

Zebra Finches and cognition

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Abstract. In spite of attracting significant attention as a model for song learning, sexual imprinting and mate-choice, there has been surprisingly little research on the general cognitive abilities of Zebra Finches (*Taeniopygia guttata*), from spatial memory and social learning to more complex tests of social cognition such as Theory of Mind. This is perhaps surprising given the logistical benefits of the species: they are fairly cheap to house and easy to maintain in the laboratory, and they can be readily bought or bred on demand and consequently large sample sizes are readily achievable. The explanation probably lies with the model market for cognition already being fully occupied by rats and pigeons, with decades of research into learning and memory in these species, whereas tests of more complex cognition have traditionally been conducted on primates and more recently extended to corvids, pigs and dogs. Although it is not clear whether Zebra Finches are going to be useful for examining the role of cognition in mate-choice, this species does seem to be a good choice for some tests of cognitive abilities, particularly given the existing neurobiological tools for examining the neural correlates of song learning and sexual imprinting in this species, and that much is already known about the neuroanatomy and connectivity of the Zebra Finch brain.

Zebra Finches have long been a valuable tool for addressing questions about song production and learning in the field (e.g. Clayton *et al.* 1991; Dunn and Zann 1996a, 1996b; Zann 1996; Runciman *et al.* 2005) and in the laboratory (e.g. Nordeen and Nordeen 1988; Bottjer and Sengelaub 1989; Kirn and Devoogd 1989; Clayton and Bischof 1990; Burek *et al.* 1991; Marler and Slabberkoom 2004; Catchpole and Slater 2008; Zann and Cash 2008). Given the involvement of learning in song, one might expect that Zebra Finches would also be a preferred species for studies of avian cognition, for tests of spatial memory and social learning for example, especially given the knowledge we have about their behaviour in the field, thanks to Richard Zann's seminal studies (Zann 1996). The logistical features that have made pigeons and rats the model species for investigating various aspects of animal learning and cognition would also apply to Zebra Finches, namely that they are fairly cheap to house, are easily domesticated, and are easy to maintain in the laboratory. Furthermore, they can be readily purchased or bred on demand so that large sample sizes are readily obtained for study and stocks can be readily replenished.

Another advantage of using Zebra Finches is that we know a lot about their social and vocal behaviour, how these develop and the extent to which they are controlled by learning, as well as the underlying neurobiology of such behaviours. This makes the Zebra Finch an excellent model for investigating the role of cognition during early development (including in the egg) and, indeed, there is now an extensive literature on song learning and sexual imprinting using Zebra Finches as the classic model. Further, although by the time they are three years old these birds are considered elderly, Zebra Finches do live long enough to make

an investment in lengthy training for an experiment, as is the case with pigeons, for which thousands of training trials are required for some of the experiments on testing of visual discrimination and delayed matching to sample. This also means that experiments can be repeated on the same birds to test memory capacity, duration and other aspects over time. For all these reasons, Zebra Finches have proved to be an excellent model for addressing many questions about the role of learning in behavioural development, particularly of sexual preferences and song, the neural mechanisms underpinning song learning and, to a lesser extent, sexual imprinting. An obvious next step would be to test Zebra Finches on other aspects of animal cognition, such as spatial memory and social learning. It would also be possible to test more complex cognitive abilities, such as the ability to remember what happened where and when and, as they are social animals and live in flocks, their social memory (e.g. remembering which individual did or saw what) and social cognition (e.g. keeping track of what another individual has and has not seen and does and does not know), extending the work traditionally conducted on primates (Tomasello and Call 1997; Hampton *et al.* 2005) and, more recently, corvids (Clayton and Dickinson 1998; Emery and Clayton 2001; Hunt and Gray 2003; Dally *et al.* 2006; Bugnyar 2008; Seed *et al.* 2008; Stulp *et al.* 2009). Other advantages of conducting research on Zebra Finches is that because they are so strikingly sexually dimorphic it would be easy to test for sexual differences in cognition, and they live long enough to enable investigations into the role of aging in cognition and cognitive decline.

Nonetheless, Zebra Finches have simply not been used to any extent to examine many of the classic cases of animal cognition.

We suspect that the lack of favour for Zebra Finches in cognitive studies is connected to the way in which mechanistic questions (as are many of the questions addressing cognitive abilities) rely on model systems. Again, the work on the behaviour and neurobiology of song learning provides support: the Zebra Finch and the Common Canary (*Serinus canaria*) are the two exemplars of the two major kinds of song learning (i.e. closed and open learners). They have become the models because they are relatively easy to keep in the laboratory and to test. Furthermore, once the behavioural component of the song of these two species was broadly characterised it was possible to take such features for granted in order to look more deeply into the mechanistic bases for song learning. For broader cognitive questions, the pigeon was already available as an avian model and the rat was the mammalian model. Early investment into the use of these two animals went into designing appropriate tasks to examine cognition from which the interesting mechanistic questions can be asked. There is now such a wealth of data on all aspects of cognition of pigeons, rats and mice, it seems more cost-effective to build on this wealth of data rather than to add an alternative species for which the initial data collection must begin (rather than citing individual work, a Web of Knowledge search returned 7403 hits for 'rat cognition', 3734 for 'mouse cognition', 163 for 'pigeon cognition' and 20 for 'corvid cognition'). Additionally, given the assumption is that the mechanisms underpinning cognition are going to apply generally across the vertebrates, including understanding cognitive mechanisms in humans, there must be considerable value either logistically or biologically for making that investment. The case of significant biological interest has been made for the primates and, more latterly, the corvids although the logistical issues surrounding these groups are such that they are unlikely ever to be the most common model for animal cognition.

The mechanistic model system, however, focused as it is on understanding in great detail how one, or perhaps two, systems work, is not appropriate to address the kinds of questions in which behavioural ecologists are most interested (i.e. functional or ultimate questions, directed to providing explanations for the diversity we see in behaviour, such as in song). Looking for explanations for how and why song is produced has, thus, left us with knowing quite a lot about how song varies in amount, complexity of notes, compositions, within and among species and so on, and a remarkable amount about the neurobiological underpinnings of song learning and production in Zebra Finches and Common Canaries (the model systems for song). We know considerably less about whether the striking diversity in behaviour is reflected at the neural level (or in the learning of those notes and songs). The working assumption is, largely, that it is not so reflected, and that the same basic neural structures (the anatomy and connectivity) enables the behavioural diversity (in song), although whether that is achieved via increased volume of structures (e.g. DeVoogd *et al.* 1993) or more or different connectivity is still not clear.

Model systems and spatial cognition

Rather than continue to lament the absence of a large body of work on cognition in Zebra Finches, it seems more useful to examine what is known and what questions can usefully be addressed in the future using Zebra Finches, both as a species of significant interest

in its own right and as a model system. Much of the work to date using Zebra Finches to examine cognitive abilities has been done in the context of a model system, so as to address questions that are less accessible using other species, although it is the biology of those other species that is of interest. The most prominent aspect of cognition for which Zebra Finches have been used is spatial cognition and some of the neurobiology underpinning that kind of cognition. We will, therefore, focus most of our discussion on spatial cognition and the role Zebra Finches have played, and may play in the future, with regard to this particular aspect of cognition.

Tests of and, indeed, interest in spatial cognition in birds were confined almost entirely to laboratory pigeons until the 1980s when behavioural ecology and experimental psychology came together in the addressing the role of spatial cognition in two 'real' world behaviours: homing and food-storing (Shettleworth 1995). The readily trained ability of pigeons to return to their home loft offers ample opportunity to investigate a wide variety of questions as to what information (cues) the birds use to determine where they are (the release site), in which direction they should leave the release site, how to navigate to the vicinity of the home loft, and how to recognise home itself, as well as when they learn the information and from whom, how they integrate different types of (potentially conflicting) information. Although the roles of olfaction, magnetism and the sun had previously attracted all the attention with regard to pigeon homing, work, especially by Bingman, Gagliardo, Guilford and their teams, continues to show the significant role played in successful homing by memory for spatial information and the role of the area of the brain of especial interest in spatial cognition, the hippocampus (Bingman and Yates 1992; Gagliardo *et al.* 1996; Meade *et al.* 2005). Navigation, however, although undoubtedly achieved at a local level by wild Zebra Finches returning to nests, good foraging sites and so on, is not readily used as an experimental system by most people working on Zebra Finches in captivity, maintaining their birds as they do far from the natural habitat of these birds (e.g. the northern hemisphere; but see Voss *et al.* 2007; Keary *et al.* 2009). It has, therefore, been food-storing, the second of the real behaviours, that has formed the basis for the work on spatial cognition in Zebra Finches.

Food-storing is an unlikely basis for investigation into spatial cognition because Zebra Finches do not store food in external caches. They also do not carry out any of the other behaviours that have been proposed to require more than the average amount or degree of spatial ability (e.g. memory of nests for nest parasitism, migration). The work on the neurobiology of Zebra Finch song learning has, however, provided a great deal of technical background for access to the Zebra Finch brain, also in a cognitive context.

One of the first forays into using Zebra Finches as a model for spatial cognition was an attempt to determine whether hippocampal transplants could reverse lesion-induced spatial memory deficits (Patel *et al.* 1997). In one of the first tests of spatial cognition of Zebra Finches, Patel and colleagues used an experimental tray, containing cardboard covered wells, one or more of which contained food. The test was composed of two phases, in the first of which only one of 50 cardboard-covered wells contained food (the exploration phase). Six other randomly chosen wells were also covered but were empty. Having discovered and eaten some, but not all, of the food, the tray was removed for

30 min and subsequently returned with all seven flaps again covering the same wells used in the exploration phase. Only the well that contained food in the exploration phase contained food in the second phase (the test). Performance was assessed by comparing the number of pieces of cardboard that needed to be moved to locate the food in the test phase with chance performance, which is the level of performance a bird should have attained during the exploration phase when it did not know which well contained the food. Birds were also tested on a colour version of the task, in which the rewarded well was identified by its colour rather than its location. The alternative, unrewarded wells were covered by pieces of cardboard of different colours from that of the rewarded well. In the test phase the wells that are covered differ from those used in the sample phase and the bird must have learned the correct colour in the first phase to make the correct choice.

Usefully for testing spatial cognition and examining its relationship with its neural correlate, the hippocampus, this particular task appears to be dependent on hippocampal integrity for successful completion: lesioned birds performed more poorly on this task than did unlesioned and sham-lesioned control birds (Patel *et al.* 1997). Importantly, for this particular experiment, the transplant of embryonic hippocampal tissue specifically improved performance on the spatial task only to levels comparable with pre-lesion levels. Additionally, transplants of embryonic non-hippocampal telencephalic tissue did not affect performance on either task. This work, then, did two key things: it provided a logistically useful cognitive task and it demonstrated that it was a hippocampal-dependent task.

Sanford and Clayton (2008) used a version of this task to determine whether Zebra Finches were capable of associating the location of a reward with the colour of the location and with the reward type. In the first experiment, the well covers the birds had to move to uncover food rewards were either heavy or light. Birds made fewer errors if they had to move the heavy covers to access food, demonstrating that performance on a task can be the outcome of a combination of factors only one of which is cognitive ability itself (Sanford and Clayton 2008). The birds were also tested on the task after a single exploration phase and after 10 trials in which the rewarded wells were in the same locations and with the same colour cover over those 10 trials. Not surprisingly, birds lifted fewer covers to find food after repeated trials than they did after a single trial. The extra feature to this experiment was that birds were faced with two sequential tray presentations in the exploration phase, in which the trays were placed in different locations in the cage, rewarded wells covered with different colours and the reward differed. This allowed for feeding of one or other of the rewarded foods before the experiment to determine whether the birds had learned which food was in each of the two locations. Feeding to satiation on one type of food before embarking on the day's trial(s) in which more than one type of food is available is a useful way of determining whether birds differentiate between types of food, either in attention or in memory. Zebra Finches pre-fed with one food did not preferentially search for the other food in the test phase after a single exploration phase although they did learn to do this over the course of 10 trials.

Western Scrub-Jays (*Aphelocoma californica*), on the other hand, can make this association between type of food and location

(Clayton and Dickinson 1998). They can also remember when one food is the more appropriate to search for, given the passing of different periods of time (i.e. after 4 h, look for mealworms; if 120 h, look for peanuts). The discovery that Scrub-Jays could associate the type of food, place and time together (what, where and when) opened up new avenues of thought and experiment on the ability of animals to remember the what, where and when of trial-unique events, which Clayton and Dickinson (1998) termed 'episodic-like' memory, and on other complex cognitive tasks in birds. That Zebra Finches, however, could not make this association after a single trial may say something about the relative cognitive abilities of the two species, either because the task is inherently more difficult for Zebra Finches or because they were required to use a learning rule that is inconsistent with their usual foraging strategy. The task may be more difficult for Zebra Finches because by requiring them to learn new information each trial means they must deal with increasing levels of proactive interference, that is where information learned previously interferes with the ability to remember information relevant to the current trial. The possibility of interference underpinning cognitive differences has previously been proposed for Black-capped Chickadees (*Parus atricapillus*) performing better than did Dark-eyed Juncos (*Junco hyemalis*) on a spatial task (Hampton *et al.* 1998).

Sanford and Clayton (2008) also suggested that Zebra Finches might utilise a win-stay foraging strategy, given the way in which wild Zebra Finches forage. Food-storing birds, such as scrub-jays, are thought to have a win-shift strategy, which would be more consistent with single-trial learning tasks such as this one. Performances based on foraging strategy have otherwise largely been considered in the context of nectarivorous birds (Cole *et al.* 1982; Wunderle and Martinez 1987; Sulikowski and Burke 2007), all of which tend to have a win-shift strategy and appear to find it more difficult to learn tasks that require a win-stay strategy. However, whereas these data are consistent with foraging strategy appearing to be a species-level trait, even nectarivores such as hummingbirds learn either strategy very quickly (Healy and Hurly 1995, 1998; Hurly 1996; Hurly and Healy 1996).

Hormones and cognition

Given the swathe of work on hormonal influences on song learning, Zebra Finches have been relatively little used to examine the role of hormones on spatial memory. The key hormones with regard to spatial cognition, in mammals at least, are the stress hormones (e.g. corticosterone) and the sex hormones (e.g. testosterone and oestrogen). It appears that corticosterone can affect spatial cognition in Zebra Finches, as in Mountain Chickadees (*Parus gambeli*) (Pravosudov 2003). Zebra Finches bred to express varying levels of corticosterone performed differently on a spatial task, depending on their baseline corticosterone levels: birds with high levels of corticosterone did not remember spatial locations (covered wells, as in Patel *et al.* 1997, above) as well as control birds, whereas there were no differences between birds from the two lines on the colour version of the task (Hodgson *et al.* 2007). Although the birds did not differ in plasma corticosterone levels immediately after the task, those with high levels of corticosterone had lower mineralocorticoid receptor

mRNA expression in the hippocampus, which may mean that stress hormones play some kind of regulatory role in spatial cognition in birds (as they do in mammals; see Harris *et al.* 2009). There is also some evidence that acute corticosterone manipulation can reduce neural proliferation in the ventricular layer surrounding the ventricles in the brain of male Zebra Finches. Cells from this layer migrate to other parts of the brain, including the hippocampus (at least in mammals) where they become functional neurons (Alvarez-Buylla and Garcia-Verdugo 2002; Katz *et al.* 2008).

Zebra Finches have often been subjected to manipulations of their sex hormones (Arnold 1975; Adkins-Regan and Ascenzi 1990; Vockel *et al.* 1990; Adkins-Regan *et al.* 1994; Wade and Arnold 1994), which, like corticosterone, have a significant impact on spatial memory in mammals although such effects have been little explored in birds. In mammals, both testosterone and oestrogen can cause changes in spatial cognition, both to increase and to decrease performance. The data are few at this point for Zebra Finches (although there are more for Zebra Finches than for any other avian species) but oestrogen certainly appears to affect spatial cognition: castrated male Zebra Finches with oestradiol implants learned a spatial task more rapidly than did control birds, whereas testosterone implants (as dihydrotestosterone) did not bring about the same effect (Oberlander *et al.* 2004). As dihydrotestosterone is not converted to oestrogen by aromatase but testosterone is, it seems possible that effects of testosterone are mediated via oestrogen. However, although the two hormones had different effects on performance, they seemed to exert similar effects on cells in the hippocampus: cells in the rostral part of the hippocampus were larger in all implanted birds than they were in control birds. In the oestradiol-treated birds, this enlargement of cell size was associated with a decrease in density of cells. Oestrogen may also act in the cerebellum to affect spatial cognition in Zebra Finches: after cerebellar lesions, oestrogen treatment appeared to improve cognitive ability somewhat relative to that of birds given oestrogen plus fadrozole, an oestrogen inhibitor (Spence *et al.* 2009).

The demonstration that sex hormones affect spatial cognition in Zebra Finches opens up several avenues of research. For example, oral administration of either testosterone and oestrogen to Great Tits (*Parus major*; both male and female) for 5 days led to enhanced performance on a one-trial spatial version of a well-task (Breuner *et al.* 1998; Hodgson *et al.* 2008). Oral administration allows for a rather precise manipulation of cognitive ability, as does injection, but without the stressful side effects of the injection process. For all of the logistical reasons outlined above, it would seem that the Zebra Finch would be a very suitable candidate for addressing the role that activational hormonal effects play in causing variation in spatial cognition in birds, far more so than would Great Tits or some other wild species. Additionally, Zebra Finches appear ideal for examining the role of organisational effects of the sex hormones on later spatial cognition as the hormone levels in eggs can be far more readily manipulated than can *in utero* early development of mammals.

Neurobiology of spatial cognition

The neurobiological underpinnings of song learning are often considered to be separate from those involved in other kinds of

cognition, including spatial memory. However, although there is no evidence yet for direct connections between these areas, the occurrence of immediate early gene (IEG) expression in the hippocampus in response to song suggests there may be some functional relationship (Bailey *et al.* 2009). Quite what relationship is still far from clear, because hippocampal IEG expression appears to depend on the immediate early gene expressed and the stimulus used. For example, c-fos is expressed in the hippocampus of 30-day-old female Zebra Finches (song learning begins ~25 days) specifically in response to conspecific song (in contrast to heterospecific song), an effect that is not significant at 45 days (when production of song begins). C-fos is not expressed in the hippocampus of juvenile males, at either 30 or 45 days of age (Bailey *et al.* 2002; Bailey and Wade 2003, 2005). ZENK levels in 30-day-old juvenile females in response to conspecific song, however, were not different to those in control females exposed to silence (Bailey and Wade 2003) and hippocampus has been used as a control region when examining ZENK expression in song regions (Kruse *et al.* 2004). Mate-calls, however, can lead to increased ZENK expression in the hippocampus (Vignal *et al.* 2008; Gobes *et al.* 2009). It would now be helpful to know more about IEG expression in the hippocampus with regard to spatial cognition, or cognition more generally, before we can appropriately interpret the current variation in hippocampal IEG expression in response to variation in song features. fMRI also promises to be useful in determining which regions of the brain respond, and to what extent, to variation in behaviour (e.g. Boumans *et al.* 2008).

Although the IEG data support a relationship between song learning and hippocampal function, data from hippocampal lesion do not. Lesions made during differing stages of song development appear to affect only spatial performance and not song learning, suggesting that the hippocampus is not playing a major role in song learning (Bailey *et al.* 2009). Bailey *et al.* (2009) looked at both the accuracy of performance and latency to make a correct choice by Zebra Finches trained to find the baited cup from six alternatives. Latency is commonly used to assess cognitive performance. Indeed, this is the measure used in the Morris water-maze task, the classic test of spatial cognition in rats in which animals are required to swim in water to a platform hidden just below the surface of the water. However, there is some concern that the speed to respond may be more susceptible to effects of extraneous variables, such as stress. Variation in levels of stress in rats, at least, can lead to apparent variation in cognitive performance (e.g. Beiko *et al.* 2004). In the case of laboratory rats, females respond more poorly to acute stress than do males, and the stress of swimming in a Morris water-maze leads the females to take longer to swim to the platform than do males (Harris *et al.* 2008a, 2008b). The strength of this effect varies with age and strain of rat: the effect is more marked in younger rats and in albinos (Luine *et al.* 2007).

One reason for suggesting this alternative explanation for the outcome of the effect of hippocampal lesions on the performance of the Zebra Finches is that performance (as assessed by the number of mistakes and latency) increased in those birds across the course of testing, which one would not expect if the lesion had incapacitated the hippocampus. Additionally, control females made more mistakes than did control males, an outcome that suggests that female Zebra Finches, like female rodents may be

more susceptible to acute stress (the stress of testing) than are males. In another study in which birds had to locate a rewarded feeder (of four visually similar feeders) in a room when released from one of four different release points, hippocampal lesions led to both the predicted accuracy effects as well as to an unexpected outcome with regard to latency. As expected, birds lesioned before spatial training did not learn the location of the reward whereas control birds did (within four training sessions; Watanabe and Bischof 2004). Furthermore, birds lesioned after they had learned which location held the reward were much poorer at locating the reward than were the control (sham-lesioned) birds. In both cases, however, the lesioned birds took no more time to arrive at the correct location than did the control birds although they made more mistakes (visiting and revisiting unrewarded locations) in doing so. Quite why damage to the hippocampus would lead to birds appearing to be more motivated to do the task is not yet clear, not least because Zebra Finches with hippocampal lesions could learn what was the rewarded feeder when it was distinguishable by a unique visual pattern and at a rate similar to that of control birds (Watanabe *et al.* 2008).

That stress may underlie some of the apparent hippocampal involvement in the performance of some of these tasks was suggested by Sadananda and Bischof (2004) upon finding increases in expression of hippocampal IEG (c-fos) during sexual imprinting of 100-day-old males (females were not tested) following isolation from Day 40. Sadananda and Bischof also found that the hypothalamus, which is associated with increases in corticosterone levels, also expressed higher levels of c-fos. An effect of long-term stress specifically on males would be consistent with the mammalian data, although these effects need to be examined in females before this can be confirmed (e.g. Bowman 2005).

Such effects lend a cautionary note to the interpretation of all cognitive data: stress may negatively affect cognitive performance either as a result of acute causes, such as the testing context, or to chronic causes, such as regular handling or inappropriate caging.

Mate-choice

Not only have there been few direct studies of cognition in Zebra Finches, the role of cognition in mate-choice, which is one of the major uses to which Zebra Finches have been put, has also been largely disregarded. There are two ways in which cognition may play a role in mate-choice. The first is directly, as a valuable trait on which mate-choice might be based, the second indirectly, as it enables and affects exactly which choice is made.

With regard to the first role, few data are available, in spite of the suggestion that the cognitive ability required to learn multiple, complex songs may reflect a more general cognitive competency, which could be used by females to assess the quality of a male (Nowicki *et al.* 2000; DeVogd 2004). Boogert *et al.* (2008) trained male Zebra Finches to find food in the covered wells of a tray and measured performance by the number of trials taken to learn how to remove those covers. Those male Zebra Finches that sang more complex songs (number of unique and total song elements per phrase and duration of song-phrases) when presented with a female were faster to learn how to lift covers. The rate of learning is, however, a problematic measure of perfor-

mance susceptible to concerns similar to those raised by measures of latency (see below). Additionally, as pointed out by Pearce (1987), the rate of learning tends to be negatively correlated with brain-size (usually thought of as being associated with complex cognition): shorter-lived animals with smaller brains learn much sooner than do longer-lived animals with larger brains.

There is still much to be explored concerning rates of learning and innovation, not least whether learning different mechanical tasks, such as the one used by Boogert *et al.* (2008), differ in their cognitive demand from tasks of the kind more typically used by experimental psychologists to test cognitive abilities (e.g. tasks that require memory for one or more features). As noted already, we still have much to learn about the relationship between song learning and memory and other cognitive abilities.

That cognition may play a more indirect role in mate-choice is little explored in any species. On the face of it, Zebra Finches would seem a prime target for such investigation. They have, after all, played a significant role in determining the role that perception may play in mate-choice. Zebra Finches were the subject of the first experiment examining the role of ultraviolet light in mate-choice (Bennett *et al.* 1996), the importance of which was eventually established (e.g. Hunt *et al.* 2001): that UV is but one of many components of the displays of a Zebra Finch, such as the amount, complexity and rate of song, size and bill-colour, that conspecifics can assess during mate-choice (e.g. Collins and ten Cate 1996).

Zebra Finches (and Bengalese Munias (*Lonchura striata* vars. *domestica*)) may well be useful for examining the role of cognition in mate-choice, for two major reasons: (1) convincingly determining how cognition acts in mate-choice is going to be most readily achieved in the laboratory where a variety of relevant variables can be measured and manipulated, such as imprinting, prior experience, and the choice of potential partners; and (2) Zebra Finches readily choose mates in the laboratory and preference for mates can be used as a proxy for actual mate-choice (e.g. ten Cate and Mug 1984; Collins 1994; Witte 2006). This allows much easier experimental manipulation than is possible when actual pairing, mating and producing of young occurs (Clayton 1990).

These significant logistical advantages notwithstanding, there is a serious downside to studying how cognition of a Zebra Finch affects mate-choice: female Zebra Finches have so many male traits to choose from (and which are assumed to be correlated; Birkhead *et al.* 1998). This is a disadvantage because it is unlikely (although not impossible) that females would assess a possible mate on the basis of each and every one of those traits, not because they are small-brained and incapable but rather because that would be a highly inefficient process (Tversky 1969; Tversky and Simonson 1993; Shafir 1994). Indeed, human decision-making shows that we most certainly would not do this when we make choices, even with our large brains and apparently sophisticated cognition, and especially when the options we have to choose among have multi-dimensional properties. When we attempt to choose among items that vary along multiple dimensions (e.g. cameras, restaurants, mates), we tend to use heuristics, that is, a rule of thumb, to reach a solution, such that we choose the option that is as close to the best (optimal) answer at the time (Sedikides *et al.* 1999; Hutchinson and Gigerenzer 2005). When it comes to choosing a restaurant, for example, it becomes clear that

the best choice is context-dependent, that is dependent on variables that differ from one decision opportunity to another. Sometimes the cheapest restaurant is the best solution, sometimes a more expensive but closer one seems best, and on yet other occasions it is neither of these options.

Whereas it may seem obvious that human choices (of mates, food, housing and so on) might vary depending on the context, animals have long been assumed to be rational, especially when it comes to choice (i.e. always choose the best; Bateson *et al.* 2002; Shafir *et al.* 2002; Bateson and Healy 2005). However, data on mate-choice from Zebra Finches have shown empirically that females do not always appear to do this. Variation among, and even within, laboratories in what features of a male used by female Zebra Finches to choose a partner is considerable (e.g. Burley and Coopersmith 1987; Houtman 1992; Swaddle and Cuthill 1994; Riebel 2000; Roberts and Gosling 2003). Some of this variation will be explained by methodology. In some, but not all, choice experiments males can see or hear the females and thus have the opportunity to respond according to the behaviour, morphology or band-colour of the female. Further, males may change rates of display depending on whether they are the extra-pair male or not (Swaddle and Page 2007). Additionally, the time over which females can make their choice will differ, which may or may not affect their preference and, importantly, a female's choice will depend on the number of males from which she can choose. Whereas it is typical in laboratory tests for females to have to choose between two males, several experiments have been conducted in which females are offered the choice of more than two males (e.g. Halliday 1983; Collins 1995; Schielzeth *et al.* 2008).

The assumption underpinning the variation in testing conditions (i.e. number of males that a female views) is that the number of males would not have a qualitative effect on which male the female preferred (and who would be assumed, therefore, to be the best male). However, the context-dependent evidence from humans in mate-choice contexts and from foraging non-human animals would predict differences in the preference the same female exhibits for a particular male, depending on how many other males with which that female is presented (Sedikides *et al.* 1999). Not only might the degree of female preference change but which male she prefers might even change, such that a male preferred when presented with one set of males, is avoided when presented with another set of males. In essence, the heuristic she uses is likely to be affected by several things: the range across which the features she is assessing varies, the number of features, whether she is paying attention to one feature more than others and so on. For example, the two (or more) males with which she happens to be presented may have little variation in colour of bill but may have very different songs. Song may then provide her with a lot more information as to their quality than the colour of their bills and so she would choose among those particular males on the basis of their song. When faced with another set of males, however, with much variation in bill-colour as well as in song, the female will have other information to use. This time she could choose among them on the basis of song or bill-colour, or a combination of the two, all of which would occur in the absence of any prior experience (learning and memory). If the features are not positively correlated, as they may not be (e.g. Birkhead *et al.* 1998), then predicting which male she should

prefer becomes problematic. Although such context-dependence has not been shown to explain the diversity of male features that female Zebra Finches prefer, such effects do occur in mate-choice in Green Swordtails (*Xiphophorus helleri*): females changed which male they preferred when a third male was added (Royle *et al.* 2008; Castellano 2009; Reaney 2009).

To conclude, then, Zebra Finches may offer one of the most promising models to investigate the effects of context on mate-choice (rather than cognition alone), although one problem with attempting to take context-dependent choice into account in mate-choice experiments in Zebra Finches is that so many aspects of an experiment can be considered as context. Indeed, context may even have led to the multiplicity of features available to female Zebra Finches (Campbell and Hauber 2009). Added to the many features directly associated with the male (his morphology and his behaviour) and those of the males with which he is being compared, there are multiple aspects that the female herself brings to the party. A contribution by her visual capacities to her choice of mate is now regularly considered but as, or more, important are her cognitive capacities. One of these is her memory: her memory of her father and any male siblings and their traits learned during sexual imprinting as well as her own experience (Collins 1995; Rutstein *et al.* 2007; Vyas *et al.* 2009).

Sexual imprinting has long been recognised as shaping female preferences and has been investigated more recently in mate-choice experiments in light of the possible role sexual imprinting may play in reproductive isolation (e.g. Burley 2006): females are expected to choose the 'best' male but what she considers to be the best male will depend on how good her father was and how he looked and sounded (Vos 1995; Witte and Sawka 2003; ten Cate *et al.* 2006; Witte and Caspers 2006). Added to the effect of her father will be her own adult experiences of males, which may be those males she has seen and heard (across her lifetime, perhaps?) or be of those males with whom she has previously paired. Her own experience of a hard-working male and the successful fledging of her nestlings may well bear on her subsequent choice and lead her to ignore an apparently fabulous but unknown male for her own more dowdy but familiar male. Mate-choice experiments in Zebra Finches (and all other animals) are going to be more complex in the future when cognitive abilities of the subjects are taken into consideration.

Conclusions

Zebra Finches appear to be a very useful model for examining spatial cognition and the underlying neurobiology in birds, not least because the species is so logistically useful and the neuroscientific techniques are rather well known. With regard to the value of Zebra Finches as a model system for the role of cognition in mate-choice, the advantages are less clear: again, the logistic benefits are tremendous but they may well be offset or exceeded by the problems incurred by addressing this issue with a bird that has such an extensive array of signals used for mate-choice.

Acknowledgements

We thank Kate Buchanan, Simon Griffiths and two anonymous reviewers for thoughtful comments on earlier drafts of the manuscript and the Wellcome Trust for funding (OH).

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Manuscript received 21 January 2010, accepted 13 July 2010