

# Is more choice always desirable? Evidence and arguments from leks, food selection, and environmental enrichment

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## ABSTRACT

Recent studies on humans show that too much choice can make subjects less likely to choose any item. I consider general adaptive and non-adaptive explanations of why such choice aversion, or its converse, might occur in animals. There are three questions: is more choice always preferred, does it ever lead to less consumption (or a lower probability of consumption), and may it result in worse items being selected? A preference for choice is one of the main explanations for lek formation and I draw attention to previously unrecognised parallels with models of human shopping behaviour. There is indeed evidence of female preference for larger leks, although much of the observational data are open to other interpretations. Unfortunately nobody has looked for choice aversion where it is most to be expected, in leks larger than normally occur. Evidence that too much choice of males confuses females is strongest in acoustically advertising frogs, but the widespread decrease of mating skew in larger leks might also have this explanation. A model reanalyses data on skew in black grouse *Tetrao tetrix* and suggests that considering only a random subset of a large lek may increase the chances of selecting the better males: larger leks are more likely to include better males, but these are less likely to be selected. These opposing effects may lead to an optimum lek size, but only with a sufficient decline in choice accuracy with size. With food choice, very few studies have avoided confounding choice with food quality, by manipulating only flavour. The widespread phenomena of stimulus-specific satiety and novelty seeking imply that monotonous diets are aversive, but no studies test whether animals choose sites where they know food diversity to be greater. Operant experiments that demonstrate mild preferences for free choice concern choice about the means to get food rather than the food itself. In some insect species even moderate choice of diet can be deleterious, and studies on search images and the confusion effect may be evidence of this in vertebrates. Environmental enrichment of captive animals often relies on increasing the options available, but it need not be the choice itself that is beneficial. I consider briefly further areas in biology where choice preference or aversion are potentially important.

*Key words:* choice aversion, female preference hypothesis, free choice, male-buffet, mate choice, mating skew, stimulus-specific satiety, cafeteria diet, confusion effect, search image.

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## I. INTRODUCTION

Modern western culture seems devoted to the maxim that the more choice the better. Thus it is not surprising that certain explanatory models in both biology and economics are generated by the assumption that animals and humans prefer choice. However, recently Iyengar & Lepper (2000) have shown that too much choice is aversive in humans, and that some cultures are less desirous of personal choice (Iyengar & Lepper, 1999). In the light of their results, this paper examines the evidence for whether animals prefer choice and whether choice stimulates consumption. Besides preference and consumption, a third issue is performance—how does degree of choice affect the appropriateness of the items selected? The three issues are interrelated because the quality of the items chosen should drive the evolution both of preference for different degrees of choice and of rules deciding how much to consume. However, the issues are logically distinct and the three aspects of behaviour do not necessarily covary. Thus we will encounter cases in which the preference for choice leads to a reduced performance when too much choice is available, and where choice is preferred but results in less consumption.

The focus will be on choice of discrete options that are simultaneously available. I largely avoid considering choice about when and how. In some situations, archetypally when a female chooses a mate, only one item must be chosen and we judge consumption by the probability of a selection being made. In other situations, archetypally herbivory, many items are chosen and we judge consumption by the number or mass chosen. Both cases are considered here; there is often some continuum between them (e.g. bees visiting flowers) and the same explanations may apply to both.

I show that choice aversion could have important consequences in various biological contexts. However, it is fair to warn readers that the evidence both for and against choice aversion in animals is surprisingly inconclusive. Conclusions will be tentative, but I will highlight some questions that further research could readily answer.

The review starts by considering a classic argument for why leks form: that males in leks are more successful because females prefer to choose a male when they have a more extensive choice. I highlight analogies with explanations in the social sciences of why shops cluster. I then describe data from psychology and marketing which question whether choice always results in greater consumption or better selections, and draw up a list of reasons why more choice may lead to less consumption. Evidence from mate choice is then reviewed, asking first whether more choice of males results in better partners, and secondly whether females prefer larger aggregations of males and are more likely to mate once in them. The review next turns to food choice and then to environmental enrichment.

## II. PREFERENCE FOR CHOICE AS AN EXPLANATION FOR GROUPING: LEKS AND SHOPPING CENTRES

In a wide variety of animals, males seeking females form aggregations. Especially when males are not guarding resources needed by the females, these aggregations are termed leks (Wiley, 1991; Höglund & Alatalo, 1995). Why should a male display beside his competitors? One ultimate explanation amongst several is that females prefer to choose males from a group, rather than from amongst solitary males (the female preference hypothesis: e.g. Bradbury, 1981; Bradbury & Gibson, 1983; Wickman, Garcia-Barros & Rappe-George, 1995). This begs the question of why this preference evolved, and the explanation of interest to us here is that females on leks choose better mates through having more choice and being better able to compare (Alexander, 1975; Kokko, 1997). It has been called the male-buffet hypothesis (Wiley, 1991). The same argument has been applied to explain female preferences for: denser clusters of males within a lek (Hovi *et al.*, 1994), resident males with more attendant satellite males in ruff leks (*Phalacrocorax pugnax*; Hugie & Lank, 1997), and temporal clumping of calling in Orthoptera (Walker, 1983*a*).

There are several reasons why selecting from a group may facilitate choosing a high-quality male, and thus why a preference to select from a group should evolve.

(1) Travel times within a cluster of males are short, so a female visiting several males will tend to have a shorter total journey by preferring to visit clustered males, even if an isolated male lies closer to her in another direction. She will thus require less time (or energy or risk) to find a male exceeding a fixed acceptance threshold, or, with a fixed time spent searching, the more males she can inspect. Preferring clusters containing more males has these same advantages of reducing travel costs as preferring clustered over unclustered. It may often be a good policy for females to examine only one cluster, so as to avoid travel costs to another (Hutchinson & Halupka, *in press*).

(2) Thus larger leks allow more males to be inspected. The more males inspected, the more likely that at least one member exceeds any particular quality level (Kokko, 1997) and the better the best male is expected to be (Bednekoff, 2002). Even if the heuristics of choice do not allow returning to previously inspected males, checking more males gives an increased expected reward (Janetos, 1980), at least if we ignore search and inspection costs, which are relatively small within a lek. These arguments argue for visiting larger leks if leks are random samples of the population, but there may be an additional advantage if low-quality males avoid larger leks because they compete less effectively there (Sutherland, 1996; Kokko, 1997; but see Hernandez, Houston & McNamara, 1999).

(3) The travel time saved on a lek, if not used to sample more males, can allow longer observation of each male (Fiske & Kålås, 1995), allowing greater accuracy of assessment (Sullivan, 1994). Furthermore, returning to previously examined males is easier. Repeat visits are a typical feature of mate sampling, particularly on leks (Jennions & Petrie, 1997). They allow information gathering to be concentrated on the males that remain potential choices after a preliminary inspection (Luttbeg, 1996, 2002), and checking the consistency of performance over a period may be particularly revealing of weaknesses (Hutchinson, McNamara & Cuthill, 1993).

(4) Accurate ranking of quality is facilitated by not having to remember the qualities of previously encountered males for so long and by even being able to compare males alongside one another. In the cricket *Oecanthus nigricornis*, females move towards the calls of all males, and exhibit a preference for larger males only when two are singing at the same time (Brown *et al.*, 1996). Svensson, Petersson & Forsgren (1989) argue that the fly *Empis borealis* can compare sizes of potential mates only within a lek, ignoring sizes encountered in leks visited earlier. The proximity of males in a lek facilitates repeated alternating bouts of inspection of two rivals, which is a pattern frequently observed in leks and also noted with food choice (Langen, 1999). Such a pattern may facilitate accurate comparison relative to spending the same total time in two single blocks of observation of each male. Even in species with the cognitive abilities to remember and compare males encountered separately, comparing alongside has the advantage of factoring out sources of variation in male appearance or performance, such as light, weather, time of day, and habitat. In some lekking species, accurate comparison of male qualities is further facilitated by information from the decisions of other, maybe more experienced, females (Gibson, Bradbury & Vehrencamp, 1991), or from the outcome of contests between neighbouring males (e.g. Hovi, Alatalo & Siikamäki, 1995; Sæther, 2002), which may be indicated indirectly by a male's position in the lek (Kokko *et al.*, 1999; but see Höglund & Robertson, 1990). Even in the non-lekking eagle owl *Bubo bubo*, conflict between neighbouring males makes their calling more revealing of quality in areas of high density than of low density (Penteriani, 2003).

(5) Because of the ease and accuracy of inspecting many males on a lek, a better estimate can be made of the current distribution of quality in the population. If this distribution varies temporally or spatially, an acceptance threshold that adjusts according to an estimate of the current distribution will outperform one based on a fixed acceptance threshold (e.g. Mazalov, Perrin & Dombrowsky, 1996; Hutchinson & Halupka, in press).

(6) If leks at traditional sites fluctuate in size, revisiting a small lek may be unattractive for a female because it might currently contain no males (H. Kokko, personal communication). Similarly, fluctuation in numbers increases the risk that a lek of small average size will contain no high-quality males. Hutchinson (1999) made the related argument that if targets disappear unpredictably, heading for a pair of targets means that if one of them disappears the other is likely to be available as a replacement. The

argument also holds with other sources of uncertainty, for instance if the female is initially uncertain of male qualities, and in other domains, such as selecting a prey item. In general, opting for a group over a singleton defers a final choice, which can be adaptive if circumstances change so as to alter which option suits the chooser best (*cf.* Bown, Read & Summers, 2003).

Quite independently, economists proposed identical explanations for why cities typically develop local concentrations of, for instance, antique shops, clothes shops or restaurants (e.g. Chamberlin, 1933, p. 197; Eaton & Lipsey, 1979; Stuart, 1979). It can help an antique dealer to have rivals locate nearby, because customers will then prefer to shop in that locality than in the next town where there is less choice. Department stores may even insist that specialist shops in the same shopping centre are independent competitors, so that customers come to comparison shop (Foster, 1968).

Geographers have proposed this mechanism to explain the clustered locations of street prostitutes within red-light districts (Ashworth, White & Winchester, 1988), which makes the analogy with leks particularly striking. But caution about this claim is due. Prostitutes have alternative reasons to cluster, notably police toleration, as well as other reasons that parallel alternative explanations for leks such as mutual protection and the hotspot model (Bradbury, Gibson & Tsai, 1986). Nevertheless on the local scale it appears that prostitutes actually space themselves out, or at most form pairs (McKeganey & Barnard, 1996). Maybe the difference with shopkeepers is that the latter, however enraged by a rival setting up across the street, cannot immediately relocate or scare off their rival, and thus they get the chance to discover through experience the benefits of clustering. In fact the naive territoriality of a shopkeeper might have justification, because the empirical evidence that shoppers visit a location because of the choice available is less established than the theoretical models have us assume. A number of studies suggest that, even with goods such as televisions, as much as half the purchases occur in the first store visited, although this may to an extent be an artefact of interviewees forgetting to report other visits (reviewed by Brown, 1988; Miller, 1993*a, b*).

Both biology and the social sciences might benefit from recognition that each has been examining the same process, but economists have been ahead in developing formal models of how preference for choice favours clustering (e.g. Stuart, 1979; Stahl, 1982; Wolinsky, 1983). Most advanced are the models of Miller & Finco (1995) and Miller (1996) which estimate simultaneously a shopper's optimal choice of route and the optimal rule for when to stop search and buy. They found that clustering of shops favours the examination of more shops and that shops within a cluster usually sell more than isolated rivals, but the advantages of clustering are not so universal as we might naively expect.

The computational demands of such optimality models mean both that rather few scenarios have been modelled and that the optimised behaviour may not well represent the behaviour of people. So economists might benefit from a simple, more intuitive, argument from biologists, the black-hole explanation of lek formation (Stillman, Clutton-Brock

& Sutherland, 1993; Stillman *et al.*, 1996). The basis of the explanation is that if a female (*cf.* customer) rejects one male (*cf.* shop) it will usually make sense to examine the closest male next. Simulations suggest that this is an excellent rule of thumb (Maier, 1991) and empirical data from avian and ungulate leks show that males visited in succession lie closer than expected by chance (Trail & Adams, 1989; Clutton-Brock, Price & MacColl, 1992). The consequence of females moving between neighbouring males is that a male attracts more visits by being one of the closest males to other males, which favours ever tighter clustering. Females once in such clusters remain there, moving between the males within them (hence the name 'black hole'). Thus female behaviour, selected by reducing travel time between males, and based only on a preference for nearer males, looks like a preference for clusters and selects for male clustering. In the original formulation the stimulus to leave each male was harassment, but Stillman *et al.* (1996) claimed that the argument holds if the stimulus is the aim to sample a number of males. Unfortunately, the models have not checked how well the mechanism works if movements are biased to unvisited males.

In two other explicitly spatial models of leks (Bradbury, 1981; Gibson, Taylor & Jefferson, 1990) the female preference for groups is prescribed rather than emerging, but part of the justification behind this assumption is also selection for a reduction in travel time.

### III. DATA FROM HUMAN PSYCHOLOGY

Data from human psychology (in domains other than mate choice) have supported these explanations of grouping by establishing how widespread is the preference for choice (e.g. Bown *et al.*, 2003). In many domains a choice, even about trivial aspects of the task (e.g. Cordova & Lepper, 1996), has an immense and consistent motivating influence on human behaviour (Perlmutter & Monty, 1977; Deci & Ryan, 1985). This is interpreted as a human motivation for self-determination.

But recently Iyengar & Lepper (2000) pointed out that earlier experiments compared choices of rather few items (up to about six) with no-choice alternatives. In a series of three experiments comparing different degrees of choice, they found that extensive choice was less motivating than moderate choice. In one experiment, a stall in a supermarket invited shoppers to taste exotic jams from a display of either six or 24. Although the richer display stimulated more shoppers to visit the stall, they were more likely subsequently to buy a jam from the normal shelves when the stall had displayed fewer. In both conditions shoppers at the stall chose to taste almost the same average number of jams (1.4 and 1.5), so they seem no more likely to have been put off by a distasteful jam. In another experiment, after being asked to choose one chocolate from six or 30 different flavours, subjects expressed more satisfaction with their decision in the moderate-choice case even though they reported more enjoyment in the extensive-choice case; moreover when subsequently offered a choice of chocolates

or money as payment for participation, the moderate-choice subjects were more likely to take chocolates. Students offered a choice from 30 essay titles or from subsets of six titles, were more likely to write an essay, and wrote better ones, in the moderate-choice condition.

Evidently, although extensive choice may initially be attractive, subsequently it can be demotivating, perhaps because people feel more uncertain that they will make, or have made, the best choice and so anticipate or feel regret, or because the cognitive work involved in making a good choice is aversive. Such an aversion to making difficult decisions indeed intuitively seems typical of human behaviour in many contexts: other reasons include the fear of being blamed for a bad decision (Beattie *et al.*, 1994). One potential source of cognitive burden is keeping many options in memory, but another is the comparison itself. The larger the number of options, the closer in quality the best two options are likely to be, and thus the more difficult the decision (although in some situations it could become easier since some option is more likely to match an ideal closely). Other studies with small numbers of options (e.g. Dhar, 1997) have shown that making the best choice more difficult by adding options of similar attractiveness prompts subjects to delay selecting an item (or alternatively to take one of each option, if allowed). Redelmeier & Shafir (1995) showed that adding a third option in various medical situations made respondents more likely to choose the *status quo* option. Similarly when legislators were asked whether to recommend closing a hospital, adding a second hospital of similar merit made it more likely that they would choose to defer judgement (Redelmeier & Shafir, 1995).

Keeping one's options open by deferring choice may well be adaptive in most contexts, but can also easily lead to choosing worse options by the process of 'luring'. Bown *et al.* (2003) allowed subjects to choose between three options A, B and the lure L, which can be clearly inferior to (dominated by) B. If the experimenters somehow paired B and L, so that subjects first had to make a choice between A *versus* a subsequent choice of B or L, then more subjects ended up choosing B over A than if L was paired with A. So some subjects must have chosen the option of a subsequent choice between B and L over option A, even though they considered A better than both B and L. One example concerned three types of bank account: if B and L were both available from the same bank, more subjects decided to visit this bank and B was more likely to be chosen than if L were instead offered by the bank offering A.

Besides a group of many items luring us away from another better item, also choice within the group might be worse if too many items confuse. In the 1970s the school of J. Jacoby claimed that consumers chose less well when offered too many brands (Jacoby, 1975). As a response to earlier criticism (e.g. Russo, 1974), accuracy of choice was measured by the correlation of each subject's preference ranking of options with the ranking predicted from an earlier questionnaire about what features mattered most to them. For brands of rice, the decline in correlation occurred between 12 and 16 brands (Jacoby, Speller & Berning, 1974), whereas for shirts it was between 14 and 21 or between 21 and 28, depending on subject pool (Moreno,

1974). No such decline was observed with up to 16 brands of prepared dinners (Jacoby *et al.*, 1974).

However, a reduced accuracy of choice in large sets need not imply a reduction in the quality of items chosen, because larger choice sets will tend to contain some better options. Moreno (1974) measured the difference between each subject's chosen shirt and their 'ideal' shirt based on an earlier questionnaire. With one set of students, this measure of performance peaked with 21 shirts on offer (*versus* 7, 14 or 28), but a second set showed no clear pattern. Another analysis is possible using the probability that the subject picked the item which they were expected to find most desirable. For instance, with brands of rice (Jacoby *et al.*, 1974) 15 out of 48 subjects chose the best item when offered 16 brands. If they instead saw only a random subset of eight brands, this would contain their best brand in half the cases; 31 out of 48 subjects offered only eight brands chose the best item of these eight, so we expect  $31/2 = 15.5$  to have ended up with the best of 16, effectively the same chances as if they had chosen from all 16. Nor do the other such datasets convincingly suggest an advantage in reducing choice.

So in summary, in humans too extensive a choice can decrease the probability of choosing any item. It also reduces the ability to choose accurately, but maybe not enough to reduce the quality of items chosen. I know of no evidence that humans are attracted more to a site with moderate choice than one with extensive choice; indeed Iyengar & Lepper's (2000) results with the jams show the reverse. Also, we should not lose sight of the conventional positive effects of choice on performance, preference, and consumption when comparing moderate choice against little or no choice.

#### IV. ADAPTIVE EXPLANATIONS FOR CHOICE AVERSION

I explained above why we expected that in larger leks females could more readily select a higher-quality male and have more confidence that it is high quality relative to others. These arguments generalise to other situations where a single item is to be chosen (e.g. lions selecting prey or a bird choosing a nest site), so that the more different options available, the more likely it is to pay to select one of them rather than to wait for another opportunity.

These arguments should also apply when several options may be chosen, such as when foraging or ovipositing: we would generally expect at least as much consumption in a patch with several types of item than when any subset of those types is available at the same individual densities. A simple reason is that the total density of food items, and thus the forager's encounter rate with them, is lower without the extra types. An extra reason why a diversity of types is desirable is that types may serve different purposes (e.g. foods contain necessary nutrients in different quantities; Pulliam, 1975), and one option may even complement another. Thus we might consume both more bread and more water if both were available than if either were alone.

With folivores a varied diet avoids over-ingesting toxins specific to particular plants (Freeland & Janzen, 1974; Singer, Bernays & Carrière, 2002) and may maintain a gut flora able to cope with sudden dietary switches necessitated by the disappearance of a major dietary component (Alm, Birgersson & Leimar, 2002). Lastly, animals may end up consuming more items when a mixture is provided for the non-adaptive reason that some low-value items are accidentally consumed when confused with the better ones (or perhaps deliberately consumed if the animal is adapted to gather information on alternatives—discussed below).

However, it is also possible to devise several general adaptive reasons to explain the opposite pattern, why it is adaptive for total consumption to be less when there are more options than when a subset of options is offered.

(1) If availabilities of different options vary partially independently, extensive choice now often indicates the likely continuing availability of at least one option in the future. So if there are other benefits for deferring selection, more choice now may favour such deferment over immediate consumption. One such benefit is simply that better options may appear later. Suppose that you are looking for a flat: if you find only two available, you might well rush to rent one before both disappear; if you find many, there is little risk to waiting in the hope of a better one. Similarly male katydids are more likely to reject females, and wait longer to accept them, when previously exposed to many females (Shelly & Bailey, 1992; Jennions & Petrie, 1997, provide other examples). The argument still applies when the decision is how much to consume. In a feeding context, a possible benefit for deferring some consumption is that too full a stomach has costs in terms of efficiency of digestion or risk of predation (Witter & Cuthill, 1993), and many other situations have been considered where intensity of foraging must be traded off against predation risk (Houston, McNamara & Hutchinson, 1993).

(2) If more options are present, even if none disappear and no new ones appear, the best of them now is less likely to be the best in the future when the environment or the chooser's requirements have changed. (The more options, the more chances that one of them changes enough to become best; also the more options, the closer packed they are in quality, so that less change is necessary for ranks to switch.) This increased likelihood of change could favour deferring choice until needed. This is the case if one choice precludes others (e.g. as in female mate choice), but the argument also works when it is a quantitative question how much to commit to the best current choice. Dhar (1997) used the same argument to explain in adaptive terms why his human subjects were more likely to defer choice when an option was added that made the better options more similar in attractiveness.

(3) If we provide extra food items all of inferior quality, the optimal policy may be to reject them when encountered, because their handling times are not worth the benefit they bring. If it takes time to distinguish whether an item is in the rejection category, or if you sometimes mistake a poor item for a good one, adding the extra options can thus decrease the overall consumption rate (Hughes, 1979). An extreme case would be if the extra option was the toxic

model for the nutritious mimic already present. If you sometimes confuse model with mimic, the addition of toxic models should make you more picky about which mimics to risk eating (Getty, 1985). Furthermore, because animals are adapted to spatial and temporal heterogeneity, encountering many poor items is liable to lead to the conclusion that it would be better to look elsewhere or wait for better times. This latter argument applies equally when the task is to select a single item (Mazalov *et al.*, 1996; Hutchinson & Halupka, in press).

(4) By offering more items from the same quality distribution, there is potentially more to gain from assessment, for instance because the best of the choice set will tend to be better (Bednekoff, 2002). Therefore longer assessment may be worthwhile. This relationship between assessment time and degree of choice has been found with jays *Aphelocoma californica* selecting heavy peanuts to hoard (Langen, 1999). Because the longer assessment succeeded in finding heavier nuts, the expected rate at which nut mass would be hoarded was higher, but consumption would have appeared lower if only the number of hoarded nuts had been observed.

(5) An alternative explanation for fewer but better items being consumed is that fewer better items are needed to satiate the animal. This is not always a straightforward possibility to recognise because we often do not know exactly what leads to satiation. As an example from food choice, with a diet of few options, all options may be poor in some limiting nutrient, so that large quantities have to be eaten to satisfy a minimum nutrient requirement. With more options it is more likely that one option is richer in the nutrient so that less food need be consumed (Raubenheimer & Simpson, 1993, provide an example in the locust *Locusta migratoria*). If in ignorance of the nutritive values, a forager should still eat more when fewer options are available because it is more likely that they are all poor.

(6) Some items to be chosen are not inanimate, and too many may hinder the chooser. Thus predators may break off more attacks on larger groups of prey because of their better defensive abilities. With mate choice, male harassment at high male densities may be extremely costly to females (e.g. Davies & Halliday, 1979; Réale, Boussès & Chapuis, 1996). Nevertheless I know of no demonstrations of a resultant female preference for smaller male groups, and once she is in a large group the harassment usually accelerates her mating, although it is feasible that interference between males might have the opposite consequence.

Note that with all except (3) and (6) of these adaptive explanations for reduced consumption, the more diverse set of options should nevertheless be preferred. Indeed Iyengar & Lepper (2000) did not demonstrate that environments with less extensive choice are preferred (indeed quite the opposite), only that consumption in them is higher. It would be wrong, although tempting, to conclude from experiments measuring consumption something about preference, and *vice versa*.

None of the listed adaptive explanations for choice reducing consumption seem very convincing for Iyengar & Lepper's (2000) experimental scenarios; their mechanistic

explanation based on cognitive overload, and a consequent lack of confidence or sense of regret about the decision, appears more appropriate. If too much choice does overwhelm us and lead to worse items being selected (rather than merely a decreased ability to spot the top items from a larger set), it could then be adaptive that we avoid a choice and wait for an easier decision involving fewer options. This explanation remains puzzling from the viewpoint of what might be the constraint preventing a more appropriate response to excessive choice. If the extra choices overload our decision-making processes, by the apparently simple procedure of ignoring some of the options we should be no worse off than in the limited-choice condition. In fact, in both humans and animals, decision processes with many options often seem to involve an initial winnowing that reduces the choice set (Tversky, 1972; McClelland *et al.*, 1987; Gibson, 1996*b*; Uy, Patricelli & Borgia, 2001). This winnowing is postulated to be imperfect by involving only a subset of attributes, but nevertheless will leave a set of more closely matched alternatives than a random selection, making them harder to decide between (Dhar, 1997). If it is adaptive that humans change the heuristics of choice as the number of options increase (Timmermans, 1993), perhaps our discomfort with too many options serves to stop us wasting time in inspecting every option as thoroughly as if there were fewer, but the discomfort may have a maladaptive side-effect when it mistakenly becomes associated with the whole decision-making process.

## V. EVIDENCE IN ANIMALS: MATE CHOICE

Naturally there is much interest in these results from marketing, and economists might also think whether shoppers can find places like Hay-on-Wye (a small English village with almost 40 bookshops) too much of a good thing. If shoppers feel burdened by a duty to visit every shop, could a restriction on the number of shops increase the number of visitors? However, the concern of the present paper is whether such effects occur in animals other than humans. If we with our exceptional cognitive abilities find 24 jams excessive, does a female bird feel similarly overwhelmed on a lek of 24 males?

One might suppose that the simpler brains of animals would find extensive choice more confusing than we do, and thus perform best with, and prefer, fewer options. But a lekking bird might have evolved specifically to cope with extensive choice. For instance, one problem we face in comparing many options is remembering them, but some animals have evolved specific memory capabilities that may exceed our own (e.g. food-storing birds: Balda & Kamil, 1992). Also, if animals use different heuristics from humans to make decisions, the confusion may be absent altogether. Thus some proposed heuristics of mate choice involve only sequential choice in which each option is inspected one at a time and accepted if it exceeds a threshold (Real, 1990; Dombrovsky & Perrin, 1994; Dudey & Todd, 2001; Hutchinson & Halupka, in press). Even if the threshold is updated depending on the qualities of options encountered

earlier, there may be no need to remember many individual qualities, but only statistics, such as the maximum quality so far encountered, or the quality of the preceding male. The cognitive load at each step can then be independent of the number of options inspected.

The bushcricket *Tettigonia viridissima* provides another example of how simple organisms can avoid confusion caused by extensive choice (Römer & Krusch, 2000). An individual may be within range of many calling males, but the sensitivity of certain synapses in the auditory pathway depends on the loudness of the loudest caller, so as to block transmission of quieter calls. Thus an individual has to decide at any time between a maximum of two males (the loudest at each ear). In various animals there is an analogous blocking of signals that follow others too closely (Snedden & Greenfield, 1998). It seems to be a constraint rather than an adaptation to select better males, but either way it has the consequence of limiting the perceived choice and thus the ability of too much choice to confuse. Thus in the fiddler crab *Uca annulipes*, females visit males from several patches but rapidly identify just one male to visit from each patch on the basis of which individual leads the synchronised claw waving (Backwell *et al.*, 1998).

In the next section we examine the evidence whether animals choose better or worse when given more choice. A reanalysis of various published datasets calculates whether a decreased ability to spot the best male in a large aggregation is counteracted by larger aggregations tending to contain better males. A better performance at intermediate lek sizes would suggest that natural selection would favour a female preference for such sizes. Conversely, a female preference for mating in leks of a particular size suggests that they gain a better mate in such leks. However, the two issues of preference and performance are logically distinct because animals are not necessarily perfectly adapted. Thus it is in a later section that we examine the more extensive evidence whether females preferentially visit larger aggregations and whether they are more likely to mate once on them.

### (1) The efficacy of choice in leks of different sizes

In some frogs the background noise from the many males in a typical mating aggregation makes all but a few of the nearest calling males undetectable to a female at any one time (Gerhardt & Klump, 1988; Wollerman, 1999). Moreover, the louder the background noise, the fewer males stand out against it (mostly merely those that happen to be closest) and the less selective is the female about other qualities of the call (Schwartz, Buchanan & Gerhardt, 2001). In playback experiments of different calls without background noise, selectivity decreases when increasing the number of loudspeakers even from two to four (Gerhardt, 1987; Bishop, Jennions & Passmore, 1995) and becomes undetectable in choruses over nine (Telford, Dyson & Passmore, 1989), so this provides the clearest example of choice being less accurate when there are too many competing options available. An analysis at the end of this section shows that female frogs may consequently select worse males in larger aggregations. It would be interesting if the feedback volume control in bushcrickets mentioned in the previous section

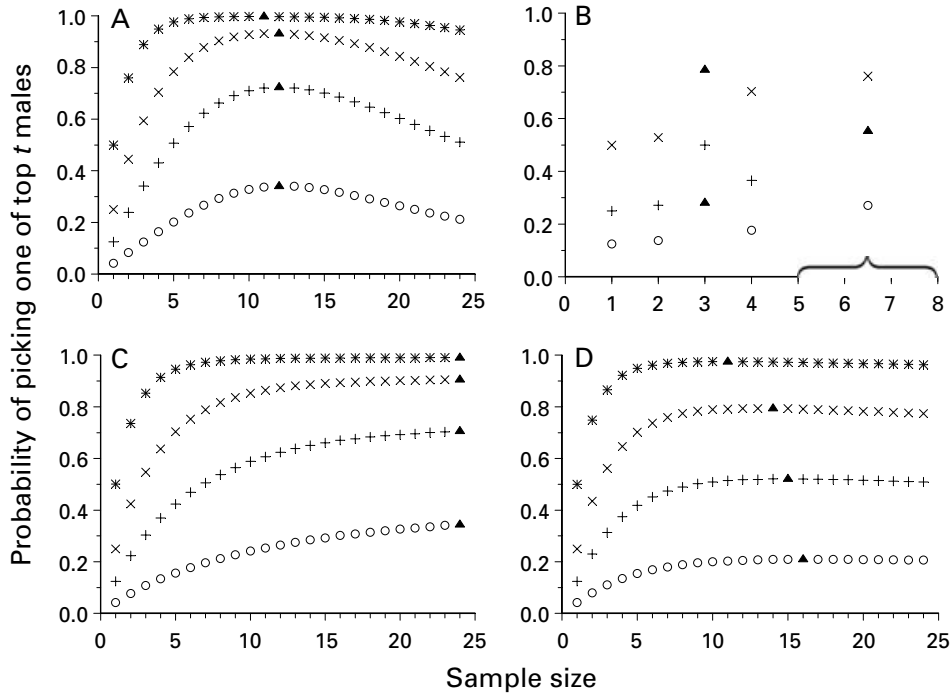
(Römer & Krusch, 2000) succeeds in avoiding this decrease in performance with large chorus size.

In frogs another factor hindering choice as density increases is that females may be grasped by a male before they can express any choice (Arak, 1983; Wagner & Sullivan, 1992). Nevertheless male–male competition can be as, or more, effective as female choice in ensuring that females mate with high-quality males (Telford & Van Sickle, 1989). However, in water striders increased harassment at high male densities leads to a reduction in female resistance, and thus mating that is more random with respect to quality (Lauer, Sih & Krupa, 1996).

As with frog aggregations, bird leks can be noisy places in which acoustic signals might interfere, but female mobility may help to overcome this, and often visual signalling seems important. Are there nevertheless indications that females are confused by larger aggregations and consequently choose worse males? Petrie (1989) directly addressed whether female moorhen *Gallinula chloropus* chose better males from flocks of about 20 males or from smaller flocks of about 10. Small females chose better males from the larger flocks, but only when the analysis took into account their ability to compete with other females, which might cloud the issue of interest here. Few other studies in any taxa have compared how the quality of selected mates depends on the group size from which they were selected (but see Svensson & Petersson, 1994, discussed below), no doubt partly because of the difficulty of establishing the relevant measure of quality. However, within each lek a crude ranking of male quality is possible using mating success itself as an assay. A rather consistent pattern emerges that mating skew, the unanimity of choice for some males above others, tends to decrease with increasing lek size (Kokko *et al.*, 1998). This suggests that females are choosing the best male less accurately in larger leks. However, there are alternative explanations: that in larger leks the top male is less able to interfere with the mating of rivals (Widemo & Owens, 1999); that, because larger leks attract more females, the most popular males in them are fully occupied (Deutsch, 1994) or become sperm depleted (Sæther, Fiske & Kålås, 2001), causing females to choose alternatives; or that in leks where skew is high, the risks of attending may outweigh the benefits for most males so that they attend less (Boyko, Gibson & Lucas, 2004).

We can use data on the relationship between skew and lek size to calculate whether a female could do better to select a male from a small group (because she is then more accurate) than from a large group (even though these contain more good males). My underlying assumption is that low skew reflects high assessment error. Kokko & Lindström (1997) and Kokko *et al.* (1998) measured mating skew in a lek by fitting a geometric distribution to the number of females choosing each male. The mating skew  $\lambda$  is measured by the rate of decrease of success with rank (itself judged from success), so that from  $\lambda$  one can readily estimate the probability that a female chooses the  $n$ th most popular male from a group of  $n$ :

$$\frac{\lambda(1-\lambda)^{r-1}}{1-(1-\lambda)^n} \quad (1)$$



**Fig. 1.** The probability of selecting, from a subset of  $m$  males, a mate in the ‘top’  $t$  of a group of  $M$  males. In B,  $M=8$ ,  $t=1$  ( $\circ$ ),  $t=2$  ( $+$ ),  $t=4$  ( $\times$ ); otherwise  $M=24$ ,  $t=1$  ( $\circ$ ),  $t=3$  ( $+$ ),  $t=6$  ( $\times$ ),  $t=12$  ( $*$ ). A triangle indicates the optimal size of subset. A is based on a function for the probability of a female choosing the  $r$ th most popular male, derived by Kokko & Lindström (1997) from data on black grouse *Tetrao tetrix* leks; ‘top’ here means most popular. B is based on data on the sex-role-reversed fly *Empis borealis* (Svensson & Petersson, 1994) giving the probability of a female choosing the  $r$ th largest male in leks of size 2–8; ‘top’ here means largest. Because of limited data on leks of 5–8 females, the results for these values of  $m$  were averaged (weighting by sample size). C is derived from a model by Johnstone and Earn (1999) assuming that females choose the apparently best male but assess quality with an error  $d$  given by the probability density function  $5 \exp(-10|d|)$ . ‘Top’ here means true quality, which is uniformly distributed between 0 and 1. D is an elaboration of C in which the error is normally distributed with s.d. =  $0.3 (M/m)^{0.5}$ . C and D are each based on  $10^6$  simulations, in each of which 24 qualities were generated, and one subset drawn independently for each value of  $m$ .

Using data from 11 black grouse leks (*Tetrao tetrix*) varying in size from six to 23 males, Kokko & Lindström (1997) related skew to the number of males in a lek, using a sigmoid function:

$$\lambda = 1/(1 + 0.00027n^3). \quad (2)$$

It is now straightforward to estimate the probability of a female choosing one amongst the most popular  $t$  males in a lek of 24. Then consider a random subset of  $m$  males drawn from this group of 24. The probability of this group containing exactly  $s$  males of the  $t$  most popular is

$$\binom{m}{s} \frac{t!}{(t-s)!} \frac{(24-t)!}{(24-t-m+s)!} \frac{(24-m)!}{24!}. \quad (3)$$

I then multiply this by the probability that a female in a lek of size  $m$  chooses one of these  $s$  top males, which I assume will be the  $s$  most popular males in this subgroup (i.e. a male that was more popular than another in the group of 24 remains more popular in the subgroup; this assumption might be violated if females extensively copy each other’s choices—Höglund *et al.*, 1995):

$$\sum_{r=1}^s \frac{\lambda(1-\lambda)^{r-1}}{1-(1-\lambda)^m}. \quad (4)$$

Summing the product of these probabilities for all  $s$  less than  $t$  and  $m$  gives the probability that a female looking only at the subgroup will choose one of the  $t$  most popular males in the original group. It turns out that she can do better than looking at the whole group, with the optimal subgroup size being around 12, depending only slightly on the value of  $t$  (Fig. 1A).

Using a group size of 24 in this analysis is arbitrary, and a similar shaped set of curves is obtained by using a very large number, representative of the entire population. Such an analysis indicates that a lek size of 12 males also maximises the chances of choosing a male in the top  $T\%$  of the entire population, where  $0 < T < 33$ . So we predict a female preference for this lek size over both smaller and larger leks.

This result confirms the idea that too extensive choice can result in poorer choice. Why can a female in a group of 24 males not select as well as in a group of 12 by simply ignoring half the males chosen at random? Perhaps she cannot avoid being confused by their presence. However, note that the analysis rests on the assumption that the composition of small leks is well represented as random samples from large leks, whereas some models predict other patterns (e.g. Sutherland, 1996; empirical support seems lacking). The exact position of the maximum in Fig. 1A is sensitive to the form of Kokko & Lindström’s (1997)



Table 1. A reanalysis of data on the frog *Hyperolius marmoratus* from Bishop *et al.* (1995). The left-hand side of the table shows the observed probability of selecting a louder speaker from a group of four. The right-hand side predicts this same probability were the frogs first randomly to choose a subset of two speakers and then to select the louder of these two with an ability measured in separate two-speaker experiments. In all but one case (that with the most different sound levels), the predicted performance using this mechanism is higher than that observed

Four-option choice (dB)	Observed probability choose 104 dB from four options	Two-option subset (dB)	Probability of two-option subset	Probability choose 104 dB from subset	Predicted probability choose 104 dB from four options
104 + 3 × 101	8/32 = 0.250	{ 104 + 101 101 + 101	1/2 1/2	{ 11/13 0	0.423
104 + 3 × 98	8/29 = 0.275	{ 104 + 98 98 + 98	1/2 1/2	{ 11/12 0	0.458
104 + 3 × 92	19/28 = 0.678	{ 104 + 92 92 + 92	1/2 1/2	{ 10/10 0	0.500
2 × 104 + 2 × 101	14/31 = 0.452	{ 104 + 104 104 + 101 101 + 101	1/6 2/3 1/6	{ 1 11/13 0	0.731
2 × 104 + 2 × 98	17/30 = 0.567	{ 104 + 104 104 + 98 98 + 98	1/6 2/3 1/6	{ 1 11/12 0	0.778

fitted functions, so I claim here only that it is feasible that females would not always do better to prefer the largest leks. Kokko *et al.* (1998) present mating skew data from another population of black grouse and these indicate a more shallow decline of skew with lek size, so that larger leks may then be best for the females. Data from other species are more sparse, but the value of  $\lambda$  is rather consistent across species for bird and mammal leks of the same size (Kokko *et al.*, 1998). This could reflect shared cognitive constraints.

A decrease in mating skew with lek size is not a sufficient condition for leks of intermediate size to be best for female choice. Johnstone & Earn (1999) present a model in which mating skew declines simply because the more individuals, the more likely that the better ones are similar enough in quality for them to be ranked differently by different females. This is a sort of null model. Putting Johnstone & Earn's (1999) functions into my analysis leads to females now being consistently more likely to choose the better males the larger the lek (Fig. 1C). So the decline in skew caused by Johnstone & Earn's (1999) mechanism is insufficient to make large leks worse for choosing. I have then introduced into this framework one obvious reason for poorer choice in larger leks: more males mean fewer observations of each male's quality. Assuming independence of observations, the deviation of an observed mean from the true value scales as the square root of sample size; so if all males in a lek are observed equally often and there is a constrained total number of observations, error in quality assessment would scale with  $(\text{lek size})^{1/2}$ . This would now lead to a very slight disadvantage in considering all 24 males rather than some subset of them (Fig. 1D). Although this difference is a little more pronounced if we assume less accurate assessment, to match the pattern in Fig. 1A

would evidently require postulating further difficulties when choosing between many males.

Another such analysis was possible using Svensson & Petersson's (1994) data on the fly *Empis borealis*, in which males choose from a lek of females. Males prefer larger females. Once a male selected a female, the whole lek was captured and measured. So for each lek size we know the proportion of matings with the largest female, with the second largest, etc. As with the black grouse, we can ask what are the chances of one of the largest  $t$  females in a lek of eight being mated by a male if he only has access to a subgroup of this eight, selected at random. This was calculated for each size of lek observed, as well as for the theoretical case of a lek of size 1 when only one female can be selected (Fig. 1B). Three was the subset size giving the highest possibility of finding the best female of eight. However, the relationship of performance and subset size seems inconsistent, so I am not confident whether males really would end up with worse females selecting from a group of eight females than from a subset.

The last data set to be reanalysed in this way concerns female frogs (*Hyperolius marmoratus*) choosing between either two or four loudspeakers playing calls at different volumes (Bishop *et al.*, 1995). The ability to choose the speaker broadcasting the loudest call (104 dB) was greater in the two-speaker than four-speaker experiment. Bishop *et al.* (1995) hypothesised that this might be because females placed equidistant from four speakers were initially confused, so that they initially moved off at random. Females would then find themselves closer to a subset of two speakers, which now appeared the loudest two, and females could then choose between them with an efficiency the same as in the two-speaker experiment. My reanalysis in Table 1

shows that by choosing two-speaker subsets at random and ignoring all others, females would generally perform better than observed, so the extra speakers seem to be causing more distraction than Bishop *et al.*'s (1995) proposed mechanism of choice can explain. Performance was better when the four speakers each played at a different intensity, but these trials cannot be included in Table 1 because the required data on some of the corresponding two-speaker choices are lacking. Without such data and information on natural variation of calls in the wild, we cannot conclude what size of aggregation best suits females.

## (2) Are larger leks always more attractive?

The evidence in the previous section suggests that sometimes in larger leks not only may choice be less accurate but also the chance of finding a good male may be reduced. Thus it may be adaptive for females not to have an open-ended preference for larger leks. This section examines direct evidence about female preferences for lek size.

The usual evidence put forward to support the male-buffet hypothesis is that more females visit larger leks. The concern often has been to examine whether the total number of female visits to the lek *per male on the lek* increases with lek size, because many studies are concerned with why it might pay males to join larger leks. But to examine whether females find larger leks more attractive it would seem sufficient to show merely that the absolute number of female visits increases with lek size. Whether using this less stringent condition is justified depends on what is the more reasonable null hypothesis of female visitation. If it is that females sample leks or geographical locations at random, the weaker test is appropriate, and I consider that this is usually the case. But if a realistic null hypothesis is that females sample males independently of their relative positions (plausible for females inspecting singing individuals in forest—Westcott & Smith, 1997), then the more stringent condition is necessary (because under this null hypothesis two males at one location leads to that location—but not each male—being visited twice as often).

The more stringent condition also tends to rule out some of the many alternative explanations for why female visits correlate with number of males on a lek: larger leks may be easier to notice (passive attraction: Bradbury, 1981); males may be attracted to where most females occur (hot-spot hypothesis: Bradbury *et al.*, 1986); if leks have coalesced from a uniform density of males, a larger lek will be spaced further from other leks and thus be the closest lek to more female territories; or aspects of the local environment may attract both males and females similarly (Deutsch, 1994). Similarly, if observations of leks are made in different years, or at different times of year, or from different populations, there is a risk that higher population densities increase both the size of leks and the absolute numbers of females visiting (Bradbury & Gibson, 1983). Tests of the female preference hypothesis with amphibians have often relied on how many of each sex come to one pond on different days; a common response to weather conditions explains a correlation in absolute numbers of each sex, and higher proportions of females when male densities are

higher can be explained by females being more picky about the right conditions than males (Wagner & Sullivan, 1992; Murphy, 2003).

Even if larger leks are deliberately chosen, it need not be to facilitate choice between the constituent males. Instead females may prefer leks where high numbers of males dilute the risk of predation (Ryan, Tuttle & Taft, 1981; Wittenberger, 1981; Gibson, Aspbury & McDaniel, 2002). Or preference for large leks could be an arbitrary preference selected by runaway Fisherian sexual selection (Queller, 1987).

Often studies report not visitation rate but instantaneous counts of females on each lek; such data are open to further interpretations because they confound visitation rate and time spent on the lek. If females spend longer on larger leks (e.g. Höglund, Montgomerie & Widemo, 1993; Deutsch, 1994), this could be interpreted as their preferring to select a mate from such leks; but when females have spent shorter periods on large leks before mating, it has also been interpreted as a preference to mate on larger leks (Jones & Quinnell, 2002). Thus such data are perhaps not appropriate to test hypotheses about preference.

In most observational studies the relationship between female visitation rate and lek size is positive, as is often that between female visits per male and lek size (Table 2). Our results above on choice efficacy being maximised at an intermediate lek size, as well as the findings of choice aversion in humans, prompt the hypothesis that female visitation might increase and then decrease with lek size. No such decline shows up in these animal studies. However, if the decline were strong, males should have evolved to prefer to join smaller leks, so that leks large enough to put females off would not exist to be observed. It is suggestive that most vertebrate leks typically contain only 10–20 males (Bradbury, 1981), which could be explained by larger leks prompting the kind of aversion observed in humans with similarly many choices. Although there are species with larger leks (up to 400 males in sage grouse), these may be divided into subleks (Kokko, 1997).

This problem of lack of variation can be avoided, as also can some of the alternative explanations for a correlation between female visits and lek size, by experimental studies in which the apparent male numbers are increased, either by adding caged males (Doolan, 1981; Walker, 1983*b*; Lank & Smith, 1992; Hovi *et al.*, 1994; Aspi & Hoffmann, 1998; deRivera *et al.*, 2003), adding mounted specimens (Kruijt, de Vos & Bossema, 1972; Petersson & Sivinski, 2003), or by playback experiments (Schwartz, 1994; Hovi *et al.*, 1997; and several studies on phonotactic insects, e.g. Morris, Kerr & Fullard, 1978; Aiken, 1982). Such experiments have usually agreed with the non-experimental data in demonstrating the attractiveness of larger aggregations, although Telford (1985) found that female frogs preferred a single speaker over a pair, Murphy (2003) found that removing almost all calling male frogs had no effect on female attendance, and in two Orthoptera there was no significant effect of the number of speakers (Otte & Loftus-Hills, 1979; Shelly & Greenfield, 1991). Unfortunately size manipulations have generally not aimed to exceed natural lek sizes, so we have not learnt more about whether the

Table 2. Observational studies on the relationship between increasing lek size and female visitation rate and the proportion of visits leading to matings. Studies are excluded in which so few leks were observed that it is unclear whether their size was the important difference, and also, for reasons given in the text, data merely on the number of females on a lek at a time (sage grouse is an exception because peak numbers were calibrated against visitation rate). Studies comparing visitation rate between days at the same lek are also excluded. In the sex-role reversed *E. borealis*, the fifth column refers to rate of visits per female. Italics indicate where I have calculated new statistics from data in the original publication

Species	Number of leks observed	Range of lek size	Rate of visits	Rate of visits per male	% visits leading to matings	Reference
<i>Chironomus plumosus</i> (midge)	17	c.50–6000	increase	maximum at 4000	—	Neems <i>et al.</i> (1992)
<i>Empis borealis</i> (empid fly)	22	1–12	increase	flat	increase	Svensson & Petersson (1988, 1992)
<i>Drosophila grimshawi</i>	>8	1–12	peak at 4	decline	flat	Droney (1994)
<i>Drosophila mycetophaga</i>	16	1 and 8	—	—	increase	Aspi & Hoffman (1998)
<i>Kobus kob thomasi</i> Uganda kob (antelope)	7	7–25	flat	decline	—	Deutsch (1994)
<i>Centrocercus urophasianus</i> sage grouse	7	2–50	increase	flat	—	Gibson (1996 <i>a</i> )
<i>Tetrao tetrix</i> black grouse	9	2–19	increase	? increase, then flat	increase	Alatalo <i>et al.</i> (1992)
<i>Tympanuchus cupido</i> greater prairie chicken	many	<4–>25	increase	decline	± flat to 15, then decline	Hamerstrom & Hamerstrom (1955)
<i>Philomachus pugnax</i> ruff	11	1–9	increase	flat	increase	Höglund <i>et al.</i> (1993)
<i>Miionectes oleagineus</i> ochre-bellied flycatcher	41	1–5	increase	flat	—	Westcott & Smith (1997)

attractiveness of larger leks continues to increase indefinitely. Doolan (1981) is an exception: cicada density was increased from the usual one or two males per bush to 12. This doubled female attendance, but then the high male density inhibited females from producing a pheromone necessary to complete the mating process.

The behaviour of females once on a lek is thus another important line of evidence. A common observation is that only a minority of the males on a lek are visited before the female makes her choice: typical mean numbers are 3–5 (Gibson & Langen, 1996). This might imply that females do not seek a wider choice (perhaps because of time or energetic costs), and that a wider choice would therefore have no benefit. However, the supposedly non-inspected males may in reality also be screened, either by a phase of long-distance assessment from trees around the lek (e.g. Wiley, 1991; Rintamäki *et al.*, 1995), or by using different quality cues, such as size or position or calls, that also do not require visiting individual territories (e.g. Gibson, 1996*b*; Murphy & Gerhardt, 2002). Several studies have tested whether the size of lek affects the proportion of female visits that include a copulation (Table 2). One study on greater prairie chicken (*Centrocercus urophasianus*; Hamerstrom & Hamerstrom, 1955) is notable in showing a peak for intermediate-sized leks of about 11–15 males, which is evidence for choice aversion at larger sizes. However, studies of other species show an increasing tendency for females to copulate in larger leks (Table 2). Allied with reports that females regularly visit more than one lek (at least in some species: Lanctot *et al.*, 1997), this pattern suggests that females more often succeed in finding high-quality males when given more choice—or at least that they have more confidence in their selections.

## VI. ANIMAL FOOD CHOICE: CONSUMPTION, PREFERENCE, PERFORMANCE

If it were a general constraint that ability to choose well declines as number of choices increases, an aversion to extensive choice should occur in domains other than mate choice. Indeed it ought to be easier to demonstrate in laboratory experiments involving food choice. For some animals, like lions for instance, food choice resembles female mate choice in that a single item must be chosen, but most data comes from herbivores in which choice is quantitative. Because feeding typically involves consumption of several items, and because food quality is multidimensional, the potential to select several different items to create a balanced diet provides extra advantages to having a choice that are less applicable to mate choice, although there can be benefits of mating with diverse partners (Bernasconi, 2003; Fox & Rauter, 2003).

Although what matters to the animal is how it reacts to the diversity of food qualities available in nature, it is also interesting to investigate its reaction to choice *per se*, even in the absence of quality variation. It is possible that laboratory studies might show that too much choice amongst similar options can confuse, and decrease consumption deleteriously, but that nevertheless in natural environments the range of qualities of possible options are such that animals nearly always increase consumption beneficially when more options become available. Similarly with mate choice one could ask whether choice promotes mating even when all mates on offer are of identical quality; no experiments have examined this situation. Such unnatural experiments would bear only on the proximate mechanism

of response to choice, not on whether the response is normally adaptive.

One pitfall in the domain of food choice is that the advantages of a mixed diet can confound the question of whether choice decreases consumption because it is aversive. Thus Bernays *et al.* (1994) showed that grasshoppers able to choose between two foods ate less than those offered either one alone. However, this need not have been due to choice aversion: the foods were complementary in nutrients, and so the grasshoppers on the mixture needed to eat less to obtain adequate nutrients, yet grew faster.

As in human psychology, the common belief is that animals consume more the more varied the diet. Thus diets to make rats obese contain many different foods ('cafeteria diets'), but most tests of their efficacy have compared consumption with that of standard rat food (which, besides providing no choice, differs dramatically in composition; Lladó *et al.*, 1995). If the extra components of the diet are much tastier, it may be their provision, not choice, that is responsible for greater consumption. So perhaps experiments should also examine choice between foods that taste the same and have the same nutrients (although then animals might not perceive them as different foods even if their appearance differed). Closest to this are a very few animal experiments in which the same food was used and only its flavouring varied to provide choice (Raynor & Epstein, 2001). Le Magnen (1960) found that rats offered three flavours ate more than when they had earlier been offered no choice. But only four of the 10 rats showed a noticeable difference in this direction, and the effect disappeared after a few days. The other such study (Naim *et al.*, 1985) compared between groups of 13–15 rats and found no effect of variety. (However, Rogers, 1990, pointed out a design flaw; consumption of a choice of flavours was always compared with that of an unflavoured food, but the unflavoured one was not always available in the choice set, so that any preference for variety might have been reversed if the unflavoured version tasted best.) A handful of other studies have demonstrated higher consumption when different flavours were presented sequentially in a regular schedule (Raynor & Epstein, 2001), but it is unclear whether animals perceive sequential presentations as allowing choice. Rather it seems possible that they interpret them as instability of the environment, in which it makes sense to eat more now in case the environment changes for the worse.

In these studies showing more consumption when there is variety, the proposed mechanism is that satiety is flavour specific. Much other research has supported this mechanism, in humans and other primates as well as rats (Raynor & Epstein, 2001). In the grasshopper *Taeniopoda eques*, a single meal on one flavour is enough to stimulate it to switch foods and eat more of a different flavour (Bernays *et al.*, 1992). Alternation between similar food items and a preference for novel foods is widespread in animals (Bernays *et al.*, 1992). Stimulus-specific satiety works in humans with the appearance or smell of the food alone (e.g. Rolls, 1985), and indeed it seems likely that in domains other than feeding a similar stimulus-specific habituation could be a widespread mechanism that causes less motivation when tasks are less varied.

Stimulus-specific satiety may be advantageous in favouring a mixed diet, but its value may often be more to cause the organism to sample its environment. Generalist herbivores fed a nutritionally optimal diet typically try out novel foods and then continue regularly to eat small quantities of them even though they are inferior (Freeland & Janzen, 1974; Behmer, Raubenheimer & Simpson, 2001), so choice of diet can decrease performance in a laboratory setting. But there is a presumed ultimate function in the wild: when the favoured food deteriorates or becomes unavailable, the animal knows the best alternatives and where to find them. Such learning about the environment provides a general adaptive explanation for the widespread phenomena of exploratory activity and novelty seeking. As a non-food example of novelty seeking, captive pigs preferred to open a door behind which novel play items had previously appeared, over one that always revealed a familiar play item (Wood-Gush & Vestergaard, 1991). However, novelty seeking has risks, and too much novelty suggests environmental instability, so we should not expect it to be a universal or unregulated tendency. Thus frightened laboratory rats reverse their usual preference for novelty, and rats from wild stock generally avoid novel objects, making them difficult to trap or poison (Barnett, 1975).

If degree of variety varies spatially, novelty seeking and stimulus-specific satiety would tend to lead to a biased diffusion away from more monotonous areas. However, for animals we still seem to lack an unambiguous demonstration that prior knowledge of the variety of food at a site makes it be chosen over a site with less variety. The closest is a study on sheep *Ovis aries* (Scott & Provenza, 1998). Lambs were allowed to wander between a site where a food was flavoured in three different ways and a site where only the most preferred flavour was available. In the 15 min allowed, they spent more time at the site with variety, but this might be because they fed more once they reached there rather than because they initially chose the site which they knew to be more varied.

Also relevant here are a series of operant experiments involving pigeons (Catania, 1980). They had to choose between pecking one 'free-choice' key which led to two terminal keys lighting up, either of which could be pecked to obtain food, or another 'fixed-choice' key which led to only one terminal key lighting up, which also produced food when pecked (i.e. a concurrent-chain design). There was a preference for the free-choice key, but it was typically rather small, less than 10% (Catania, 1980), and not found in all experiments (Ono, 2000). Generally the food reward was the same and was provided at the same hopper regardless of which of the lit keys in the free-choice option were pecked or whether the free-choice or fixed option was chosen. (The one exception involved a free choice between food and water compared with the fixed choice always providing just one; since food and water are not substitutable and both necessary, it would be surprising if the free choice had not been preferred.) So the free choice is really about the means to obtain a food rather than about the food itself. There are three combinations of successive key presses that produce the reward, so if pigeons viewed the choice as between these three alternatives, rather than as an

initial choice between free choice or fixed choice, the two alternatives involving the free-choice key were chosen less often than expected by chance.

The preference was not stronger if the free choice involved more keys (up to four), although there was also a preference for free choice yielding four alternatives over two (Catania, 1980). Interestingly the preference was stronger if pecking the terminal keys produced food only probabilistically rather than with certainty (Ono, 2000). It is understandable that in a situation where one option sometimes does not work pigeons should exhibit a greater preference for having an alternative option, even though in the experiment this alternative was never available once the other had been tried. By contrast, Hayes *et al.* (1981) identified circumstances where fixed choice was very strongly preferred over free choice: one of the two keys available in the free-choice condition was the same as in the fixed-choice condition, but the alternative provided food for so brief a time that usually none could be obtained. Although this terminal key was almost never chosen (even if the fixed-choice option was removed), and thus the rewards from free choice were similar as from fixed choice, pigeons seemed unwilling to put themselves at risk of pecking it.

Analogous experiments with macaques (*Macaca fascicularis*) and humans (Suzuki, 1997, 1999, 2000) have produced broadly similar results, but not the fixed-choice preference found by Hayes *et al.* (1981). Another experiment which is often compared involved rats in a maze (Voss & Homzie, 1970). They slightly preferred a branch that led to a further choice of routes over one that involved no further branch point (59:41). All routes led to the same food supply, so this experiment may reveal merely a preference for an environment with an escape route.

I can find no animal experiments analogous to Iyengar & Lepper's (2000) in comparing consumption or preference between moderate and extensive choice of food. However, in some animals there is evidence of cognitive overload even with very few options, with the consequence of decreased consumption and performance. Choice can be a blessing if you are adapted to make use of it (as are, for instance, many polyphagous herbivorous insects such as grasshoppers which are superb at maintaining a balanced diet even when to do so they must mix several foods: e.g. Behmer *et al.*, 2001, and references therein), but in other species it may become a curse. Because extreme specialists may not react to potential alternatives, perhaps moderately polyphagous species are often the most vulnerable to too much choice. For instance, a specialist variety of the butterfly *Polygonia c-album* was not only both better at identifying good food plants of its host species and faster at doing so, but also, unlike more polyphagous conspecifics, was not tempted by a lethal host (Janz & Nylin, 1997; Nylin, Bergström & Janz, 2000; Janz, 2003). Of particular relevance to us is when it is the cognitive processes that cannot cope as well with multiple food types (rather than, say, physiological processes such as digestion). Bernays (1999*b*) provides an example of a homopteran which, although able to feed on many plant species, produced fewer eggs in the presence of three species of host plants (compared with when only one host was

present) because it was stimulated to move too often. Other problems may be in attending to the right cues to identity or quality, or in making good decisions based upon these cues, or in recalling previous knowledge, such as how to deal quickly with each option. Repeatedly relearning these skills in the presence of a mixture of options is wasteful of time. Furthermore, the presence of different rewarding options may hinder learning the recognition cues associated with each (Papaj, 1990; Dukas & Real, 1993; Bernays, 1998, 1999*a*). These ideas are well reviewed by Bernays & Wcislo (1994) and Bernays (1999*a*). The solution to the problem is to ignore alternative options, with the option selected either fixed or learnt during development. Such avoidance of interference was Darwin's (1876) explanation for flower constancy—individuals of many flower-feeding insects have their own preferred type of flower, ignoring types that conspecifics prefer (Goulson, Stout & Hawson, 1997).

The same principle lies behind the idea of a search image or selective attention, which has been most thoroughly investigated in birds: with cryptic prey, concentrating the search on one type may find items at a higher rate than looking for several types (Langley *et al.*, 1996; Dukas & Kamil, 2001). If the ability to specialise is incomplete, which may well be adaptive in the long term (Papaj, 1990), providing extra options could distract (e.g. lead to a loss of the search image), and decrease consumption. Unfortunately, published experiments on search image do not unequivocally demonstrate this, because they lower the density of the existing option when adding an extra option (Plaisted & Mackintosh, 1995).

Such interference would disappear if the options were similar enough to be covered by the same search image. With identical options, it does not matter which is chosen. Nevertheless a choice still has to be made (if only on the order of consumption), and research on humans has found that the closer the options, the more we deliberate (Dhar, 1997; *cf.* time to select a mate in the lekking fly *E. borealis*, Svensson *et al.*, 1989). Could this play a role in the 'confusion effect' (as suggested also by Bernays, 1999*a*)? Numerous studies have shown a predator attacking a shoal of fish to be less likely to capture any prey than when attacking isolated members of the shoal (e.g. Landeau & Terborgh, 1986). Accordingly, predatory fish may prefer to attack single prey than those in groups, especially if they have another task to perform simultaneously such as to look out for predators (Milinski, 1990). The process is not restricted to fast-moving prey moving in three dimensions: it also occurs with geckos and primates feeding on mealworms and beetles (Schradin, 2000), and with students touching static paper dots with a pointer (Milinski, 1990). The conventional explanation is that the confusion comes from an inability to concentrate on any one item through an overload of the perception system (e.g. Krakauer, 1995), and this is supported by the tendency for odd-looking prey to be most vulnerable (Landeau & Terborgh, 1986). However, Iyengar & Lepper's (2000) results should make us test whether discomfort and delay over making a choice between many similar targets is also part of the problem.

## VII. CHOICE AND ENVIRONMENTAL ENRICHMENT

Captive animals have often traditionally been kept in plain cages and enclosures. Increasingly it is being shown that environmental enrichment of such cages can bring welfare, health, and economic benefits (Newberry, 1995). Such enrichments can often be interpreted as increasing the animal's choice: maybe more types of food or toys are provided, or extra perches, or the enclosure might be subdivided by partitions so that all positions in it are no longer equivalent. There are at least five reasons why such provision of choice can be beneficial.

(1) Having two perches provides an alternative if, for instance, another animal already occupies one; choice itself is not the important factor.

(2) The extra options may include some that were better than those available before. It is again not then the choice that is important, but it usually requires a contrived experimental setting to distinguish these effects, which most studies do not attempt. In any case, even though each individual could be happy to have all but its favoured option removed, which is the favoured option may differ between individuals, so the provision of variety benefits the animals and saves keepers from having to identify individual preferences.

(3) The preferred option of an animal may change during the day, possibly often and unpredictably. Preferred options may change because of the animal's earlier activities: for instance, eating one food may prompt an appetite for another, so as to balance nutrient intake and/or because of stimulus-specific habituation. Provision of choice allows the animal to match its activities closely to its immediate needs. But many needs can be satisfied equally well a little later, and thus similar benefits could in theory be achieved by providing different options at different times, without providing a simultaneous choice. Whether having to wait for the right option to become available causes undue stress perhaps depends on the level of choice in the natural environment.

(4) Choice of options might be attractive in exercising the mind of a 'bored' animal and maybe therefore also in taking up time. Captive animals will tackle tasks requiring problem solving without any reward (e.g. Harlow, Harlow & Meyer, 1950), although this is nowadays interpreted as exploration of the environment rather than amusement seeking (Inglis, Forkman & Lazarus, 1997). Because it is difficult to provide different options day after day, any intellectual stimulation from making a choice is likely to wane rapidly; intellectual stimulation seems easier to provide by getting the animal to search for food, or extract it from inaccessible places. Nevertheless, the pleasure of intellectual stimulation might be a reason not to observe aversive effects of extensive choice in captive animals, even if it did occur in wild animals that do not have too little to do and think about. However, a more likely explanation for any such difference would be that aversive effects of too much choice reduce as the options become more familiar.

(5) For humans one important attraction of choice is that we feel in control (Deci & Ryan, 1985). It is often proposed that animals may also seek to be in control (e.g. Perlmuter & Monty, 1977; Markowitz, 1982; Chamove, 1989), although the main experimental evidence cited is the suffering of animals unable to avoid aversive stimuli such as electric shocks (Seligman, Maier & Solomon, 1971). Probably better evidence would be the slight preference for free choice in operant experiments (discussed above: Catania, 1980; Suzuki, 1999).

One recent experiment on choice in the context of environmental enrichment concerned pecking behaviour in chickens *Gallus gallus* (Jones, Carmichael & Rayner, 2000). (In plain cages this urge can be directed deleteriously towards pecking out feathers.) String, beads and chain were offered either singly or in combination. All were pecked more when all three were present. Slower habituation does not seem to be the explanation because pecking increased with time. However, unfortunately the choice condition was confounded by the total stimulus being three times as large. In any case more pecking need not imply that chickens are happier—the housewife who feels a duty to keep her windows clean is probably not happier to have more windows to deal with (although it is unlikely that she would then spend longer on each window). We cannot directly ask animals about their happiness, but we can study their preferences. In follow-up experiments, Jones *et al.* (2000) discovered that yellow and white were the colours of string that elicited most pecking. When offered a simultaneous choice at different positions in their cage, chickens preferred (i.e. more pecking bouts) both all-yellow and all-white bunches of string over a mixture, which is interpretable as an aversion to having an immediate choice (but the greater visual complexity of the mixed stimulus is a confounding factor). At least this is a warning to be even more circumspect with animals than with humans in predicting that extra choice is always pleasurable.

## VIII. FURTHER APPLICATIONS

Frustratingly often this review has had to conclude that the right experiments have not been done to address the questions of concern. The lack of research on whether animals prefer choice contrasts with the extensive research on risk sensitivity (Kacelnik & Bateson, 1996) in which the question is likewise whether animals prefer variety, but the variable option is offered in a way that excludes choice between its components. Nevertheless, choice requires variety, so in the wild the two are often confounded. It is conceivable that some experimental findings of preference for risk arise because the animal mistakenly associates more variable options with providing choice as well as variety. In the wild the animal can expect to be able to choose to skip the poor items and concentrate on the good, which the laboratory studies prevent.

I expect that any tendency for extensive choice to be aversive will vary between taxa depending on the species' cognitive capabilities, but also for ecological reasons. The

latter could lead to different patterns in different domains (e.g. food and mate choice) even within the same species. Demonstrating whether choice preference or aversion occurs can be relevant to understanding a range of biological phenomena. Thus, how many potential mates are inspected, and the consistency in selecting the best one, has consequences for population genetics and responses to selection. Too much insistence on having a choice of mates can cause breeding failure when population density falls to low levels which would otherwise still be viable; it also presents problems for captive breeding (Møller & Legendre, 2001). Other important consequences for ecology follow from whether animals seek choice in their diet. One issue is habitat choice: do animals seek out and remain in areas which are diverse in food or environment? Another consequence is the population dynamics of predator and prey. If animals prefer not to be bothered by too many choices, they may not switch from favoured prey items even if they become heavily depredated. Conversely, a preference for choice combined with stimulus-specific satiety will lead rare prey species to be disproportionately depleted, but the predator itself may be less sensitive to environmental disturbances by being a generalist. I have already discussed the welfare issues associated with whether absence of choice disturbs animals, but even a farmer motivated purely by profit should be interested in whether diversifying at least the flavours in the diet stimulates feeding.

Another practical application is experimental design. As Raffa, Havill & Nordheim (2002) discuss, preference tests are widely used in many areas of biology and there are often logistical advantages to offering many choices simultaneously in each test. In experiments on caterpillars, Raffa *et al.* (2002) found that the likelihood of detecting a preference for lower concentrations of a feeding inhibitor was greater in two-option tests than in four-option tests, and five-option tests were sufficiently poorer again as to suggest a non-linear effect. Unfortunately it is unclear to me to what extent their finding is due to extra confusion with more choice, or simply to a reduction in statistical power caused by a proportional dilution of feeding effort on each option. Interestingly Bateson (2002) proposed that providing extra options had the opposite effect, that they clarified the preference for one option over another, because random decisions by choosers that are indifferent between two options are diluted over the extra options. Various animal researchers have found that a preference for one option over another can be reversed when a third option is added (e.g. Bateson, Healy & Hurly, 2002; Shafir, Waite & Smith, 2002), so care must be taken in extrapolating preference tests to the wild.

Raffa *et al.*'s (2002) comparisons were all between different concentrations of the same chemical, so that ranking the options may be less demanding a task than when comparing between different flavours, or between options that vary multidimensionally. If more choices in concentration cause more confusion, what is the situation when there are infinitely many choices, as when there is a continuous gradient of concentration or temperature? Perhaps in a gradient the obvious ranking, and its association with a spatial cue, make choice not such a confusing task. In this

context it is interesting that Raffa *et al.* (2002) found an effect of spatial arrangement on the strength of preference, although this was not always greatest in configurations in which the concentrations over the dish matched a monotonic gradient.

A review of choice aversion in animals would not be complete without mention of the apocryphal Buridan's ass (Rescher, 1969), which starved to death unable to decide between two equally wonderful bales of hay. This ancient fable was meant to illustrate a philosophical point about choosing without a preference. Alternatives with identical pay-offs should not be so rare in biology whenever a better option is more heavily exploited so that its yield is differentially depressed (the basis of the ideal free distribution: e.g. Tregenza, 1995). In humans it seems not difficult to find examples from literature or real life of dithering between two suitors or two careers leading to the disastrous loss of both. Are there real examples of such asinine paralysis amongst the animals?

## IX. CONCLUSIONS

(1) This review was stimulated by results from psychology showing that humans prefer to have some choice over no choice and are motivated to consume more when choice is offered, but that too much choice can reduce consumption and the accuracy of choice, perhaps because decision making is then more difficult.

(2) Biologists and social scientists both might profit from recognising the strong similarities between certain models of mate choice and of shopping behaviour, which in both cases rest on the assumption of a preference for choice.

(3) There are many potential adaptive explanations both for diversity of choice increasing consumption and for it decreasing consumption, although cognitive constraints are also a likely explanation for the latter pattern.

(4) My main conclusion is that there is surprisingly little clear-cut evidence whether or not choice is aversive in animals. Research needs to address three interrelated, but logically distinct, issues: whether individuals prefer to have more choice, whether more choice stimulates consumption, and whether more choice enables better options to be selected.

(5) The issue has been addressed most often when considering mate choice on leks, because the assumption of a preference for choice underlies one of the main explanations of why leks form. Most studies have found that larger leks attract more females, and a few studies have found that females are more likely to mate when in a large lek than when in a small one. There is little evidence of this preference reversing at larger lek sizes, but the problem is a lack of studies that experimentally increase leks above their natural sizes.

(6) The consistency, and therefore perhaps efficacy, of choice declines in larger leks. This argues that it may not be in the best interests of females to have an open-ended preference for larger leks. Evidence of confusion with too much choice is clearest in acoustically advertising amphibians.

(7) With diet selection, stimulus-specific satiety seems to be a widespread phenomenon in stimulating greater consumption if there is variety, but we lack experiments on whether this makes animals prefer sites where this variety exists. Particularly in insects there is evidence that dealing with more than one food can be cognitively challenging, so that there are advantages to being able to concentrate on a single type of food; the phenomena of search image and the confusion effect may be evidence of similar limitations in vertebrates.

(8) Operant experiments, mostly in pigeons, usually show only slight preferences for free choice. This choice concerns the method to obtain a food reward rather than the food itself.

(9) Extra choice is often a component of environmental enrichment for captive animals, but it is usually unclear whether the ability to choose is itself what matters.

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## XI. REFERENCES

- AIKEN, R. B. (1982). Effects of group density on call rate, phonokinesis, and mating success in *Palmacorixa nana* (Heteroptera: Corixidae). *Canadian Journal of Zoology* **60**, 1665–1672.
- ALATALO, R. V., HÖGLUND, J., LUNDBERG, A. & SUTHERLAND, W. J. (1992). Evolution of black grouse leks: female preferences benefit males in larger leks. *Behavioral Ecology* **3**, 53–59.
- ALEXANDER, R. D. (1975). Natural selection and specialized chorusing behavior in acoustical insects. In *Insects, Science and Society* (ed. D. Pimentel), pp. 35–77. Academic Press, New York.
- ALM, U., BIRGERSSON, B. & LEIMAR, O. (2002). The effect of food quality and relative abundance on food choice in fallow deer. *Animal Behaviour* **64**, 439–445.
- ARAK, A. (1983). Male-male competition and mate choice in anuran amphibians. In *Mate Choice* (ed. P. Bateson), pp. 181–210. Cambridge University Press, Cambridge.
- ASHWORTH, G. J., WHITE, P. E. & WINCHESTER, H. P. M. (1988). The red-light district in the West European city: a neglected aspect of the urban landscape. *Geoforum* **19**, 201–212.
- ASPI, J. & HOFFMANN, A. A. (1998). Female encounter rates and fighting costs of males are associated with lek size in *Drosophila mycetophaga*. *Behavioral Ecology and Sociobiology* **42**, 163–169.
- BACKWELL, P., JENNIONS, M., PASSMORE, N. & CHRISTY, J. (1998). Synchronized courtship in fiddler crabs. *Nature* **391**, 31–32.
- BALDA, R. P. & KAMIL, A. C. (1992). Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. *Animal Behaviour* **44**, 761–769.
- BARNETT, S. A. (1975). *The Rat: A Study in Behavior* (2nd edn). University of Chicago Press, Chicago.
- BATESON, M. (2002). Context-dependent foraging choices in risk-sensitive starlings. *Animal Behaviour* **64**, 251–260.
- BATESON, M., HEALY, S. D. & HURLY, T. A. (2002). Irrational choices in hummingbird foraging behaviour. *Animal Behaviour* **63**, 587–596.
- BEATTIE, J., BARON, J., HERSHEY, J. C. & SPRANCA, M. D. (1994). Psychological determinants of decision attitude. *Journal of Behavioral Decision Making* **7**, 129–144.
- BEDNEKOFF, P. A. (2002). On hotshots and lotteries: are the best males on larger leks better than expected? *Behavioral Ecology* **13**, 580–581.
- BEHMER, S. T., RAUBENHEIMER, D. & SIMPSON, S. J. (2001). Frequency-dependent food selection in locusts: a geometric analysis of the role of nutrient balancing. *Animal Behaviour* **61**, 995–1005.
- BERNASCONI, G. (2003). Diversity effects in reproductive biology. *Oikos* **102**, 217–220.
- BERNAYS, E. A. (1998). The value of being a resource specialist: behavioral support for a neural hypothesis. *American Naturalist* **151**, 451–464.
- BERNAYS, E. A. (1999a). Plasticity and the problem of choice in food selection. *Annals of the Entomological Society of America* **92**, 944–951.
- BERNAYS, E. A. (1999b). When host choice is a problem for a generalist herbivore: experiments with the whitefly, *Bemisia tabaci*. *Ecological Entomology* **24**, 260–267.
- BERNAYS, E. A., BRIGHT, K. L., GONZALEZ, N. & ANGEL, J. (1994). Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* **75**, 1997–2006.
- BERNAYS, E. A., BRIGHT, K., HOWARD, J. J., RAUBENHEIMER, D. & CHAMPAGNE, D. (1992). Variety is the spice of life: frequent switching between foods in the polyphagous grasshopper *Taeniopoda eques* Burmeister (Orthoptera: Acrididae). *Animal Behaviour* **44**, 721–731.
- BERNAYS, E. A. & WCISLO, W. T. (1994). Sensory capabilities, information processing, and resource specialization. *Quarterly Review of Biology* **69**, 187–204.
- BISHOP, P. J., JENNIONS, M. D. & PASSMORE, N. I. (1995). Chorus size and call intensity: female choice in the painted reed frog, *Hyperolius marmoratus*. *Behaviour* **132**, 721–731.
- BOWN, N. J., READ, D. & SUMMERS, B. (2003). The lure of choice. *Journal of Behavioral Decision Making* **16**, 297–308.
- BRADBURY, J. W. (1981). The evolution of leks. In *Natural Selection and Social Behaviour* (eds. R. D. Alexander and D. W. Tinkle), pp. 138–169. Chiron Press, New York.
- BRADBURY, J. W. & GIBSON, R. M. (1983). Leks and mate choice. In *Mate Choice* (ed. P. Bateson), pp. 109–138. Cambridge University Press, Cambridge.
- BRADBURY, J., GIBSON, R. & TSAI, I. M. (1986). Hotspots and the dispersion of leks. *Animal Behaviour* **34**, 1694–1709.
- BROWN, S. (1988). Information seeking, external search and 'shopping' behaviour: preliminary evidence from a planned shopping centre. *Journal of Marketing Management* **4**, 33–49.
- BROWN, W. D., WIDEMAN, J., ANDRADE, M. C. B., MASON, A. C. & GWYNNE, D. T. (1996). Female choice for an indicator of male size in the song of the black-horned tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). *Evolution* **50**, 2400–2411.
- BOYKO, A. R., GIBSON, R. M. & LUCAS, J. R. (2004). How predation risk affects the temporal dynamics of avian leks: greater sage grouse versus golden eagles. *American Naturalist* **163**, 154–165.



- CATANIA, A. C. (1980). Freedom of choice: a behavioral analysis. *The Psychology of Learning and Motivation* **14**, 97–145.
- CHAMBERLIN, E. (1933). *The Theory of Monopolistic Competition*. Harvard University Press, Cambridge.
- CHAMOVE, A. S. (1989). Environmental enrichment: a review. *Animal Technology* **40**, 155–178.
- CLUTTON-BROCK, T. H., PRICE, O. F. & MACCOLL, A. D. C. (1992). Mate retention, harassment, and the evolution of ungulate leks. *Behavioral Ecology* **3**, 234–242.
- CORDOVA, D. I. & LEPPER, M. R. (1996). Intrinsic motivation and the process of learning: beneficial effects of contextualization, personalization, and choice. *Journal of Educational Psychology* **88**, 715–730.
- DARWIN, C. (1876). *The Effects of Cross and Self-Fertilisation in the Vegetable Kingdom*. Murray, London.
- DAVIES, N. B. & HALLIDAY, T. R. (1979). Competitive mate searching in male common toads, *Bufo bufo*. *Animal Behaviour* **27**, 1253–1267.
- DECI, E. L. & RYAN, R. M. (1985). *Intrinsic Motivation and Self-Determination in Human Behavior*. Plenum Press, New York.
- DERIVERA, C. E., BACKWELL, P. R. Y., CHRISTY, J. H. & VEHRENCAMP, S. L. (2003). Density affects female and male mate searching in the fiddler crab, *Uca beebei*. *Behavioral Ecology and Sociobiology* **53**, 72–83.
- DEUTSCH, J. C. (1994). Uganda kob mating success does not increase on larger leks. *Behavioral Ecology and Sociobiology* **34**, 451–459.
- DHAR, R. (1997). Consumer preference for a no-choice option. *Journal of Consumer Research* **24**, 215–231.
- DOMBROVSKY, Y. & PERRIN, N. (1994). On adaptive search and optimal stopping in sequential mate choice. *American Naturalist* **144**, 355–361.
- DOOLAN, J. M. (1981). Male spacing and the influence of female courtship behaviour in the bladder cicada, *Cystosoma saundersii* Westwood. *Behavioral Ecology and Sociobiology* **9**, 269–276.
- DRONEY, D. C. (1994). Tests of hypotheses for lek formation in a Hawaiian *Drosophila*. *Animal Behaviour* **47**, 351–361.
- DUDEY, T. & TODD, P. M. (2001). Making good decisions with minimal information: simultaneous and sequential choice. *Journal of Bioeconomics* **3**, 195–215.
- DUKAS, R. & KAMIL, A. C. (2001). Limited attention: the constraint underlying search image. *Behavioral Ecology* **12**, 192–199.
- DUKAS, R. & REAL, L. A. (1993). Learning constraints and floral choice behaviour in bumble bees. *Animal Behaviour* **46**, 637–644.
- EATON, B. C. & LIPEY, R. G. (1979). Comparison shopping and the clustering of homogeneous firms. *Journal of Regional Science* **19**, 421–435.
- FISKE, P. & KÅLÅS, J. A. (1995). Mate sampling and copulation behaviour of great snipe females. *Animal Behaviour* **49**, 209–219.
- FREELAND, W. J. & JANZEN, D. H. (1974). Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* **108**, 269–289.
- FOSTER, J. R. (1968). Real estate financing and the opportunity for shopping center occupancy. *Land Economics* **44**, 319–329.
- FOX, C. W. & RAUTER, C. M. (2003). Bet-hedging and the evolution of multiple mating. *Evolutionary Ecology Research* **5**, 273–286.
- GERHARDT, H. C. (1987). Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog, *Hyla cinerea*. *Animal Behaviour* **35**, 1479–1489.
- GERHARDT, H. C. & KLUMP, G. M. (1988). Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. *Animal Behaviour* **36**, 1247–1249.
- GETTY, T. (1985). Discriminability and the sigmoid functional response: how optimal foragers could stabilize model-mimic complexes. *American Naturalist* **125**, 239–256.
- GIBSON, R. M. (1996a). A re-evaluation of hotspot settlement in lekking sage grouse. *Animal Behaviour* **52**, 993–1005.
- GIBSON, R. M. (1996b). Female choice in sage grouse: the roles of attraction and active comparison. *Behavioral Ecology and Sociobiology* **39**, 55–59.
- GIBSON, R. M., ASPBURY, A. S. & MCDANIEL, L. L. (2002). Active formation of mixed-species grouse leks: a role for predation in lek evolution. *Proceedings of the Royal Society of London B* **269**, 2503–2507.
- GIBSON, R. M., BRADBURY, J. W. & VEHRENCAMP, S. L. (1991). Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behavioral Ecology* **2**, 165–180.
- GIBSON, R. M. & LANGEN, T. A. (1996). How do animals choose their mates? *Trends in Ecology and Evolution* **11**, 468–470.
- GIBSON, R. M., TAYLOR, C. E. & JEFFERSON, D. R. (1990). Lek formation by female choice: a simulation study. *Behavioral Ecology* **1**, 36–42.
- GOULSON, D., STOUT, J. C. & HAWSON, S. A. (1997). Can flower constancy in nectaring butterflies be explained by Darwin's interference hypothesis? *Oecologia* **112**, 225–231.
- HAMERSTROM, F. & HAMERSTROM, F. (1955). Population density and behavior in Wisconsin Prairie Chickens (*Tympanuchus cupido pinnatus*). In *Proceedings of the 11th International Ornithological Congress*, pp. 459–466.
- HARLOW, H. F., HARLOW, M. K. & MEYER, D. R. (1950). Learning motivated by a manipulation drive. *Journal of Experimental Psychology* **40**, 228–234.
- HAYES, S. C., KAPUST, J., LEONARD, S. R. & ROSENFARB, I. (1981). Escape from freedom: choosing not to choose in pigeons. *Journal of the Experimental Analysis of Behavior* **36**, 1–7.
- HERNANDEZ, M. L., HOUSTON, A. I. & MCNAMARA, J. M. (1999). Male rank and optimal lek size. *Behavioral Ecology* **10**, 73–79.
- HÖGLUND, J. & ALATALO, R. V. (1995). *Leks*. Princeton University Press, Princeton.
- HÖGLUND, J. & ROBERTSON, J. G. M. (1990). Female preferences, male decision rules and the evolution of leks in the great snipe *Gallinago media*. *Animal Behaviour* **40**, 15–22.
- HÖGLUND, J., MONTGOMERIE, R. & WIDEMO, F. (1993). Costs and consequences of variation in the size of ruff leks. *Behavioral Ecology and Sociobiology* **32**, 31–39.
- HÖGLUND, J., ALATALO, R. V., GIBSON, R. M. & LUNDBERG, A. (1995). Mate-choice copying in black grouse. *Animal Behaviour* **49**, 1627–1633.
- HOUSTON, A. I., MCNAMARA, J. M. & HUTCHINSON, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London B* **341**, 375–397.
- HOVI, M., ALATALO, R. V., HALONEN, M. & LUNDBERG, A. (1997). Responses of male and female black grouse to male vocal display. *Ethology* **103**, 1032–1041.
- HOVI, M., ALATALO, R. V., HÖGLUND, J., LUNDBERG, A. & RINTAMÄKI, P. T. (1994). Lek centre attracts black grouse females. *Proceedings of the Royal Society of London B* **258**, 303–305.
- HOVI, M., ALATALO, R. V. & SIIKAMÄKI, P. (1995). Black grouse leks on ice: female mate sampling by incitation of male competition? *Behavioral Ecology and Sociobiology* **37**, 283–288.

- HUGHES, R. N. (1979). Optimal diets under the energy maximization premise: the effects of recognition time and learning. *American Naturalist* **113**, 209–221.
- HUGIE, D. M. & LANK, D. B. (1997). The resident's dilemma: a female choice model for the evolution of alternative mating strategies in lekking male ruffs (*Philomachus pugnax*). *Behavioral Ecology* **8**, 218–225.
- HUTCHINSON, J. M. C. (1999). Bet-hedging when targets may disappear: optimal mate-seeking or prey-catching trajectories and the stability of leks and herds. *Journal of Theoretical Biology* **196**, 33–49.
- HUTCHINSON, J. M. C. & HALUPKA, K. (in press). Mate choice when males are in patches: optimal strategies and good rules of thumb. *Journal of Theoretical Biology*.
- HUTCHINSON, J. M. C., McNAMARA, J. M. & CUTHILL, I. C. (1993). Song, sexual selection, starvation and strategic handicaps. *Animal Behaviour* **45**, 1153–1177.
- INGLIS, I. R., FORKMAN, B. & LAZARUS, J. (1997). Free food or earned food? A review and fuzzy model of contrafreeloading. *Animal Behaviour* **53**, 1171–1191.
- IYENGAR, S. S. & LEPPER, M. R. (1999). Rethinking the value of choice: a cultural perspective on intrinsic motivation. *Journal of Personality and Social Psychology* **76**, 349–366.
- IYENGAR, S. S. & LEPPER, M. R. (2000). When choice is demotivating: can one desire too much of a good thing? *Journal of Personality and Social Psychology* **79**, 995–1006.
- JACOBY, J. (1975). Perspectives on a consumer information processing research program. *Communication Research* **2**, 203–215.
- JACOBY, J., SPELLER, D. E. & BERNING, C. K. (1974). Brand choice behavior as a function of information load: replication and extension. *Journal of Consumer Research* **1**, 33–42.
- JANETOS, A. C. (1980). Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology* **7**, 107–112.
- JANZ, N. (2003). The cost of polyphagy: oviposition decision time vs error rate in a butterfly. *Oikos* **100**, 493–496.
- JANZ, N. & NYLIN, S. (1997). The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. *Proceedings of the Royal Society of London B* **264**, 701–707.
- JENNIONS, M. D. & PETRIE, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews* **72**, 283–327.
- JOHNSTONE, R. A. & EARN, D. J. D. (1999). Imperfect female choice and male mating skew on leks of different sizes. *Behavioral Ecology and Sociobiology* **45**, 277–281.
- JONES, R. B., CARMICHAEL, N. L. & RAYNER, E. (2000). Pecking preferences and pre-dispositions in domestic chicks: implications for the development of environmental enrichment devices. *Applied Animal Behaviour Science* **69**, 291–312.
- JONES, T. M. & QUINNELL, R. J. (2002). Testing predictions for the evolution of lekking in the sandfly, *Lutzomyia longipalpis*. *Animal Behaviour* **63**, 605–612.
- KACELNIK, A. & BATESON, M. (1996). Risky theories—the effects of variance on foraging decisions. *American Zoologist* **36**, 402–434.
- KOKKO, H. (1997). The lekking game: can female choice explain aggregated male displays? *Journal of Theoretical Biology* **187**, 57–64.
- KOKKO, H. & LINDSTRÖM, J. (1997). Measuring the mating skew. *American Naturalist* **149**, 794–799.
- KOKKO, H., SUTHERLAND, W. J., LINDSTRÖM, J., REYNOLDS, J. D. & MACKENZIE, A. (1998). Individual mating success, lek stability, and the neglected limitations of statistical power. *Animal Behaviour* **56**, 755–762.
- KOKKO, H., RINTAMÄKI, P. T., ALATALO, R. V., HÖGLUND, J., KARVONEN, E. & LUNDBERG, A. (1999). Female choice selects for lifetime lekking performance in black grouse males. *Proceedings of the Royal Society of London B* **266**, 2109–2115.
- KRAKAUER, D. C. (1995). Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. *Behavioral Ecology and Sociobiology* **36**, 421–429.
- KRUIJT, J. P., DE VOS, G. J. & BOSSEMA, I. (1972). The arena system of black grouse. In *Proceedings of the 15th International Ornithological Congress*, pp. 399–423.
- LANCTOT, R. B., SCRIBNER, K. T., KEMPENAEERS, B. & WEATHERHEAD, P. J. (1997). Lekking without a paradox in buff-breasted sandpiper. *American Naturalist* **149**, 1051–1070.
- LANDEAU, L. & TERBORGH, J. (1986). Oddity and the 'confusion effect' in predation. *Animal Behaviour* **34**, 1372–1380.
- LANK, D. B. & SMITH, C. M. (1992). Females prefer larger leks: field experiments with ruffs (*Philomachus pugnax*). *Behavioral Ecology and Sociobiology* **30**, 323–329.
- LANGEN, T. A. (1999). How western scrub-jays (*Aphelocoma californica*) select a nut: effects of number of options, variation in nut size, and social competition among foragers. *Animal Cognition* **2**, 223–233.
- LANGLEY, C. M., RILEY, D. A., BOND, A. B. & GOEL, N. (1996). Visual search for natural grains in pigeons (*Columba livia*): search images and selective attention. *Journal of Experimental Psychology: Animal Behavior Processes* **22**, 139–151.
- LAUER, M. J., SIH, A. & KRUPA, J. J. (1996). Male density, female density and inter-sexual conflict in a stream-dwelling insect. *Animal Behaviour* **52**, 929–939.
- LE MAGNEN, J. (1960). Effets d'une pluralité de stimuli alimentaires sur le déterminisme quantitatif de l'ingestion chez le rat blanc. *Archives des Sciences Physiologiques* **14**, 411–419.
- LLADÓ, I., PICÓ, C., PALAU, A. & PONS, A. (1995). Protein and amino acid intake in cafeteria fed obese rats. *Physiology and Behavior* **58**, 513–519.
- LUTTBEG, B. (1996). A comparative Bayes tactic for mate assessment and choice. *Behavioral Ecology* **7**, 451–460.
- LUTTBEG, B. (2002). Assessing the robustness and optimality of alternative decision rules with varying assumptions. *Animal Behaviour* **63**, 805–814.
- MAIER, G. (1991). Modeling search processes in space. *Papers in Regional Science* **70**, 133–147.
- MARKOWITZ, H. (1982). *Behavioral Enrichment in the Zoo*. Van Nostrand Reinhold, New York.
- MAZALOV, V., PERRIN, N. & DOMBROVSKY, Y. (1996). Adaptive search and information updating in sequential mate choice. *American Naturalist* **148**, 123–137.
- McCLELLAND, G. H., STEWART, B. E., JUDD, C. M. & BOURNE, L. E. JR. (1987). Effects of choice task on attribute memory. *Organizational Behavior and Human Decision Processes* **40**, 235–254.
- McKEGANEY, N. & BARNARD, M. (1996). *Sex Work on the Streets: Prostitutes and their Clients*. Open University Press, Buckingham.
- MILINSKI, M. (1990). Information overload and food selection. In: *Behavioural Mechanisms of Food Selection*, NATO ASI Series Vol. G20 (ed. R. N. Hughes), pp. 721–737. Springer Verlag, Berlin.
- MILLER, H. J. (1993a). Consumer search and retail analysis. *Journal of Retailing* **69**, 160–192.
- MILLER, H. J. (1993b). Modeling strategies for the spatial search problem. *Papers in Regional Science* **72**, 63–85.

- MILLER, H. J. (1996). Pricing policy reactions to agglomeration in a market with spatial search. *Journal of Regional Science* **36**, 393–415.
- MILLER, H. J. & FINCO, M. V. (1995). Spatial search and spatial competition: a probability analysis of basic results from the spatially-restricted theory. *Annals of Regional Science* **29**, 67–89.
- MÖLLER, A. P. & LEGENDRE, S. (2001). Allee effect, sexual selection and demographic stochasticity. *Oikos* **92**, 27–34.
- MORENO, N. (1974). The effects of motivation on consumer information processing. Unpublished Ph.D. dissertation, Purdue University.
- MORRIS, G. K., KERR, G. E. & FULLARD, J. H. (1978). Phonotactic preferences of female meadow katydids (Orthoptera: Tettigoniidae: *Conocephalus nigropleurum*). *Canadian Journal of Zoology* **56**, 1479–1487.
- MURPHY, C. G. (2003). The cause of correlations between nightly numbers of male and female barking treefrogs (*Hyla gratiosa*) attending choruses. *Behavioral Ecology* **14**, 274–281.
- MURPHY, C. G. & GERHARDT, H. C. (2002). Mate sampling by female barking treefrogs (*Hyla gratiosa*). *Behavioral Ecology* **13**, 472–480.
- NAIM, M., BRAND, J. G., KARE, M. R. & CARPENTER, R. C. (1985). Energy intake, weight gain and fat deposition in rats fed flavored, nutritionally controlled diets in a multichoice (“cafeteria”) design. *Journal of Nutrition* **115**, 1447–1458.
- NEEMS, R. M., LAZARUS, J. & MCLACHLAN, A. J. (1992). Swarming behavior in male chironomid midges: a cost-benefit analysis. *Behavioral Ecology* **3**, 285–290.
- NEWBERRY, R. C. (1995). Environmental enrichment: increasing the biological relevance of captive environments. *Applied Animal Behaviour Science* **44**, 229–243.
- NYLIN, S., BERGSTRÖM, A. & JANZ, N. (2000). Butterfly host plant choice in the face of possible confusion. *Journal of Insect Behavior* **13**, 469–482.
- ONO, K. (2000). Free-choice preference under uncertainty. *Behavioural Processes* **49**, 11–19.
- OTTE, D. & LOFTUS-HILLS, J. (1979). Chorusing in *Syrbula* (Orthoptera: Acrididae). Cooperation, interference competition, or concealment. *Entomological News* **90**, 159–165.
- PAPAJ, D. R. (1990). Interference with learning in pipevine swallowtail butterflies: behavioural constraint or possible adaptation? *Symposia Biologica Hungarica* **39**, 89–101.
- PENTERIANI, V. (2003). Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality. *Ibis* **145** (online), E127–E135.
- PERLMUTER, L. C. & MONTY, R. A. (1977). The importance of perceived control: fact or fantasy? *American Scientist* **65**, 759–765.
- PETERSSON, E. & SIVINSKI, J. (2003). Mating status and choice of group size in the phoretic fly *Norbomia frigipennis* (Spuler) (Diptera: Spaeceridae). *Journal of Insect Behavior* **16**, 411–423.
- PETRIE, M. (1989). Mating decisions by female common moorhens (*Gallinula chloropus*). In *Proceedings of the 19th International Ornithological Congress*, pp. 947–955.
- PLAISTED, K. C. & MACKINTOSH, N. J. (1995). Visual search for cryptic stimuli in pigeons: implications for the search image and search rate hypotheses. *Animal Behaviour* **50**, 1219–1232.
- PULLIAM, H. R. (1975). Diet optimization with nutrient constraints. *American Naturalist* **109**, 765–768.
- QUELLER, D. C. (1987). The evolution of leks through female choice. *Animal Behaviour* **35**, 1424–1432.
- RAFFA, K. F., HAVILL, N. P. & NORDHEIM, E. V. (2002). How many choices can your test animal compare effectively? Evaluating a critical assumption of behavioral preference tests. *Oecologia* **133**, 422–429.
- RAUBENHEIMER, D. & SIMPSON, S. J. (1993). The geometry of compensatory feeding in the locust. *Animal Behaviour* **45**, 953–964.
- RAYNOR, H. A. & EPSTEIN, L. H. (2001). Dietary variety, energy regulation, and obesity. *Psychological Bulletin* **127**, 325–341.
- REAL, L. (1990). Search theory and mate choice I. Models of single-sex discrimination. *American Naturalist* **136**, 376–404.
- RÉALE, D., BOUSSÈS, P. & CHAPUIS, J.-L. (1996). Female-biased mortality induced by male sexual harassment in a feral sheep population. *Canadian Journal of Zoology* **74**, 1812–1818.
- REDELMEIER, D. A. & SHAFIR, E. (1995). Medical decision making in situations that offer multiple alternatives. *Journal of the American Medical Association* **273**, 302–305.
- RESCHER, N. (1969). Choice without preference: a study on the history and of the logic of ‘Buridan’s Ass’. In *Essays in Philosophical Analysis* (ed. N. Rescher), pp. 111–157. University of Pittsburgh Press, Pittsburgh.
- RINTAMÄKI, P. T., ALATALO, R. V., HÖGLUND, J. & LUNDBERG, A. (1995). Mate sampling behaviour of black grouse females (*Tetrao tetrix*). *Behavioral Ecology and Sociobiology* **37**, 209–215.
- ROGERS, P. J. (1990). Why a palatability construct is needed. *Appetite* **14**, 167–170.
- ROLLS, B. J. (1985). Experimental analyses of the effects of variety in a meal on human feeding. *American Journal of Clinical Nutrition* **42**, 932–939.
- 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). *Journal of Comparative Physiology A* **186**, 181–191.
- RUSO, J. E. (1974). More information is better: a reevaluation of Jacoby, Speller and Kohn. *Journal of Consumer Research* **1**, 68–72.
- RYAN, M. J., TUTTLE, M. D. & TAFT, L. K. (1981). The costs and benefits of frog chorusing behavior. *Behavioral Ecology and Sociobiology* **8**, 273–278.
- SÆTHER, S. A. (2002). Female calls in lek-mating birds: indirect mate choice, female competition for mates, or direct mate choice? *Behavioral Ecology* **13**, 344–352.
- SÆTHER, S. A., FISKE, P. & KÅLÅS, J. A. (2001). Male mate choice, sexual conflict and strategic allocation of copulations in a lekking bird. *Proceedings of the Royal Society of London B* **268**, 2097–2102.
- SCHRADIN, C. (2000). Confusion effect in a reptilian and a primate predator. *Ethology* **106**, 691–700.
- SCHWARTZ, J. J. (1994). Male advertisement and female choice in frogs: recent findings and new approaches to the study of communication in a dynamic acoustic environment. *American Zoologist* **34**, 616–624.
- SCHWARTZ, J. J., BUCHANAN, B. W. & GERHARDT, H. C. (2001). Female mate choice in the gray treefrog (*Hyla versicolor*) in three experimental environments. *Behavioral Ecology and Sociobiology* **49**, 443–455.
- SCOTT, L. L. & PROVENZA, F. D. (1998). Variety of foods and flavors affects selection of foraging location by sheep. *Applied Animal Behaviour Science* **61**, 113–122.
- SELIGMAN, M. E. P., MAIER, S. F. & SOLOMON, R. L. (1971). Unpredictable and uncontrollable aversive events. In *Aversive Conditioning and Learning* (ed. F. R. Brush), pp. 347–400. Academic Press, New York.
- SHAFIR, S., WAITE, T. A. & SMITH, B. H. (2002). Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behavioral Ecology and Sociobiology* **51**, 180–187.

- SHELLY, T. E. & BAILEY, W. J. (1992). Experimental manipulation of mate choice by male katydids: the effect of female encounter rate. *Behavioral Ecology and Sociobiology* **30**, 277–282.
- SHELLY, T. E. & GREENFIELD, M. D. (1991). Dominions and desert clickers (Orthoptera: Acrididae): influences of resources and male signaling of female settlement patterns. *Behavioral Ecology and Sociobiology* **28**, 133–140.
- SINGER, M. S., BERNAYS, E. A. & CARRIÈRE, Y. (2002). The interplay between nutrient balancing and toxin dilution in foraging by a generalist insect herbivore. *Animal Behaviour* **64**, 629–643.
- SNEDDEN, W. A. & GREENFIELD, M. D. (1998). Females prefer leading males: relative call timing and sexual selection in katydid choruses. *Animal Behaviour* **56**, 1091–1098.
- STAHL, K. (1982). Differentiated products, consumer search, and locational oligopoly. *Journal of Industrial Economics* **31**, 97–113.
- STILLMAN, R. A., CLUTTON-BROCK, T. H. & SUTHERLAND, W. J. (1993). Black holes, mate retention, and the evolution of ungulate leks. *Behavioral Ecology* **4**, 1–6.
- STILLMAN, R. A., DEUTSCH, J. C., CLUTTON-BROCK, T. H. & SUTHERLAND, W. J. (1996). Black hole models of ungulate lek size and distribution. *Animal Behaviour* **52**, 891–902.
- STUART, C. (1979). Search and the spatial organization of trading. In *Studies in the Economics of Search* (eds. S. A. Lippman and J. J. McCall), pp. 17–33. North-Holland, Amsterdam.
- SULLIVAN, M. S. (1994). Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Animal Behaviour* **47**, 141–151.
- SUTHERLAND, W. J. (1996). *From Individuals to Population Ecology*. Oxford University Press, Oxford.
- SUZUKI, S. (1997). Effects of number of alternatives on choice in humans. *Behavioural Processes* **39**, 205–214.
- SUZUKI, S. (1999). Selection of forced- and free-choice by monkeys (*Macaca fascicularis*). *Perceptual and Motor Skills* **88**, 242–250.
- SUZUKI, S. (2000). Choice between single-response and multichoice tasks in humans. *Psychological Record* **50**, 105–115.
- SVENSSON, B. G. & PETERSSON, E. (1988). Non-random mating in the dance fly *Empis borealis*: the importance of male choice. *Ethology* **79**, 307–316.
- SVENSSON, B. G. & PETERSSON, E. (1992). Why insects swarm: testing the models for lek mating systems on swarming *Empis borealis* females. *Behavioral Ecology and Sociobiology* **31**, 253–261.
- SVENSSON, B. G. & PETERSSON, E. (1994). Mate choice tactics and swarm size: a model and a test in a dance fly. *Behavioral Ecology and Sociobiology* **35**, 161–168.
- SVENSSON, B. G., PETERSSON, E. & FORSGREN, E. (1989). Why do males of the dance fly *Empis borealis* refuse to mate? The importance of female age and size. *Journal of Insect Behavior* **2**, 387–395.
- TELFORD, S. R. (1985). Mechanisms and evolution of inter-male spacing in the painted reedfrog (*Hyperolius marmoratus*). *Animal Behaviour* **33**, 1353–1361.
- TELFORD, S. R. & VAN SICKLE, J. (1989). Sexual selection in an African toad (*Bufo gutturalis*): the roles of morphology, amplexus displacement and chorus participation. *Behaviour* **110**, 62–75.
- TELFORD, S. R., DYSON, M. L. & PASSMORE, N. I. (1989). Mate choice occurs only in small choruses of painted reed frogs *Hyperolius marmoratus*. *Bioacoustics* **2**, 47–53.
- TIMMERMANS, D. (1993). The impact of task complexity on information use in multi-attribute decision making. *Journal of Behavioral Decision Making* **6**, 9–111.
- TRAIL, P. W. & ADAMS, E. S. (1989). Active mate choice at cock-of-the-rock leks: tactics of sampling and comparison. *Behavioral Ecology and Sociobiology* **25**, 283–292.
- TREGENZA, T. (1995). Building on the ideal free distribution. *Advances in Ecological Research* **26**, 253–307.
- TVERSKY, A. (1972). Elimination by aspects: a theory of choice. *Psychological Review* **79**, 281–299.
- UY, J. A. C., PATRICELLI, G. L. & BORGIA, G. (2001). Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *American Naturalist* **158**, 530–542.
- VOSS, S. C. & HOMZIE, M. J. (1970). Choice as a value. *Psychological Reports* **26**, 912–914.
- WAGNER, W. E. JR. & SULLIVAN, B. K. (1992). Chorus organization in the gulf coast toad (*Bufo valliceps*): male and female behavior and the opportunity for sexual selection. *Copeia* **1992**, 647–658.
- WALKER, T. J. (1983a). Diel patterns of calling in nocturnal Orthoptera. In *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (eds. D. T. Gwynne and G. K. Morris), pp. 45–72. Westview Press, Boulder.
- WALKER, T. J. (1983b). Mating modes and female choice in short-tailed crickets (*Anurogryllus arboreus*). In *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (eds. D. T. Gwynne and G. K. Morris), pp. 240–267. Westview Press, Boulder.
- WESTCOTT, D. & SMITH, J. N. M. (1997). Lek size variation and its consequences in the ochre-bellied flycatcher, *Mionectes oleagineus*. *Behavioral Ecology* **8**, 396–403.
- WICKMAN, P.-O., GARCIA-BARROS, E. & RAPPE-GEORGE, C. (1995). The location of landmark leks in the small heath butterfly, *Coenonympha pamphilus*: evidence against the hot-spot model. *Behavioral Ecology* **6**, 39–45.
- WIDEMO, F. & OWENS, I. P. F. (1999). Size and stability of vertebrate leks. *Animal Behaviour* **58**, 1217–1221.
- WILEY, R. H. (1991). Lekking in birds and mammals: behavioral and evolutionary issues. *Advances in the Study of Behavior* **20**, 201–291.
- WITTENBERGER, J. F. (1981). *Animal Social Behavior*. Duxbury Press, Boston.
- WITTER, M. S. & CUTHILL, I. C. (1993). The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London B* **340**, 73–92.
- WOLINSKY, A. (1983). Retail trade concentration due to consumers' imperfect information. *Bell Journal of Economics* **14**, 275–282.
- WOLLERMAN, L. (1999). Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. *Animal Behaviour* **57**, 529–536.
- WOOD-GUSH, D. G. M. & VESTERGAARD, K. (1991). The seeking of novelty and its relation to play. *Animal Behaviour* **42**, 599–606.