



Review

Explanations for variation in cognitive ability: Behavioural ecology meets comparative cognition

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ARTICLE INFO

Article history:
Received 3 June 2008
Received in revised form
29 September 2008
Accepted 4 October 2008

Keywords:
Adaptation
Natural selection
Cognition
Shettleworth

ABSTRACT

Sara Shettleworth has played a defining role in the development of animal cognition and its integration into other parts of biology, especially behavioural ecology. Here we chart some of that progress in understanding the causes and importance of variation in cognitive ability and highlight how Tinbergen's levels of explanation provide a useful framework for this field. We also review how experimental design is crucial in investigating cognition and stress the need for naturalistic experiments and field studies. We focus particularly on the example of the relationship among food hoarding, spatial cognition and hippocampal structure, and review the conflicting evidence for sex differences in spatial cognition. We finish with speculation that a combination of Tinbergen and Shettleworth-style approaches would be the way to grapple with the as-yet unanswered questions of why birds mimic heterospecifics.

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1. Introduction

Comparative cognition was once a field predicated on the assumption that both the presence and complexity of cognitive abilities were best explained by a kind of evolutionary tree (scale) at the top of which were perched humans. On this tree proximity (phylogenetic relatedness) was the key explanation for describing variation in cognitive abilities in animals other than humans. Often explicit in this assumption was that phylogenetic relatedness represented a scale, for example, a scale of intelligence (Hodos and Campbell, 1990). Morphing gently into animal cognition, the field is no longer dominated by this philosophy but has been significantly modified by a growing awareness of the importance that natural

selection, through adaptation to the local environment (biological and physical), is likely to have had on the production of variation in cognitive abilities. This philosophical change has enabled the formulation of functional hypotheses and the generation of predictions as to what and where variation in cognitive abilities should be expected. The use of this kind of hypothesis to drive the nature of the predictions and questions has led to a variety of conspicuous changes in the face of animal cognition, some of which we will examine here. Sara Shettleworth has been at the forefront of bringing about this fundamental change, visible, not least, at comparative cognition meetings: while a portion of the presentations continue to be descriptions of a deepening knowledge of what animals can do (especially laboratory rats and pigeons), a significant proportion of these presentations also use knowledge of the animal's natural environment as the base from which to produce functional hypotheses to explain the variation in cognitive abilities within and between species. The face of behavioural ecology has

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also changed, in increasing recognition of the role that cognition plays in many aspects of animal behaviour traditionally viewed as requiring only functional explanation, especially those involving decision making (e.g. sexual selection, Bateson and Healy, 2005; Shettleworth, 2001). Here we trace a small portion of the history of this integrative approach.

2. Cognition in the field

As an adaptationist the place where one might think to begin to investigate cognition is the field and there to look at the abilities of animals in the context in which those abilities are being put to the test. Perhaps frustratingly, at least for a behavioural ecologist, this is a difficult logistic proposition in most situations. However, rufous hummingbirds *Selasphorus rufous* have proved amenable to cognitive investigation, logistically, because males aggressively defend territories around artificial feeders and can be trained within an hour or two to feed from artificial flowers, which can then be manipulated in a variety of ways. The biological rationale for testing cognitive ability in this species is because males seem to minimise time spent feeding in order to look out for females and conspecific males. To do this efficiently it would be beneficial for them to remember from which flowers they had fed in order to avoid them. It is, indeed, the case that these birds can remember and avoid flowers they have recently emptied but will return to flowers they have not fully emptied (Healy and Hurly, 1995; Henderson et al., 2001).

One early prediction, based on an apparent preference by hummingbirds for red flowers and as hummingbird-pollinated plants commonly produce red flowers (at least in California, through which state these birds migrate), was that the rufous hummingbirds would pay more attention to colour than to spatial cues. It turns out that this is not the case, indeed, all spatial cues must be removed before hummingbirds will show that they remember colour, if the requirement is to return to flowers in the same location (Healy and Hurly, 1998). If the location changes but the colour does not, the birds very rapidly learn the colour reward association (Hurly and Healy, 1996). It appears that cue reliability makes spatial information preferable to a flower's colour. A further piece of information that a territorial male might use, if he could, is the time since he emptied a flower. This ability would be beneficial so as to return to flowers that do refill, but not for some time after being emptied (under natural conditions, some 2–4 h). Although not tested over 'real' time periods (refill durations were 10 and 20 min), hummingbirds in the field can learn refill rates of multiple flowers (Henderson et al., 2006).

However, for all that this work is allowing description of the cognitive capacities of these birds, it is not yet convincing evidence that these abilities are specific adaptations to the hummingbird's environment, rather than all-purpose abilities that other animals would exhibit if presented with analogous tests. Ideally, one would demonstrate that the birds do not have abilities they do not need. However, this then leads to the fruitless task of attempting to prove a null hypothesis. Additionally, a failure to demonstrate a capability could be due just to poor experimental design. Alternatively, rufous hummingbirds may have abilities that differ from closely related species in a way that is best explained by variation in their natural history. This would require comparisons of closely related hummingbird species, which have not yet been made. Even then, these data will only be correlational and not evidence of a causal relationship between cognitive abilities and the animal's environment. All in all, the integration of functional and mechanistic explanations for behaviour is far from straightforward (not a novel conclusion, see, for example, Bateson and Kacelnik, 1998).

3. Food storing

One of the better-known examples of using knowledge of an animal's natural history (or ecology) to formulate functional hypotheses to explain variation in cognitive ability is that of the relationship between food hoarding, spatial cognition and hippocampus structure. Food hoarding is a relatively uncommon, although taxonomically widespread, behaviour that some animals carry out when they encounter an excess of food. Some animals larderhoard that excess, requiring them to guard the pile of food they have accumulated, which is rarely hidden, due to the sheer number of food items. Scatterhoarding species, on the other hand, take one or more pieces of food away and hide them in multiple locations, often within their home range or territory. This strategy of hiding small numbers of food items in any one place reduces the loss to scavengers of any one hoard but does leave the significant problem of relocating hoards effectively. Retrieval of the food occurs after varying periods of time: some species hoard food for a few hours, days or weeks, while others do not retrieve their food for several months (the Corvidae are among the most impressive avian examples Vander Wall, 1990). The numbers of items hoarded also varies among species from a few hundreds to multiple thousands (again, the Corvidae are especially notable).

While there has been discussion and dispute as to the extent of scatterhoarder's memory capacity (Brodin, 2005; Smulders and Dhondt, 1997; Male and Smulders, 2007), there is no dispute that they do use memory for successful relocation. This has been most convincingly demonstrated in the laboratory although there are sufficient data from field tests to show that this is not an artefact of the laboratory setting (Cowie et al., 1981; Sherry et al., 1981; Stevens and Krebs, 1986). Food hoarders remember what they have hidden, where they hid the food and when they did so (e.g. Clayton and Dickinson, 1999; Sherry, 1984; Shettleworth et al., 1988, 1990; Shettleworth and Krebs, 1986, 1982).

So, the scene was set: food hoarders remembered many places in which they had hidden food and this requirement, specifically for the locations of those food items, seemed to be substantially greater than that faced by animals that did not hoard food. The hypothesis was that natural selection would have resulted in food hoarders having better spatial cognitive abilities than did nonhoarders. In the beginning this seemed such a significant difference in the natural history of the species under comparison, that it was assumed that cognitive differences would be demonstrated in any test of spatial cognition. Nonetheless, the bulk of testing began with naturalistic looking experimental set-ups using artificial trees in large rooms, bearing possible food locations that the birds had to fly among, and with tests designed to resemble food hoarding as closely as possible. Only as closely as possible, but not requiring food hoarding, because the cognitive comparisons were between hoarders and nonhoarders and it is not possible to get nonhoarding species to hoard food. In order to deal with the conspicuous problems of variation in physical abilities and motivation that are so inherent to species comparisons, the nonhoarding species were, preferably, very closely related to the hoarding species. For the both the Paridae and Corvidae, this is more readily done in Europe as both hoarding and nonhoarding relatives are often sympatric.

There was not a small amount of consternation when, in spite of the functional logic and care over experimental design, it became clear that differences in spatial cognition were not readily demonstrated. Windowshopping experiments, in which the birds were allowed to visit a number of sites where they could see a large nut and consume a small portion of it before returning at a later time to retrieve the larger portion of food, did not, for example, show that food hoarders were conspicuously better at remembering food

locations than were nonhoarders, irrespective of the number of locations or the durations before relocation was required (Krebs et al., 1990; Healy and Krebs, 1992a). It did appear that food hoarders made different kinds of errors than did the nonhoarders as hoarders made errors to previously unvisited sites, while nonhoarders made errors to sites they had previously seen to be empty but their relocation of rewarded locations was not conspicuously different.

This outcome was much as might have been expected from the history of comparative cognition as reviewed by Macphail (1982), i.e. there are no real differences in cognition across species; where perceived, differences in cognitive abilities are much more likely be due to differences in motivation or motor skills of the test subjects or, indeed, to poor experimental design. There were two kinds of response to the outcome of the comparative experiments: the sceptic's was to declare that the functional view was not an appropriate way to investigate cognition, the alternative was to 'go back to the drawing board' in the sense of examining much more carefully what variation in cognitive abilities that might be specific to food hoarding. There were several possibilities: (1) the tasks to date were not sufficiently difficult to distinguish the difference; (2) that there might be a difference in the kind of information that to which hoarders and nonhoarders paid attention; (3) that selection had not acted on all of spatial cognition but rather, on a specific component.

A variety of tasks were then developed that resembled standard spatial cognitive tests much more closely than those tasks that attempted to approximate food hoarding (e.g. Clayton and Krebs, 1994c, 1993; Healy, 1995). One of the most elegant was the radial maze analogue designed by Hilton and Krebs (1990) in which a bird flew into a dark room lit only by a light on a platform in the middle of the room. Once perched, the room lights were turned on and the bird was faced with eight platforms, each with a feeder, arranged in a circle around the middle platform. The bird flew to one feeder to locate food (or not) and once at the chosen feeder location, the room lights were again turned off so that the bird had to fly back to the central perch before the room lights were again turned on and it could make another choice. Unlike other analogues of the radial maze developed for birds (e.g. Spetch and Honig, 1988; Spetch, 1990), this one had birds moving along 'arms' of light to the centre of the array in a manner very similar to that of the radial arm using for testing rodents. In spite of the experimental elegance, however, comparisons of four tit species (two hoarding and two nonhoarding) and greenfinches (*Carduelis chloris*, nonhoarding) did not reveal any difference in spatial performance between hoarding and nonhoarding species.

A much more successful avenue of investigation proved to be that addressing the nature of the information to which hoarders and nonhoarders pay attention. Brodbeck (1994) was the first to show that food hoarders, black-capped chickadees *Poecile atricapillus*, used the spatial location of a rewarded feeder rather than the colour pattern of the feeder itself to make decisions about which was the appropriate feeder to visit. The nonhoarding dark-eyed juncos *Junco hyemalis*, however, used both colour/pattern and spatial cues to make their decision. A similar difference in cue preference was found in European hoarding and nonhoarding tits (Clayton and Krebs, 1994b). Furthermore, these preference or attentional differences were correlated with differences in memory for the different cue types: hoarders remembered spatial information better than the colour of images, whereas juncos did not differ (Brodbeck and Shettleworth, 1995). More recently, this apparently clear distinction has become less so as nonhoarding species will also prefer spatial cues over visual cues, depending on the testing context (Hodgson and Healy, 2005; Hurlly and Healy, 1996).

Some progress was also made by attempting to examine the different aspects of spatial cognition that might be used by food

hoarders to remember their hoards. Food hoarders can remember many locations, for long periods and with remarkable accuracy. It is possible that food hoarders differ from nonhoarders in only one of these components, rather than in them all (or, indeed, that the cue differences described above is the sum total of the difference). Delayed-non-matching-to-sample (DNMTS) tasks presented on touchscreens were a far cry from the naturalistic experiments previously carried out, but they proved to be a useful way forward. Wild birds can be trained to perform these tasks and capacity, duration and accuracy of memory can be tested in ways that are difficult in naturalistic tasks. Additionally, very similar versions of the task can be used to test memory for spatial or colour/pattern information. In this way food-hoarding coal tits *Poecile palustris* were found to be able to remember even a single spatial location for longer than could nonhoarding great tits *Parus major* (Biegler et al., 2001; see also McGregor and Healy, 1999). However, the species did not differ in the number of items or in the accuracy with which they remembered locations, suggesting that food hoarders are specifically better than nonhoarders at remembering even small amounts of spatial information but do not differ in memory capacity or in memory resolution. The data from the Hilton and Krebs (1990) experiment hints at this difference as the hoarders appear to have performed much better than did the nonhoarders but only after 24 h and not at the shorter durations of 30 s and 2 h. Additionally, in a version of the DNMTS task in which the birds were tested for their ability to remember what the images looked like, there were no differences in duration, capacity or accuracy of memory between hoarders and nonhoarders.

The evidence in support of the prediction that food hoarders should have better spatial cognitive abilities than do nonhoarders has come about very slowly and with what some would consider to be an excessively tenacious clinging to the functional view (e.g. Macphail and Bolhuis, 2001). The lack of progress in demonstrating cognitive differences has been, in large part, due to early naivety about the nature of variation in cognitive abilities and how to investigate cognitive abilities in 'nonmodel' organisms i.e. not pigeons or rats. Indeed, there has been little concern over addressing variation at all. It is, for example, standard procedure in psychological testing in the laboratory to test only animals that reach a set criterion of performance, potentially removing relevant variation. However, progress in science was ever thus and addressing these problems has led to convincing explanations of variation in cognitive ability between food hoarders and nonhoarders. We do note that the evidence for the relationship between the apparent memory demands of food hoarding and enhanced spatial cognition is still correlational rather than causal and future efforts should be directed into demonstrating causality.

4. Food hoarding, spatial cognition and hippocampal structure

Encouragement to stick with the functional stance came from a nearby source, which was the investigation into the structure and function of the avian hippocampus, driven by the literature implicating the mammalian hippocampus in spatial cognition. A series of correlational studies showed a relationship between hippocampal structure and memory involved in hoarding: hippocampal volume, relative to the rest of the forebrain, was found to be larger in food-hoarding species than in nonhoarders (Krebs et al., 1989; Sherry et al., 1989). The more items hoarded and the longer they are hoarded is also positively correlated with variation in hippocampal volume (Hampton et al., 1995; Healy and Krebs, 1992b, 1996) and hippocampal volume increases concomitantly with food-hoarding experience (Healy and Krebs, 1993; Healy et al., 1994). Additionally, variation in hippocampal volume is not restricted to

variation in hoarding, as it should not be if its function is to subserve spatial cognition rather than food storing *per se*. For example, brood-parasitic birds that search for host nests prior to egg laying have larger hippocampal volumes than do non parasites (Reboreda et al., 1996) and migrants with migration experience have a larger hippocampus than do birds that have not yet migrated or resident species (Healy et al., 1996). There is little known as yet as to what cognitive benefits are being conferred by these hippocampal enlargements although memory for a particular feeding site persisted for at least 12 months in a migrant (garden warbler *Sylvia borin*) whereas the closely related non-migratory Sardinian warbler *Sylvia melanocephala momus* could only remember it for 2 weeks (Mettke-Hofmann and Gwinner, 2004).

Additionally, and in spite of Shettleworth (e.g. 2003) pointing out that natural selection had supplied the reverse of the typical lesion situation in enlargement of the hippocampus, lesion data also seemed to support the notion that there was a relationship between hippocampal function and variation in demand for spatial cognition. For example, hippocampal lesions lead to impairments in spatial cognition in a range of contexts: home loft relocation in homing pigeons (Bingman et al., 1985), on spatial DMTS tasks in laboratory pigeons and relocation of hoards by black-capped chickadees (Sherry and Vaccarino, 1989). Additionally, when tested on the location/colour DMTS tasks described earlier, hippocampal-lesioned hoarders were only impaired on the spatial task. However, hippocampal lesions had the same effect on dark-eyed juncos, the nonhoarder (Hampton and Shettleworth, 1996a,b). This latter result was a reminder that one must be careful with regard to expectations of species differences. Species that vary in spatial cognition might be expected to vary in hippocampal size but not in the presence or absence of a hippocampus, nor in hippocampal function. Therefore, experiments that do not tap into a requirement for extra cognitive ability should not be expected to yield differences between hoarders and nonhoarders. An experiment that simply requires some hippocampal input for success should not be expected to result in a species difference. It seems as if the investigations into the relationship between hippocampal structure and its function are tracing a similar path as the cognitive experiments did: early naive expectations were that whole scale lesions would result in differences in spatial cognition between hoarders and nonhoarders and this is not the case. There now seem at least two obvious avenues to pursue: the effect of partial lesions and the effect of lesions on the duration of memories for spatial locations. Given the difference in relative hippocampal volume between hoarders and nonhoarders, lesions of the same size and lesions that lead to damage of a similar proportion of the hippocampus may lead to different outcomes.

Experimental substantiation of these correlational data has come from developmental work in which fledgling food hoarders were deprived of hoarding experience. The result was that their hippocampus did not develop as it did in age-matched, hoarding controls but when birds were allowed to begin hoarding at a much later date, they began to hoard and their hippocampal volume increased (Clayton and Krebs, 1994a; Clayton, 1996, 2001). Quite how plastic the hippocampus is in relation to food hoarding experience is not clear, although there is a suggestion that there is some seasonal variation (Smulders et al., 1995; see also experiments on relationship between day length and food hoarding such as Shettleworth et al., 1995).

5. Sex differences in spatial cognition

Not only is there adaptationist rationale for variation among species in cognition, there is also good reason for predicting within-species variation, although it is not always easy to dis-

tinguish between variation in information acquired and in the way it is used (perception/attention vs. memory). Pond-dwelling sticklebacks *Gasterosteus aculeatus*, for example, face a very stable environment and use spatial features to navigate, while stream-living sticklebacks pay much more attention to the flow of water and much less to spatial cues (e.g. Girvan and Braithwaite, 1998). However, it is not yet clear whether these differences in cue use are matched by differences in memory for those cues, as it appears to be in the food-hoarding example.

One well-known example of within-species variation in cognition, at least in mammals, is that males typically outperform females in tests of spatial cognition (e.g. Gaulin and FitzGerald, 1986; Williams and Meck, 1991). The frequency of this result has spawned a plethora of hypotheses to explain why sex differences in spatial cognition might have evolved, tellingly, almost as many hypotheses as species that have been tested. The critique directed at adaptationist explanations for variation in cognition would be rightly directed to this literature, which suffers from a serious lack of species/taxonomic comparison, crucial to any evolutionary explanation (unless the experiment involves evolution of the trait itself e.g. Méry, 2007). A multitude of other problems have been discussed elsewhere (Jones et al., 2003) but we would like to reiterate here the importance of attempting to exclude alternative hypotheses rather than adding new ones that generate the same or similar predictions as to the expected outcome. Currently, there does appear to be one hypothesis to explain most of the described sex differences in cognition in mammals, the 'range size hypothesis', which proposes that having to remember more landmarks, and the relationship among them, in larger territories has been the selection pressure leading to superior spatial ability in males. Supporting data come from the relationship between home range size and spatial cognition performance in two vole species: male meadow voles (*Microtus pennsylvanicus*) have larger home ranges and better spatial ability than do their conspecific females (Gaulin and FitzGerald, 1986) while male prairie voles (*M. ochrogaster*) do not differ from conspecific females in either range size or cognitive performance. Neatly, the variation in hippocampal volume matches the natural history and cognitive performance in the expected direction (Jacobs et al., 1990; Gaulin et al., 1990). However, not only is this example based on a two-sample comparison, these species also differ in mating system and, perhaps, in other ways. Indeed, range size varies because prairie vole males are monogamous and have home ranges they share with their mate while the meadow vole is polygynous with a home range that encompasses home ranges of multiple females. Range size is, then, completely confounded with mating system and it is possible that the sex differences are not due to natural selection acting on spatial cognitive abilities but rather on the mating systems of these animals, a pleiotropic result of which has been variation in spatial cognition.

In our view, it is with the sex difference literature that the importance of integrating functional and mechanistic explanations for variation in spatial cognition becomes apparent. Indeed, attention should be paid to all four of Tinbergen's levels of explanation: ontogeny, phylogeny, mechanism and function. This is because, far in excess of the literature addressing the evolutionary basis of sex differences, there is a vast body of work showing that both the sex steroids and stress hormones influence spatial abilities both developmentally (organisational or ontogenetic effects) and in adulthood (activational or mechanistic effects). Both groups of hormones affect spatial memory in a non-linear way, such that low and high levels usually lead to poor performance with best performance in the mid-range. However, the exact levels differ within and between the sexes. For example, spatial cognition is enhanced in most females with addition of testosterone, either in-

utero (Roof and Havens, 1992) or post-natally (Aleman et al., 2004) but for males, addition of testosterone may lead to a detriment in performance (Gouchie and Kimura, 1991; Roof, 1993). Seasonal fluctuations in testosterone (Galea et al., 1994) and cyclic variation in oestrogen (Warren and Juraska, 1997) lead to enhancements or declines in spatial ability, and there is some evidence that these effects are accompanied by structural changes in the hippocampus (e.g. Galea and McEwen, 1999; Gould et al., 1990; Roof and Havens, 1992; Woolley et al., 1997). Understanding the relationship between the structure and function of the hippocampus in animals in which gross morphological variation correlates with spatial memory demands seems to be one of the keys to integrating across Tinbergen's levels of explanation.

Integrating levels of explanation is far from being a straightforward problem to deal with, not least because of the role that stress plays in spatial cognition and in variation between the sexes. Sex differences in spatial cognition have been most often investigated in laboratory rodents and humans and for both groups, while the majority of authors report a male advantage (e.g. Astur et al., 2004; Silverman et al., 2000; Seymoure et al., 1996; Williams et al., 1990), there are multiple reports of no sex difference (e.g. Bucci et al., 1995; Healy et al., 1999; Kitchin, 1996; Warren and Juraska, 1997). One explanation (of several) of this variation is stress: females often respond more poorly to acute stress than do males, while males respond more poorly to chronic stress than do females (Luine et al., 2007; Shors, 2001). As the most commonly used test of spatial cognition for rats (the Morris Water Maze MWM) is considered to be sufficiently acutely stressful that the UK Home Office requires users to be licensed, it is plausible that females appear to perform more poorly because they are more stressed by being put in the brightly-lit water bath. This hypothesis becomes more plausible when it is recognised that the initial response of rats to being placed in the MWM is to swim around the edge of the pool (wall-hugging behaviour known as thigmotaxis). It appears that females may do this to a much greater extent than males (e.g. Beiko et al., 2004; Harris et al., 2008b). As performance in the MWM is measured in time or path length taken to reach a platform hidden just below the water surface, the more time females spend swimming in the periphery of the pool where the platform is never located, the poorer their cognitive abilities will appear. In some experiments, thigmotaxis in females diminishes significantly by the second swim of the day but if the test is one of reference memory (memory for the platform's location across days), the rat may get only one swim a day and, if so, will continue to perform relatively poorly (e.g. Harris et al., 2008a; 2008b). It may, therefore, be that many of the experiments in which male and female laboratory rats have been tested in the MWM have resulted in sex differences that are an artefact of the test environment. As in the comparison between the voles, it may be that differences between the sexes are due to a previously unconsidered factor (in this case, stress). The question to address, then, is why natural selection has favoured males responding better to acute stress than do females, rather than why it has favoured their superior spatial cognition. Alternatively, it might be that laboratory rodents are not the appropriate system in which to investigate functional explanations for sex differences in cognition.

The data on sex differences in spatial cognition in humans have all these problems, as well as that of emotional and political responses to any evidence for differences. One problem with the human testing paradigms, in common with the early hoarding cognitive tests, is that it is often not clear exactly what aspect of cognition is being examined, not least because the tests are often human-centric. For example, 'spatial cognition' can be tested with pen and paper (or real) objects, asking subjects to name or replace missing objects, from a list or from memory. Unfortunately, per-

formance on this kind of task is heavily dependent on the nature of the objects: different objects will result in females doing more or less well than males. Nonetheless, across a range of primarily navigational/map-based tasks, it appears that, similarly to food hoarders, male rodents and humans pay attention to distance and direction information while, like nonhoarders, females tend to pay more attention to visual landmarks (Jones and Healy, 2006; Roof and Stein, 1999; Saucier et al., 2002). There is also evidence that on top of differences in attention to different cues, men and women differ slightly but significantly in their memory for spatial and visual information. Males seem to be able remember both kinds of information equally well, while females remember visual features better they remember spatial locations (Jones and Healy, 2006). One of many questions to be answered is how stress and sex steroids affect cue use and memory for those different kinds of information. As with the rats, it may be that understanding the mechanisms underpinning sex differences will lead to the most appropriate functional explanation.

6. Vocal mimicry

Problematic though the integration of explanations for variation in spatial cognition might be, there is good reason to believe that a more complete understanding of that variation is emerging. We would like to conclude with a brief consideration of a rather different behaviour than those requiring spatial cognition but one we believe would also be best investigated with a similar across-level approach. This behaviour is vocal mimicry, which at least 20% of songbirds produce.

It is, perhaps, not surprising that the apparent accuracy of a superb lyrebird *Menura novaehollandiae* producing the sound of a camera shutter release or a chainsaw, of spotted bowerbirds *Chlamydera maculata* reproducing the sound of a kookaburra call or a starling *Sturnus vulgaris* mimicking a goat and a chicken (Marler and Slabberkorn, 2004) have led to a number of proposed functional explanations: it simply seems implausible that the sounds the birds make could be both accurate and non-functional. Functions ascribed to heterospecific vocal mimicry include sexual selection, threat avoidance, social affiliation and brood parasitism (Kelley et al., 2008). However, as yet, the only hypothesis for which all the data are consistent is Hindmarsh's learning mistakes hypothesis (Hindmarsh, 1984), whereby he proposed that birds with large repertoires are more likely to learn heterospecific sounds that are common in the acoustic environment, loud, simple, or similar to species-specific song. In this instance, it is not the natural history of the animals that is lacking but an understanding of the cognitive abilities involved. In order to determine which, if any, functional hypothesis is an appropriate explanation of vocal mimicry, we need to determine what is copied, when, from whom and the context in which the information is used. In some cases, there may even be no learning at all, for example, brood-parasitic birds that eject all host young are raised alone and appear to have arrived at similar begging calls to those of their host species through evolutionary convergence (McLean and Waas, 1987).

One of the few relevant studies to date has shown that mimics most consistently reproduce the duration of a model's call while, for example, being less accurate at mimicking features such as trill rate (Zollinger and Suthers, 2004). They tend to be least accurate at mimicking the species-specific components of calls. Even this elegant work, however, tells us more about physical difficulties involved in mimicking the calls of another species rather than necessarily adding to our understanding of the cognitive processes involved. The kind of approach to addressing this kind of knotty cognitive problem is one that Sara Shettleworth has advocated for much of her career. The of coupling functional

hypotheses to experiments fit for non-model organisms is ideally suited to the determination of just why such beautiful copying occurs.

7. Conclusion

It is due in no small part to Sara Shettleworth's contributions that behavioural ecologists now consider cognition worthy of consideration in explanations of animal behaviour and, equally, experimental psychologists are now prepared to consider variation in cognitive abilities worthy of investigation, rather than exclusion. It is not surprising that misunderstandings on both sides have arisen along the way, and will continue to do so, but the increasing familiarity of, and respect for, each party's different approach is slowly but surely leading to the completeness of understanding behaviour towards which Tinbergen so usefully directed us.

Acknowledgements

We thank Karen Hollis and two anonymous reviewers for their helpful comments on a draft of our manuscript. We also thank NERC (I.E.B. and L.A.K.), the 3 R's Liaison Group (A.P.H.) and The Wellcome Trust (O.H.) for funding.

References

- Aleman, A., Bronk, E., Kessels, R.P.C., Koppeschaar, H.P.F., van Honk, J., 2004. A single administration of testosterone improves visuospatial ability in young women. *Psychoneuroendocrinology* 29, 612–617.
- Astur, R.S., Tropp, J., Sava, S., Constable, R.T., Markus, E.J., 2004. Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. *Behavioural Brain Research* 151, 103–115.
- Bateson, M., Healy, S.D., 2005. Comparative evaluation and its implications for mate choice. *Trends In Ecology & Evolution* 20, 659–664.
- Bateson, M., Kacelnik, A., 1998. Risk-sensitive foraging: decision making in variable environments. In: Dukas, R. (Ed.), *Cognitive Ecology*. University of Chicago, Chicago, pp. 297–341.
- Beiko, J., Lander, R., Hampson, E., Boon, F., Cain, D.P., 2004. Contribution of sex differences in the acute stress response to sex differences in water maze performance in the rat. *Behavioural Brain Research* 151, 239–253.
- Biegler, R., McGregor, A., Krebs, J.R., Healy, S.D., 2001. A larger hippocampus is associated with longer-lasting spatial memory. *Proceedings of the National Academy of Sciences (U.S.A)* 98, 6941–6944.
- Bingman, V.P., Joale, P., Casini, G., Bagnoli, P., 1985. Dorsomedial forebrain ablations and home loft association behavior in homing pigeons. *Brain Behavior and Evolution* 26, 1–9.
- Brodbeck, D.R., 1994. Memory for spatial and local cues—a comparison of a storing and a nonstoring species. *Animal Learning & Behavior* 22, 119–133.
- Brodbeck, D.R., Shettleworth, S.J., 1995. Matching location and color of a compound stimulus: comparison of a food-storing and a nonstoring bird species. *Journal of Experimental Psychology: Animal Behavior Processes* 21, 64–77.
- Brodin, A., 2005. Mechanisms of cache retrieval in long-term hoarding birds. *Journal of Ethology* 23, 77–83.
- Bucci, D.J., Chiba, A.A., Gallagher, M., 1995. Spatial learning in male and female Long-Evans rats. *Behavioral Neuroscience* 109, 180–183.
- Clayton, N.S., 1996. Development of food-storing and the hippocampus in juvenile marsh tits (*Parus palustris*). *Behavioural Brain Research* 74, 153–159.
- Clayton, N.S., 2001. Hippocampal growth and maintenance depend on food-caching experience in juvenile mountain chickadees (*Poecile gambeli*). *Behavioral Neuroscience* 115, 614–625.
- Clayton, N.S., Dickinson, A., 1999. Scrub jays (*Aphelocoma coerulescens*) remember the relative time of caching as well as the location and content of their caches. *Journal of Comparative Psychology* 113, 14.
- Clayton, N.S., Krebs, J.R., 1993. Lateralization in Paridae: comparison of a storing and a non-storing species on a one-trial associative memory task. *Journal of Comparative Physiology A* 171, 807–815.
- Clayton, N.S., Krebs, J.R., 1994a. Hippocampal growth and attrition in birds affected by experience. *Proceedings of the National Academy of Sciences of the United States of America* 91, 7410–7414.
- Clayton, N.S., Krebs, J.R., 1994b. Memory for spatial and object-specific cues in food-storing and nonstoring birds. *Journal of Comparative Physiology A: Sensory Neural and Behavioral Physiology* 174, 371–379.
- Clayton, N.S., Krebs, J.R., 1994c. One-trial associative memory—comparison of food-storing and nonstoring species of birds. *Animal Learning & Behavior* 22, 366–372.
- Cowie, R.J., Krebs, J.R., Sherry, D.F., 1981. Food storing by marsh tits. *Animal Behaviour* 29, 1252–1259.
- Galea, L.A.M., Kavaliers, M., Ossenkopp, K.-P., Innes, D., Hargreaves, E.L., 1994. Sexually dimorphic spatial learning varies seasonally in two populations of deer mice. *Brain Research* 635, 18–26.
- Galea, L.A.M., McEwen, B.S., 1999. Sex and seasonal differences in the rate of cell proliferation in the dentate gyrus of adult wild meadow voles. *Neuroscience* 89, 955–964.
- Gaulin, S.J.C., FitzGerald, R.W., 1986. Sex differences in spatial ability: an evolutionary hypothesis and test. *The American Naturalist* 127, 74–88.
- Gaulin, S.J.C., FitzGerald, R.W., Wartell, M.S., 1990. Sex differences in spatial ability and activity in two vole species (*Microtus ochrogaster* and *M. pennsylvanicus*). *Journal of Comparative Psychology* 104, 88–93.
- Girvan, J.R., Braithwaite, V.A., 1998. Population differences in spatial learning in three-spined sticklebacks. *Proceedings of the Royal Society of London Series B-Biological Sciences* 265, 913–918.
- Gouchie, C., Kimura, D., 1991. The relationship between testosterone levels and cognitive ability patterns. *Psychoneuroendocrinology* 16, 323–334.
- Gould, E., Woolley, C.S., Frankfurt, M., McEwen, B.S., 1990. Gonadal steroids regulate dendritic spine density in hippocampal pyramidal cells in adulthood. *Journal Of Neuroscience* 10, 1286–1291.
- Hampton, R.R., Sherry, D.F., Shettleworth, S.J., Khurgel, M., Ivy, G., 1995. Hippocampal volume and food-storing behavior are related in Parids. *Brain Behavior and Evolution* 45, 54–61.
- Hampton, R.R., Shettleworth, S.J., 1996a. Hippocampal lesions impair memory for location but not color in passerine birds. *Behavioral Neuroscience* 110, 831–835.
- Hampton, R.R., Shettleworth, S.J., 1996b. Hippocampus and memory in a food-storing and in a nonstoring bird species. *Behavioral Neuroscience* 110, 946–964.
- Harris, A.P., D'Eath, R.B., Healy, S.D., 2008a. Sex differences in spatial cognition are not caused by isolation housing. *Behaviour* 145, 757–778.
- Harris, A.P., D'Eath, R.B., Healy, S.D., 2008b. Sex differences, or not, in spatial cognition in albino rats: acute stress is the key. *Animal Behaviour* 76, 1579–1589.
- Healy, S.D., 1995. Memory for objects and positions: delayed non-matching-to-sample in storing and nonstoring tits. *Quarterly Journal of Experimental Psychology B* 48, 179–191.
- Healy, S.D., Braham, S.R., Braithwaite, V.A., 1999. Spatial working memory in rats: no differences between the sexes. *Proceedings of the Royal Society of London B* 266, 2303–2308.
- Healy, S.D., Clayton, N.S., Krebs, J.R., 1994. Development of hippocampal specialization in 2 species of Tit (*Parus* spp.). *Behavioural Brain Research* 61, 23–28.
- Healy, S.D., Gwinner, E., Krebs, J.R., 1996. Hippocampal volume in migratory and non-migratory warblers: effects of age and experience. *Behavioural Brain Research* 81, 61–68.
- Healy, S.D., Hurly, T.A., 1995. Spatial memory in Rufous Hummingbirds (*Selasphorus rufus*): a field test. *Animal Learning & Behavior* 23, 63–68.
- Healy, S.D., Hurly, T.A., 1998. Rufous hummingbirds' (*Selasphorus rufus*) memory for flowers: patterns or actual spatial locations? *Journal of Experimental Psychology: Animal Behavior Processes* 24, 396–404.
- Healy, S.D., Krebs, J.R., 1992a. Comparing spatial memory in 2 species of tit—recalling a single positive location. *Animal Learning & Behavior* 20, 121–126.
- Healy, S.D., Krebs, J.R., 1992b. Food storing and the hippocampus in corvids: amount and volume are correlated. *Proceedings of the Royal Society of London B* 248, 241–245.
- Healy, S.D., Krebs, J.R., 1996. Food storing and the hippocampus in Paridae. *Brain Behavior and Evolution* 47, 195–199.
- Healy, S.D., Krebs, K.R., 1993. Development of hippocampal specialization in a food-storing bird. *Behavioural Brain Research* 53, 127–131.
- Henderson, J., Hurly, T.A., Bateson, M., Healy, S.D., 2006. Timing in free-living rufous hummingbirds *Selasphorus rufus*. *Current Biology* 16, 512–515.
- Henderson, J., Hurly, T.A., Healy, S.D., 2001. Rufous hummingbirds' memory for flower location. *Animal Behaviour* 61, 981–986.
- Hilton, S.C., Krebs, J.R., 1990. Spatial memory of four species of *Parus*: performance in an open-field analogue of a radial maze. *The Quarterly Journal of Experimental Psychology* 42B, 345–368.
- Hindmarsh, A.M., 1984. Vocal mimicry in starlings. *Behaviour* 90, 302–324.
- Hodgson, Z.G., Healy, S.D., 2005. Preference for spatial cues in a non-storing songbird species. *Animal Cognition* 8, 211–214.
- Hodos, W., Campbell, C.B.G., 1990. Evolutionary scales and comparative studies of animal cognition. In: Kesner, R.P., Olton, D.S. (Eds.), *Comparative Cognition, and Neuroscience: Neurobiology of Comparative Cognition*. Lawrence Erlbaum Associates, Publishers, Hillsdale, New Jersey, USA; Hove, England, UK, Illus, pp. 1–20, Xiii+476 pp.
- Hurly, T.A., Healy, S.D., 1996. Memory for flowers in rufous hummingbirds: location or local visual cues? *Animal Behaviour* 51, 1149–1157.
- Jacobs, L.F., Gaulin, S.J.C., Sherry, D.F., Hoffman, G.E., 1990. Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Sciences (U.S.A.)* 87, 6349–6352.
- Jones, C.M., Braithwaite, V.A., Healy, S.D., 2003. The evolution of sex differences in spatial ability. *Behavioral Neuroscience* 117, 403–411.
- Jones, C.M., Healy, S.D., 2006. Differences in cue use and spatial memory in men and women. *Proceedings of the Royal Society B-Biological Sciences* 273, 2241–2247.
- Kelley, L.A., Coe, R.L., Madden, J.R., Healy, S.D., 2008. Vocal mimicry in songbirds. *Animal Behaviour* 76, 521–528.

- Kitchin, R.M., 1996. Are there sex differences in geographic knowledge and understanding? *Geographical Journal* 162, 14.
- Krebs, J.R., Healy, S.D., Shettleworth, S.J., 1990. Spatial memory of Paridae: comparison of a storing and a nonstoring species, the coal tit, *Parus ater*, and the great tit, *P. major*. *Animal Behaviour* 39, 1127–1137.
- Krebs, J.R., Sherry, D.F., Healy, S.D., Perry, V.H., Vaccarino, A.L., 1989. Hippocampal specialization of food-storing birds. *Proceedings of the National Academy of Sciences (U.S.A.)* 86, 1388–1392.
- Luine, V.N., Beck, K.D., Bowman, R.E., Frankfurt, M., Macluskus, N.J., 2007. Chronic stress and neural function: accounting for sex and age. *Journal of Neuroendocrinology* 19, 743–751.
- Macphail, E.M., 1982. *Brain and Intelligence in Vertebrates*. Clarendon Press, Oxford.
- Macphail, E.M., Bolhuis, J.J., 2001. The evolution of intelligence: adaptive specializations versus general process. *Biological Reviews* 76, 341–364.
- Male, L.H., Smulders, T.V., 2007. Memory for food caches: not just for retrieval. *Behavioral Ecology* 18, 456–459.
- Marler, P., Slabberkorn, H., 2004. *Nature's Music*. Academic Press.
- McGregor, A., Healy, S.D., 1999. Spatial accuracy in food-storing and nonstoring birds. *Animal Behaviour* 58, 727–734.
- McLean, I.G., Waas, J.R., 1987. Do cuckoo chicks mimic the begging calls of their hosts. *Animal Behaviour* 35, 1896–1898.
- Méry, F., 2007. Experimental evolution of learning ability in *Drosophila melanogaster*: benefits and fitness costs of learning. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* 146, S101–S1101.
- Mettke-Hofmann, C., Gwinner, E., 2004. Differential assessment of environmental information in a migratory and a nonmigratory passerine. *Animal Behaviour* 68, 1079–1086.
- Reboreda, J.C., Clayton, N.S., Kacelnik, A., 1996. Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *Neuroreport* 7, 505–508.
- Roof, R.L., 1993. Neonatal exogenous testosterone modifies sex difference in radial arm and Morris water maze performance in prepubescent and adult rats. *Behavioural Brain Research* 53, 1–10.
- Roof, R.L., Havens, M.D., 1992. Testosterone improves maze performance and induces development of a male hippocampus in females. *Brain Research* 572, 310–313.
- Roof, R.L., Stein, D.G., 1999. Gender differences in Morris water maze performance depend on task parameters. *Physiology & Behavior* 68, 81–86.
- Saucier, D.M., Green, S.M., Leason, J., MacFadden, A., Bell, S., Elias, L.J., 2002. Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behavioral Neuroscience* 116, 403–410.
- Seymour, P., Dou, H., Juraska, J.M., 1996. Sex differences in radial maze performance: influence of rearing environment and room cues. *Psychobiology* 24, 33–37.
- Sherry, D.F., 1984. What food-storing birds remember. *Canadian Journal of Psychology-Revue Canadienne De Psychologie* 38, 304–321.
- Sherry, D.F., Krebs, J.R., Cowie, R.J., 1981. Memory for the location of stored food in marsh tits. *Animal Behaviour* 29, 1260–.
- Sherry, D.F., Vaccarino, A.L., 1989. Hippocampus and memory for food caches in black-capped chickadees. *Behavioral Neuroscience* 103, 308–318.
- Sherry, D.F., Vaccarino, A.L., Buckenham, K., Herz, R.S., 1989. The hippocampal complex of food-storing birds. *Brain Behavior and Evolution* 34, 308–317.
- Shettleworth, S.J., 2001. Animal cognition and animal behaviour. *Animal Behaviour* 61, 277–286.
- Shettleworth, S.J., 2003. Memory and hippocampal specialization in food-storing birds: challenges for research on comparative cognition. *Brain Behavior and Evolution* 62, 108–116.
- Shettleworth, S.J., Hampton, R.R., Westwood, R.P., 1995. Effects of season and photoperiod on food storing by black-capped chickadees *Parus atricapillus*. *Animal Behaviour* 49, 989–998.
- Shettleworth, S.J., Krebs, J.R., 1982. How marsh tits find their hoards: the roles of site preference and spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes* 8, 354–375.
- Shettleworth, S.J., Krebs, J.R., 1986. Stored and encountered seeds: a comparison of two spatial memory tasks in Marsh Tits and Chickadees. *Journal of Experimental Psychology: Animal Behavior Processes* 12, 248–257.
- Shettleworth, S.J., Krebs, J.R., Healy, S.D., Thomas, C.M., 1988. Spatial memory for stored and encountered food in food-storing tits. *Bulletin of the Psychonomic Society* 26, 526–526.
- Shettleworth, S.J., Krebs, J.R., Healy, S.D., Thomas, C.M., 1990. Spatial memory of food-storing tits (*Parus ater* and *Parus atricapillus*): comparison of storing and nonstoring tasks. *Journal of Comparative Psychology* 104, 71–81.
- Shors, T.J., 2001. Acute stress rapidly and persistently enhances memory formation in the male rat. *Neurobiology of Learning and Memory* 75, 10–29.
- Silverman, I., Choi, J., Mackewn, A., Fisher, M., Moro, J., Olshansky, E., 2000. Evolved mechanisms underlying wayfinding: further studies on the hunter-gatherer theory of spatial sex differences. *Evolution and Human Behavior* 21, 201–213.
- Smulders, T.V., Dhondt, A.A., 1997. How much memory do tits need? *Trends in Ecology & Evolution* 12, 417–418.
- Smulders, T.V., Sasson, A.D., Devoogd, T.J., 1995. Seasonal variation in hippocampal volume in a food-storing bird, the black-capped chickadee. *Journal of Neurobiology* 27, 15–25.
- Spetch, M.L., 1990. Further studies of pigeons' spatial working memory in the open-field task. *Animal Learning & Behavior* 18, 332–340.
- Spetch, M.L., Honig, W.K., 1988. Characteristics of pigeons' spatial working memory in an open-field task. *Animal Learning & Behavior* 16, 123–131.
- Stevens, T.A., Krebs, J.R., 1986. Retrieval of stored seeds by Marsh Tits *Parus palustris* in the field. *Ibis* 128, 513–525.
- Vander Wall, S.B., 1990. *Food Hoarding in Animals*. The University of Chicago Press, Chicago.
- Warren, S.G., Juraska, J.M., 1997. Spatial and nonspatial learning across the rat estrous cycle. *Behavioral Neuroscience* 111, 259–266.
- Williams, C.L., Barnett, A.M., Meck, W.H., 1990. Organizational effects of gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience* 104, 84–97.
- Williams, C.L., Meck, W.H., 1991. The organizational effects of gonadal steroids on sexually dimorphic spatial ability. *Psychoneuroendocrinology* 16, 155–176.
- Woolley, C.S., Weiland, N.G., McEwen, B.S., Schwartzkroin, P.A., 1997. Estradiol increases the sensitivity of hippocampal CA1 pyramidal cells to NMDA receptor-mediated synaptic input: correlation with dendritic spine density. *Journal of Neuroscience* 17, 1848–1859.
- Zollinger, S.A., Suthers, R.A., 2004. Motor mechanisms of a vocal mimic: implications for birdsong production. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271, 483–491.