing environments. Analysing the structure of the environment is usually easier than with humans because most species are more specialist. Shorter life cycles make it easier to relate the immediate consequences of a behaviour to fitness. Practical considerations also allow far more complete manipulations of an animal's environment than in humans. Moreover, as Tinbergen found, it is often the case in animals that quite crude tricks suffice, itself perhaps a reflection of animals' greater reliance on simpler rules of thumb.

Of course calls for better communication between biologists and psychologists are not original, and behavioural ecology has always had some contacts with animal psychology (e.g. Kamil and Sargent, 1981; Fantino and Abarca, 1985; Rowe and Skelhorn, 2004). One link of some relevance to ABC is the investigation of animal models that duplicate the human "biases" emphasised by the heuristics-and-biases school (e.g. Fantino, 1998; Shafir et al., 2002; Bateson et al., 2003). If these findings are related to the natural environments of these animals (not always done), this can be an avenue to test explanations of these biases as products of adaptive heuristics (e.g. Arkes and Ayton, 1999; Schuck-Paim et al., 2004).

13. Conclusions

ABC has demonstrated that simple heuristics can be a surprisingly effective way of making many decisions, both in terms of frugality and performance. Research

has also started to show that humans really use these simple heuristics in environments where they are ecologically rational. It lies ahead to discover how much of human cognition can be usefully understood in terms of ABC's algorithmic approach. Within psychology there is a wide range of opinion about the likely answer and thus about the importance of ABC's work. However, there is increasing interest from economists, who realise that their unboundedly rational optimality models often provide an inadequate prediction of human decisions.

How might ABC gain from a closer relationship with behavioural biology? Certainly biology considerably broadens the range of examples of heuristics, some of which will turn out to be shared between animals and humans. Some make particularly strong examples because they can be anchored in proven neurological mechanisms or because their adaptive value is less ambiguous than with humans. Animal examples may illuminate characteristics of natural environments that are less important to modern humans, but to which our cognitive mechanisms are still adapted: an example is our suggestion that cue orders may have as much to do with costs and accessibility of each cue as with validity. We have also discussed how the tools of optimality modelling might be reapplied to the study of heuristics.

What might biology gain from a broader knowledge of ABC's work? Rules of thumb are already part of behavioural biology's vocabulary. And biologists already use the usual ABC approach of simulating candidate heuristics to judge their performance. However, although biological examples of rules of thumb and of cue integration are not so rare, they tend to be isolated curiosities in the literature. Can some of these different rules be classified by shared building blocks, just as with ABC's simple heuristics? ABC's emphasis on simple algorithmic decision rules might provide a useful impetus both to interpret further animal behaviours in such terms, and then to expose commonalities between the examples. This is especially the case with cue integration, for which biology seems not to have developed an equivalent of ABC's theoretical framework explaining why particular methods of cue integration work well in particular types of information environments. Also largely missing from biology is the idea that simple heuristics may be superior to more complex methods, not just a necessary evil because of the sim-

plicity of animal nervous systems (but see Bookstaber and Langsam, 1985; Real, 1992; Stephens and Anderson, 2001; Stephens, 2002). The shared assumption that performance is what matters should facilitate communication between biologists and ABC.

One of the possible derivations of the phrase "rule of thumb" is from craftsmen using the size of their thumb as a measure instead of a ruler (Brewer, 1996). To finish with a pleasing parallel between humans and animals, consider this example. The sticky part of a spider's web is a spiral thread with each whorl evenly spaced from its predecessor, as one expects of a well-designed net. Just like the craftsman, the spider uses a part of its own body as a calliper. To demonstrate this, Vollrath (1987) cut off the spider's legs on one side; the legs regrew at the next moult, but smaller than before, and the spacing of the spiral was then proportionately closer.

Acknowledgements

We thank Edmund Fantino, Konstantinos Katsikopoulos, Heike Reise, Lael Schooler, Masanori Takezawa, Peter Todd and an anonymous referee for their comments on an earlier version of the manuscript, and Henry Brighton for providing Fig. 1. We also thank Randolph Grace for stimulating and facilitating this review.

References

- Anderson, J.R., 1990. *The Adaptive Character of Thought*. Lawrence Erlbaum, Hillsdale, NJ.
- Anderson, J.R., Bothell, D., Byrne, M.D., Douglass, S., Lebiere, C., Qin, Y., 2004. An integrated theory of mind. *Psych. Rev.* 111, 1036–1060.
- Arkes, H.R., Ayton, P., 1999. The sunk cost and concorde effects: are humans less rational than lower animals? *Psych. Bull.* 125, 591–600.
- Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.
- Balda, R.P., Kamil, A.C., 1992. Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. *Anim. Behav.* 44, 761–769.
- Balkovsky, E., Shraiman, B.I., 2002. Olfactory search at high Reynolds number. *Proc. Natl. Acad. Sci. U.S.A.* 99, 12589–12593.
- Barta, Z., Houston, A.I., McNamara, J.M., Székely, T., 2002. Sexual conflict about parental care: the role of reserves. *Am. Nat.* 159, 687–705.

- Basolo, A.L., Trainor, B.C., 2002. The confirmation of a female preference for a composite male trait in green swordtails. *Anim. Behav.* 63, 469–474.
- Bateson, M., Healy, S.D., Hurly, T.A., 2003. Context-dependent foraging decisions in rufous hummingbirds. *Proc. R. Soc. Lond.* 270, 1271–1276.
- Baum, K.A., Grant, W.E., 2001. Hummingbird foraging behavior in different patch types: simulation of alternative strategies. *Ecol. Mod.* 137, 201–209.
- Bélisle, C., Cresswell, J., 1997. The effects of a limited memory capacity on foraging behavior. *Theor. Pop. Biol.* 52, 78–90.
- Benhamou, S., 1992. Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *J. Theor. Biol.* 159, 67–81.
- Bonduriansky, R., 2003. Layered sexual selection: a comparative analysis of sexual behaviour within an assemblage of piophilid flies. *Can. J. Zool.* 81, 479–491.
- Bookstaber, R., Langsam, J., 1985. On the optimality of coarse behavior rules. *J. Theor. Biol.* 116, 161–193.
- Bradbeer, J.W., 1988. *Seed Dormancy and Germination*. Blackie, Glasgow.
- Brancazio, P.J., 1985. Looking into Chapman's homer: the physics of judging a fly ball. *Am. J. Phys.* 53, 849–855.
- Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. *Classification and Regression Trees*. Wadsworth, Belmont, CA.
- Brewer, E.C., 1996. *Brewer's Dictionary of Phrase and Fable*, 15th ed. Cassel, London.
- Bröder, A., 2000. Assessing the empirical validity of the "Take-the-Best" heuristic as a model of human probabilistic inference. *J. Exp. Psychol. Learn. Mem. Cogn.* 26, 1332–1346.
- Bröder, A., 2003. Decision making with the "adaptive toolbox": influence of environmental structure, intelligence, and working memory load. *J. Exp. Psychol. Learn. Mem. Cogn.* 29, 611–625.
- Bröder, A., Schiffer, S., 2003. Take The Best versus simultaneous feature matching: probabilistic inferences from memory and effects of representation format. *J. Exp. Psychol. Gen.* 132, 277–293.
- Buntine, W., Caruana, R., 1992. *Introduction to IND Version 2.1 and Recursive Partitioning*. NASA Ames Research Centre, Moffett Field, CA.
- Burke, D., Fulham, B.J., 2003. An evolved spatial memory bias in a nectar-feeding bird? *Anim. Behav.* 66, 695–701.
- Calkins, J.D., Burley, N.T., 2003. Mate choice for multiple ornaments in the California quail, *Callipepla californica*. *Anim. Behav.* 65, 69–81.
- Camazine, S., Deneubourg, J.-L., Franks, N.R., Sneyd, J., Theraulaz, G., Bonabeau, E., 2001. *Self-Organization in Biological Systems*. Princeton University Press, Princeton, NJ.
- Candolin, U., 2003. The use of multiple cues in mate choice. *Biol. Rev.* 78, 575–595.
- Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.* 9, 129–136.
- Chater, N., Oaksford, M., 1999. Ten years of the rational analysis of cognition. *Trends Cogn. Sci.* 3, 57–65.
- Chater, N., Oaksford, M., Nakisa, R., Redington, M., 2003. Fast, frugal, and rational: how rational norms explain behavior. *Organ. Behav. Hum. Decis. Process.* 90, 63–86.
- Cheverton, J., Kacelnik, A., Krebs, J.R., 1985. Optimal foraging: constraints and currencies. In: Hölldobler, B., Lindauer, M. (Eds.), *Experimental Behavioral Ecology*. Fischer Verlag, Stuttgart, pp. 109–126.
- Cresswell, W., Hilton, G.M., Ruxton, G.D., 2000. Evidence for a rule governing the avoidance of superfluous escape flights. *Proc. R. Soc. Lond. B* 267, 733–737.
- Czerlinski, J., Gigerenzer, G., Goldstein, D.G., 1999. How good are simple heuristics? In: Gigerenzer, G., Todd, P.M., the ABC Research Group (Eds.), *Simple Heuristics that Make Us Smart*. Oxford University Press, New York, pp. 97–118.
- Davies, N.B., Houston, A.I., 1981. Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. *J. Anim. Ecol.* 50, 157–180.
- Davis, J.N., Todd, P.M., Bullock, S., 1999. Environment quality predicts parental provisioning decisions. *Proc. R. Soc. Lond. B* 266, 1791–1797.
- Dawes, R.M., 1979. The robust beauty of improper linear models in decision making. *Am. Psychol.* 34, 571–582.
- Dawkins, R., 1982. *The Extended Phenotype*. Freeman, San Francisco.
- Detrain, C., Deneubourg, J.-L., 2002. Complexity of environment and parsimony of decision rules in insect societies. *Biol. Bull.* 202, 268–274.
- de Vries, H., Biesmeijer, J.C., 2002. Self-organization in collective honeybee foraging: emergence of symmetry breaking, cross inhibition and equal harvest-rate distribution. *Behav. Ecol. Sociobiol.* 51, 557–569.
- Dhami, M.K., 2003. Psychological models of professional decision making. *Psychol. Sci.* 14, 175–180.
- Dieckmann, A., Todd, P.M., 2004. Simple ways to construct search orders. In: Forbus, K., Gentner, D., Regier, T. (Eds.), *Proceedings of the 26th Annual Conference of the Cognitive Science Society*. Lawrence Erlbaum, Mahwah, NJ, pp. 309–314.
- Driessen, G., Bernstein, C., 1999. Patch departure mechanisms and optimal host exploitation in an insect parasitoid. *J. Anim. Ecol.* 68, 445–459.
- Dukas, R. (Ed.), 1998. *Cognitive Ecology: the Evolutionary Ecology of Information Processing and Decision Making*. University of Chicago Press, Chicago.
- Dusenbery, D.B., 2001. Performance of basic strategies for following gradients in two dimensions. *J. Theor. Biol.* 208, 345–360.
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y., Sgerdahl, N., 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Anim. Behav.* 10, 1–14.
- Fairhurst, S., Gallistel, C.R., Gibbon, J., 2003. Temporal landmarks: proximity prevails. *Anim. Cogn.* 6, 113–120.
- Fantino, E., 1998. Judgement and decision making: behavioral approaches. *Behav. Anal.* 21, 203–218.
- Fantino, E., Abarca, N., 1985. Choice, optimal foraging, and the delay-reduction hypothesis. *Behav. Brain. Sci.* 8, 315–362 (including commentaries).
- Fawcett, T.W., 2003. Multiple cues and variation in mate-choice behaviour. D.Phil. Thesis. University of Cambridge.
- Fawcett, T.W., Johnstone, R.A., 2003. Optimal assessment of multiple cues. *Proc. R. Soc. Lond. B* 270, 1637–1643.

- Fortin, D., 2003. Searching behavior and use of sampling information by free-ranging bison (*Bos bison*). *Behav. Ecol. Sociobiol.* 54, 194–203.
- Fraenkel, G.S., Gunn, D.L., 1940. *The Orientation of Animals: Kineses, Taxes and Compass Reactions*. Oxford University Press, Oxford.
- Franks, N.R., Mallon, E.B., Bray, H.E., Hamilton, M.J., Mischler, T.C., 2003. Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* 65, 215–223.
- Gibson, R.M., 1996. Female choice in sage grouse: the roles of attraction and active comparison. *Behav. Ecol. Sociobiol.* 39, 55–59.
- Gigerenzer, G., 2000. *Adaptive Thinking: Rationality in the Real World*. Oxford University Press, New York.
- Gigerenzer, G., 2004. Fast and frugal heuristics: the tools of bounded rationality. In: Koehler, D.J., Harvey, N. (Eds.), *Blackwell Handbook of Judgment and Decision Making*. Blackwell, Oxford, pp. 62–88.
- Gigerenzer, G., Goldstein, D.G., 1996. Reasoning the fast and frugal way: models of bounded rationality. *Psychol. Rev.* 103, 650–669.
- Gigerenzer, G., Goldstein, D.G., 1999. Betting on one good reason: the Take The Best heuristic. In: Gigerenzer, G., Todd, P.M., the ABC Research Group (Eds.), *Simple Heuristics that Make Us Smart*. Oxford University Press, New York, pp. 75–95.
- Gigerenzer, G., Selten, R. (Eds.), 2001. *Bounded Rationality: The Adaptive Toolbox*. MIT Press, Cambridge, MA.
- Gigerenzer, G., Todd, P.M., the ABC Research Group, 1999. *Simple Heuristics that Make Us Smart*. Oxford University Press, New York.
- Gill, F.B., 1988. Trapline foraging by hermit hummingbirds: competition for an undefended, renewable resource. *Ecology* 69, 1933–1942.
- Gilovich, T., Griffin, D.W., Kahneman, D. (Eds.), 2002. *Heuristics and Biases: The Psychology of Intuitive Judgment*. Cambridge University Press, New York.
- Goldstein, D.G., Gigerenzer, G., 2002. Models of ecological rationality: the recognition heuristic. *Psychol. Rev.* 109, 75–90.
- Gould, J.L., Gould, C.G., 1988. *The Honey Bee*. Scientific American Library, New York.
- Gould, S.J., 1991. *Bully for Brontosaurus: Reflections in Natural History*. W.W. Norton, New York.
- Gould, S.J., Lewontin, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* 205, 581–598.
- Goulson, D., 2000. Why do pollinators visit proportionally fewer flowers in large patches? *Oikos* 91, 485–492.
- Grafen, A., 1990. Biological signals as handicaps. *J. Theor. Biol.* 144, 517–546.
- Green, R.F., 1984. Stopping rules for optimal foragers. *Am. Nat.* 123, 30–40.
- Hammerstein, P., 2003. Why is reciprocity so rare in social animals? A protestant appeal. In: Hammerstein, P. (Ed.), *Genetic and Cultural Evolution of Cooperation*. MIT Press, Cambridge, MA, pp. 83–93.
- Hankinson, S.J., Morris, M.R., 2003. Avoiding a compromise between sexual selection and species recognition: female sword-tail fish assess multiple species-specific cues. *Behav. Ecol.* 14, 282–287.
- Hasson, O., 1991. Sexual displays as amplifiers: practical examples with an emphasis on feather decorations. *Behav. Ecol.* 2, 189–197.
- Hauert, C., Stenull, O., 2002. Simple adaptive strategy wins the prisoner's dilemma. *J. Theor. Biol.* 218, 261–272.
- Hebets, E.A., 2005. Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behav. Ecol.* 16, 75–82.
- Henrich, J., Boyd, R., 1998. The evolution of conformist transmission and the emergence of between-group differences. *Evol. Hum. Behav.* 19, 215–241.
- Hertwig, R., Hoffrage, U., Martignon, L., 1999. Quick estimation: letting the environment do the work. In: Gigerenzer, G., Todd, P.M., the ABC Research Group (Eds.), *Simple Heuristics that Make Us Smart*. Oxford University Press, New York, pp. 209–234.
- Hertwig, R., Todd, P.M., 2003. More is not always better: the benefits of cognitive limits. In: Hardman, D., Macchi, L. (Eds.), *Thinking: Psychological Perspectives on Reasoning, Judgement and Decision Making*. Wiley, Chichester, UK, pp. 213–231.
- Hill, J.A., Enstrom, D.A., Ketterson, E.D., Nolan, V., Ziegenfus, C., 1999. Mate choice based on static versus dynamic secondary sexual traits in the dark-eyed junco. *Behav. Ecol.* 10, 91–96.
- Hills, T.T., Adler, F.R., 2002. Time's crooked arrow: optimal foraging and rate-biased time perception. *Anim. Behav.* 64, 589–597.
- Hoffmann, R., 2000. Twenty years on: the evolution of cooperation revisited. *J. Artif. Soc. Soc. Simul.* 3 (2).
- Hoffrage, U., Hertwig, R., Gigerenzer, G., 2000. Hindsight bias: a by-product of knowledge updating? *J. Exp. Psychol. Learn. Mem. Cogn.* 26, 566–581.
- Houston, A., Kacelnik, A., McNamara, J., 1982. Some learning rules for acquiring information. In: McFarland, D.J. (Ed.), *Functional Ontogeny*. Pitman, London, pp. 140–191.
- Hutchinson, J.M.C., Halupka, K., 2004. Mate choice when males are in patches: optimal strategies and good rules of thumb. *J. Theor. Biol.* 231, 129–151.
- Hutchinson, J.M.C., McNamara, J.M., Cuthill, I.C., 1993. Song, sexual selection, starvation and strategic handicaps. *Anim. Behav.* 45, 1153–1177.
- Iwasa, Y., Higashi, M., Yamamura, N., 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *Am. Nat.* 117, 710–723.
- Janetos, A.C., 1980. Strategies of female mate choice: a theoretical analysis. *Behav. Ecol. Sociobiol.* 7, 107–112.
- Janetos, A.C., Cole, B.J., 1981. Imperfectly optimal animals. *Behav. Ecol. Sociobiol.* 9, 203–209.
- Jennions, M.D., Petrie, M., 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* 72, 283–327.
- Johnson, E.J., Meyer, R.J., Ghose, S., 1989. When choice models fail: compensatory models in negatively correlated environments. *J. Market. Res.* 26, 255–270.
- Kacelnik, A., Todd, I.A., 1992. Psychological mechanisms and the Marginal Value Theorem: effect of variability in travel time on patch exploitation. *Anim. Behav.* 43, 313–322.

- Kahneman, D., Tversky, A., 1979. Prospect theory: an analysis of decision under risk. *Econometrica* 47, 263–291.
- Kahneman, D., Tversky, A., 1996. On the reality of cognitive illusions. *Psychol. Rev.* 103, 582–591.
- Kamil, A.C., Sargent, T.D., 1981. *Foraging Behavior: Ecological, Ethological and Psychological Approaches*. Garland STPM Press, New York.
- Kareev, Y., 2000. Seven (indeed, plus or minus two) and the detection of correlations. *Psychol. Rev.* 107, 397–402.
- Karsai, I., Péntzes, Z., 2000. Optimality of cell arrangement and rules of thumb of cell initiation in *Polistes dominulus*: a modeling approach. *Behav. Ecol.* 11, 387–395.
- Keasar, T., Rashkovich, E., Cohen, D., Shmida, A., 2002. Bees in two-armed bandit situations: foraging choices and possible decision mechanisms. *Behav. Ecol.* 13, 757–765.
- Kennedy, J.S., 1983. Zigzagging and casting as a programmed response to wind-borne odour: a review. *Physiol. Entomol.* 8, 109–120.
- Kodric-Brown, A., Nicoletto, P.F., 2001. Female choice in the guppy (*Poecilia reticulata*): the interaction between male color and display. *Behav. Ecol. Sociobiol.* 50, 346–351.
- Körding, K.P., Wolpert, D.M., 2004. Bayesian integration in sensorimotor learning. *Nature* 427, 244–247.
- Krebs, J.R., Erichsen, J.T., Webber, M.I., Charnov, E.L., 1977. Optimal prey selection in the great tit (*Parus major*). *Anim. Behav.* 25, 30–38.
- Krebs, J.R., Stephens, D.W., Sutherland, W.J., 1983. Perspectives in optimal foraging. In: Bush, A.H., Clark, G.A. (Eds.), *Perspectives in Ornithology: Essays Presented for the Centennial of the American Ornithologists' Union*. Cambridge University Press, Cambridge, UK, pp. 165–221.
- Künzler, R., Bakker, T.C.M., 2001. Female preferences for single and combined traits in computer animated stickleback males. *Behav. Ecol.* 12, 681–685.
- Lawler, E.L., Lenstra, J.K., Rinnooy-Kan, A.H.G., Shmoys, D.B. (Eds.), 1985. *The Traveling Salesman Problem*. Wiley, New York.
- Lifjeld, J.T., Slagsvold, T., 1988. Female pied flycatchers *Ficedula hypoleuca* choose male characteristics in homogeneous habitats. *Behav. Ecol. Sociobiol.* 22, 27–36.
- Lima, S.L., 1994. Collective detection of predatory attack by birds in the absence of alarm signals. *J. Avian Biol.* 25, 319–326.
- Logue, A.W., 1988. Research on self-control: an integrating framework. *Behav. Brain. Sci.* 11, 665–704 (including commentaries).
- Luttbeg, B., 1996. A comparative Bayes tactic for mate assessment and choice. *Behav. Ecol.* 7, 451–460.
- MacKay, D.J.C., 1992. Bayesian interpolation. *Neural Comput.* 4, 415–447.
- McLeod, P., Dienes, Z., 1996. Do fielders know where to go to catch the ball or only how to get there? *J. Exp. Psychol. Hum. Percept. Perform.* 22, 531–543.
- McNamara, J.M., Houston, A.I., 1985. Optimal foraging and learning. *J. Theor. Biol.* 117, 231–249.
- McNamara, J.M., Houston, A.I., 1987a. Partial preferences and foraging. *Anim. Behav.* 35, 1084–1099.
- McNamara, J.M., Houston, A.I., 1987b. Memory and the efficient use of information. *J. Theor. Biol.* 125, 385–395.
- McNamara, J.M., Barta, Z., Houston, A.I., 2004. Variation in behaviour promotes cooperation in the Prisoner's Dilemma game. *Nature* 428, 745–748.
- Mallon, E.B., Franks, N.R., 2000. Ants estimate area using Buffon's needle. *Proc. R. Soc. Lond. B* 267, 765–770.
- Marchetti, K., 1998. The evolution of multiple male traits in the yellow-browed leaf warbler. *Anim. Behav.* 55, 361–376.
- Marr, D., 1982. *Vision*. Freeman, San Francisco.
- Martignon, L., Hoffrage, U., 2002. Fast, frugal, and fit: simple heuristics for paired comparisons. *Theor. Decis.* 52, 29–71.
- Martignon, L., Laskey, K.B., 1999. Bayesian benchmarks for fast and frugal heuristics. In: Gigerenzer, G., Todd, P.M., the ABC Research Group (Eds.), *Simple Heuristics that Make Us Smart*. Oxford University Press, New York, pp. 169–188.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, UK.
- Menzel, R., 2001. Searching for the memory trace in a mini-brain, the honeybee. *Learn. Mem.* 8, 53–62.
- Menzel, R., Giurfa, M., 2001. Cognitive architecture of a mini-brain: the honeybee. *Trends Cogn. Sci.* 5, 62–71.
- Menzel, R., Greggers, U., Hammer, M., 1993. Functional organization of appetitive learning and memory in a generalist pollinator the honey bee. In: Papaj, D.R., Lewis, A.C. (Eds.), *Insect Learning: Ecological and Evolutionary Perspectives*. Chapman & Hall, New York, pp. 79–125.
- Moyer, R.S., Landauer, T.K., 1967. Time required for judgements of numerical inequality. *Nature* 215, 1519–1520.
- Mugford, S.T., Mallon, E.B., Franks, N.R., 2001. The accuracy of Buffon's needle: a rule of thumb used by ants to estimate area. *Behav. Ecol.* 12, 655–658.
- Müller, M., Wehner, R., 1988. Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. U.S.A.* 85, 5287–5290.
- Nakata, K., Ushimaru, A., Watanabe, T., 2003. Using past experience in web relocation decisions enhances the foraging efficiency of the spider *Cyclosa argenteoalba*. *J. Insect Behav.* 16, 371–380.
- Newell, B.R., Shanks, D.R., 2003. Take the best or look at the rest? Factors influencing “one-reason” decision making. *J. Exp. Psychol. Learn. Mem. Cogn.* 29, 53–65.
- Oudejans, R.R.D., Michaels, C.F., Bakker, F.C., Davids, K., 1999. Shedding some light on catching in the dark: perceptual mechanisms for catching fly balls. *J. Exp. Psych. Hum. Percept. Perform.* 25, 531–542.
- Partan, S., Marler, P., 1999. Communication goes multimodal. *Science* 283, 1272–1273.
- Patricelli, G.L., Uy, J.A.C., Borgia, G., 2003. Multiple male traits interact: attractive bower decorations facilitate attractive behavioural displays in satin bowerbirds. *Proc. R. Soc. Lond. B* 270, 2389–2395.
- Payne, J.W., Bettman, J.R., Johnson, E.J., 1993. *The Adaptive Decision Maker*. Cambridge University Press, Cambridge, UK.
- Pratt, S.C., Mallon, E.B., Sumpter, D.J.T., Franks, N.R., 2002. Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* 52, 117–127.
- Proctor, C.J., Broom, M., Ruxton, G.D., 2001. Modelling antipredator vigilance and flight response in group foragers when warning signals are ambiguous. *J. Theor. Biol.* 211, 409–417.

- Quinlan, J.R., 1993. C4.5: Programs for Machine Learning. Morgan Kaufmann, San Mateo, CA.
- Raguso, R.A., Willis, M.A., 2002. Synergy between visual and olfactory cues in nectar feeding by naïve hawkmoths, *Manduca sexta*. Anim. Behav. 64, 685–695.
- Real, L.A., 1990a. Predator switching and the interpretation of animal choice behavior: the case for constrained optimization. In: Hughes, R.N. (Ed.), Behavioural Mechanisms of Food Selection. NATO ASI Series, vol. G20. Springer, Berlin, pp. 1–21.
- Real, L., 1990b. Search theory and mate choice. I. Models of single-sex discrimination. Am. Nat. 136, 376–404.
- Real, L.A., 1992. Information processing and the evolutionary ecology of cognitive architecture. Am. Nat. 140, S108–S145.
- Rechten, C., Avery, M., Stevens, A., 1983. Optimal prey selection: why do great tits show partial preferences? Anim. Behav. 31, 576–584.
- Reimer, T., Katsikopoulos, K.V., 2004. The use of recognition in group decision-making. Cogn. Sci. 28, 1009–1029.
- Rieskamp, J., Hoffrage, U., 1999. When do people use simple heuristics, and how can we tell? In: Gigerenzer, G., Todd, P.M., the ABC Research Group (Eds.), Simple Heuristics that Make Us Smart. Oxford University Press, New York, pp. 141–167.
- Rieskamp, J., Otto, P.E. Adaptive strategy selection in decision making: the learning rule theory, submitted for publication.
- Roitberg, B.D., Reid, M.L., Li, C., 1993. Choosing hosts and mates: the value of learning. In: Papaj, D.R., Lewis, A.C. (Eds.), Insect Learning: Ecological and Evolutionary Perspectives. Chapman & Hall, New York, pp. 174–194.
- Römer, H., Krusch, M., 2000. A gain-control mechanism for processing of chorus sounds in the afferent auditory pathway of the bushcricket *Tettigonia viridissima* (Orthoptera; Tettigoniidae). J. Comp. Physiol. A 186, 181–191.
- Rosander, K., von Hofsten, C., 2002. Development of gaze tracking of small and large objects. Exp. Brain Res. 146, 257–264.
- Rowe, C., 1999. Receiver psychology and the evolution of multi-component signals. Anim. Behav. 58, 921–931.
- Rowe, C., Skelhorn, J., 2004. Avian psychology and communication. Proc. R. Soc. Lond. B 271, 1435–1442.
- Sato, Y., Saito, Y., Sakagami, T., 2003. Rules for nest sanitation of a social spider mite, *Schizotetranychus miscanthi* Saito (Acari: Tetranychidae). Ethology 109, 713–724.
- Schuck-Paim, C., Pompilio, L., Kacelnik, A., 2004. State-dependent decisions cause apparent violations of rationality in animal choice. PLoS Biol. 2 (12), e402.
- Seeley, T.D., 1995. The Wisdom of the Hive. Harvard University Press, Cambridge, MA.
- Seeley, T.D., 2003. Consensus building during nest-site selection in honey bee swarms: the expiration of dissent. Behav. Ecol. Sociobiol. 53, 417–424.
- Seeley, T.D., Visscher, P.K., 2003. Choosing a home: how scouts in a honey bee swarm perceive the completion of their group decision making. Behav. Ecol. Sociobiol. 54, 511–520.
- Seeley, T.D., Visscher, P.K., 2004. Quorum sensing during nest-site selection by honeybee swarms. Behav. Ecol. Sociobiol. 56, 594–601.
- Shaffer, D.M., Krauchunas, S.M., Eddy, M., McBeath, M.K., 2004. How dogs navigate to catch frisbees. Psychol. Sci. 15, 437–441.
- Shafir, S., Waite, T.A., Smith, B.H., 2002. Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). Behav. Ecol. Sociobiol. 51, 180–187.
- Shanteau, J., Thomas, R.P., 2000. Fast and frugal heuristics: what about unfriendly environments? Behav. Brain. Sci. 23, 762–763.
- Shettleworth, S.J., 1998. Cognition, Evolution and Behavior. Oxford University Press, New York.
- Shine, R., Phillips, B., Wayne, H., LeMaster, M., Mason, R.T., 2003. The lexikon of love: what cues cause size-assortative courtship by male garter snakes. Behav. Ecol. Sociobiol. 53, 234–237.
- Simão, J., Todd, P.M., 2002. Modeling mate choice in monogamous mating systems with courtship. Adapt. Behav. 10, 113–136.
- Simon, H.A., 1956. Rational choice and the structure of the environment. Psychol. Rev. 63, 129–138.
- Simon, H.A., 1990. Invariants of human behavior. Ann. Rev. Psychol. 41, 1–19.
- Simpson, G.G., Genadall, A.R., Dean, C., 1999. When to switch to flowering. Ann. Rev. Cell. Dev. Biol. 99, 519–550.
- Sirota, E., 2001. Mate-choice copying by females: the advantages of a prudent strategy. J. Evol. Biol. 14, 418–423.
- Stephens, D.W., 2002. Discrimination, discounting and impulsivity: a role for an informational constraint. Phil. Trans. R. Soc. Lond. B 357, 1527–1537.
- Stephens, D.W., Anderson, D., 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. Behav. Ecol. 12, 330–339.
- Tauber, M.J., Tauber, C.A., 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Ann. Rev. Entomol. 21, 81–107.
- Thompson, K., Grime, J.P., 1983. A comparative study of germination responses to diurnally-fluctuating temperatures. J. Appl. Ecol. 20, 141–156.
- Thomson, J.D., 1996. Trapline foraging by bumblebees: I. Persistence of flight-path geometry. Behav. Ecol. 7, 158–164.
- Thuijsman, F., Peleg, B., Amitai, M., Shmida, A., 1995. Automata, matching and foraging behavior of bees. J. Theor. Biol. 175, 305–316.
- Tinbergen, N., 1958. Curious Naturalists. Country Life, London.
- Todd, I.A., Kacelnik, A., 1993. Psychological mechanisms and the Marginal Value Theorem: dynamics of scalar memory for travel time. Anim. Behav. 46, 765–775.
- Todd, P.M., 1999. Simple inference heuristics versus complex decision machines. Minds Mach. 9, 461–477.
- Todd, P.M., Dieckmann, A. Heuristics for ordering cue search in decision making. Adv. Neural Inform. Process. Syst. 18, in press.
- Todd, P.M., Miller, G.F., 1999. From pride and prejudice to persuasion: satisficing in mate search. In: Gigerenzer, G., Todd, P.M., the ABC Research Group (Eds.), Simple Heuristics that Make Us Smart. Oxford University Press, New York, pp. 287–308.
- Tversky, A., 1972. Elimination by aspects: a theory of choice. Psychol. Rev. 79, 281–299.
- van Alphen, J.J.M., Bernstein, C., Driessen, G., 2003. Information acquisition and time allocation in insect parasitoids. Trends. Ecol. Evol. 18, 81–87.

- Vicario, D.S., Naqvi, N.H., Raksin, J.N., 2001. Sex differences in discrimination of vocal communication signals in a songbird. *Anim. Behav.* 61, 805–817.
- Vollrath, F., 1987. Altered geometry of webs in spiders with regenerated legs. *Nature* 328, 247–248.
- Volz, K.G., Schubotz, R.I., Raab, M., Schooler, L., Gigerenzer, G., von Cramon, D.Y. Recognition heuristic and the brain. EPOS/NOW workshop: control in attention and action: neurocognitive systems and mechanisms. Amsterdam, in press.
- Wajnberg, E., Fauvergue, X., Pons, O., 2000. Patch leaving decision rules and the Marginal Value Theorem: an experimental analysis and a simulation model. *Behav. Ecol.* 11, 577–586.
- Wajnberg, E., Gonsard, P.-A., Tabone, E., Curty, C., Lezcano, N., Colazza, S., 2003. A comparative analysis of patch-leaving decision rules in a parasitoid family. *J. Anim. Ecol.* 72, 618–626.
- Wald, A., 1947. *Sequential Analysis*. Wiley, New York.
- Wallraff, H.G., 2001. Navigation by homing pigeons: updated perspective. *Ethol. Ecol. Evol.* 13, 1–48.
- Webb, B., Reeve, R., 2003. Reafferent or redundant: integration of phonotaxis and optomotor behavior in crickets and robots. *Adapt. Behav.* 11, 137–158.
- Wells, M.S., 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. *Anim. Behav.* 36, 321–326.
- Wiegmann, D.D., Mukhopadhyay, K., 1998. The fixed sample search rule and use of an indicator character to evaluate mate quality. *J. Theor. Biol.* 193, 709–715.
- Wiegmann, D.D., Real, L.A., Capone, T.A., Ellner, S., 1996. Some distinguishing features of models of search behavior and mate choice. *Am. Nat.* 147, 188–204.
- Wilke, A., Hutchinson, J.M.C., Todd, P.M., 2004. Testing simple rules for human foraging in patchy environments. In: Forbus, K., Gentner, D., Regier, T. (Eds.), *Proceedings of the 26th Annual Conference of the Cognitive Science Society*. Erlbaum, Mahwah, NJ, p. 1656.
- Williams, C.M., 1956. Physiology of insect diapause. X. An endocrine mechanism for the influence of temperature on the diapausing pupa of the cecropia silkworm. *Biol. Bull.* 110, 201–218.
- Wiltschko, R., Wiltschko, W., 2003. Avian navigation: from historical to modern concepts. *Anim. Behav.* 65, 257–272.
- Ydenberg, R.C., 1982. Great tits and giving-up times: decision rules for leaving patches. *Behaviour* 90, 1–24.
- Zuk, M., Ligon, J.D., Thornhill, R., 1992. Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. *Anim. Behav.* 44, 999–1006.