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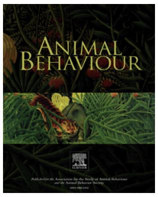

Female hummingbirds do not relocate rewards using colour cues

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Males generally outperform females in spatial tasks. This difference in spatial performance may reflect differences in cue preference because males often use both spatial cues (distance and direction) and feature cues, whereas females prefer to use feature cues. However, studies in birds are few and results are conflicting. As wild male rufous hummingbirds, *Selasphorus rufus*, prefer to use spatial cues to relocate a rewarded flower, in the present study we tested free-flying wild female hummingbirds of three different species (rufous, white-eared, *Hylocharis leucotis*, and magnificent hummingbird, *Eugenes fulgens*) and males of one species (white-eared) for their cue preference in the same task in which rufous males have been tested previously. Birds were allowed to feed once from a four-flower array in which only one flower was rewarded. When the birds returned, the colour and the spatial cue designating the rewarded flower had been dissociated. Although we had expected females to visit the flower of the correct colour (feature cue) first, during the test phase most of the birds (males and females) went to the correct spatial location (spatial cue). It appears, then, that preference for spatial cues is not specific to males and it seems more likely to depend on the relevance or value of a cue to the solution of the task.

Males typically outperform females on a range of spatial learning tasks. One consistent feature of the males' performance is that they use distance, direction and feature cues whereas females prefer to use mainly feature cues to solve the task (Collins & Kimura, 1997; Gaulin & Fitzgerald, 1986; Jozet-Alves, Modéran, & Dickel, 2008; Kavaliers et al., 1996; Lacreuse, Herndon, Killiany, Rosene, & Moss, 1999; Schmidtke & Esser, 2011; Seymoure, Dou, & Juraska, 1996). This effect appears to hold across both species and tasks. For example, when returning to a platform in a Morris water maze male rats outperform conspecific females when extramaze landmark cues are absent but not when a landmark is made available (Roof & Stein, 1999). Similarly, on a computer screen version of a delayed non-matching-to-sample task, women were more likely to use feature than location cues, whereas men used both types of information equally (Jones & Healy, 2006). Even when describing the location of a place, men tend to provide Euclidean information (distance and direction) whereas women provide information on landmarks (Dabbs, Chang, Strong, & Milun, 1998). Furthermore, for male rats Euclidian information overshadows landmark information but for female rats the opposite is true (Rodríguez, Chamizo, & Mackintosh, 2011).

This male advantage in spatial cognition is so typical that there are multiple evolutionary hypotheses purporting to explain these differences, typically by relating sex differences in spatial abilities to the use of space (e.g. range size: Gray & Buffery, 1971; male foraging: Silverman et al., 2000; see Jones, Braithwaite, & Healy, 2003). In particular, since polygynous males cover a larger home range than their conspecific females, it has been suggested that selection has favoured those males with better spatial abilities (Gaulin & Fitzgerald, 1986, 1989; Perdue, Snyder, Zhihe, Marr, & Maple, 2011).

The sex difference in cue use appears not to be confined to mammals as male domestic chicks, *Gallus gallus domesticus*, used position cues to relocate a food reinforcement whereas female chicks used colour cues more readily (Vallortigara, 1996) and female shiny cowbirds, *Molothrus bonariensis*, retrieved food rewards faster than males only when the food was associated with a colour cue (Astié, Kacelnik, & Reboreda, 1998). But the avian data are more mixed than are the data from the mammalian literature. For example, both male and female great tits, *Parus major*, used a position cue to relocate a reward hidden in one of three wells rather than the colour of a cloth on top of each well (Hodgson & Healy, 2005). Furthermore, if cue preference is associated with selection pressure for better spatial ability, then in the cowbirds one would expect the females to be the sex that prefers/uses spatial rather than feature information as it is the females that appear to have the great spatial memory demand (as they alone search for nests to

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parasitize; Reboreda, Clayton, & Kacelnik, 1996) and the better spatial memory: female brown-headed cowbirds, *Molothrus ater*, outperformed conspecific males in a spatial memory task (Guigueno, Snow, MacDougall-Shackleton, & Sherry, 2014). The lack of a compelling association between spatial demand/performance and preferential use of spatial information in birds led Hodgson and Healy (2005) to suggest that cue use/preference might be due to the relative value of those cues in the specific context in which the animals were tested, i.e. that cue use might be context dependent rather than favoured by selection.

Hummingbirds are a useful group in which to address sex differences in cue use because in most species the sexes differ in foraging behaviour and their use of space. Males are typically territorial, defending and feeding from hundreds of flowers within their territories every day (Kodric-Brown & Brown, 1978) and in most species are considered to be polygynous. Females, on the other hand, are not usually territorial, are thought to forage by trap lining (Temeles, Shaw, Kudla, & Sander, 2006) and provide all of the parental care. Consistent with this expectation, wild male rufous hummingbirds, *Selasphorus rufus*, preferentially used spatial information to return to a previously rewarded artificial flower (Hurly & Healy, 1996).

To determine whether female hummingbirds preferred to use feature rather than spatial cues we tested female hummingbirds of three different species using a similar task to that used by Hurly and Healy (1996). In this test birds visited a four-flower array in which all four artificial flowers were a different colour and only one of them contained reward. Prior to the birds' return, we emptied the flower and switched it with one of the other flowers. If the birds preferred to use feature cues to choose the flower it expected to contain reward (the original flower contained more sucrose than the bird could consume in a single visit), it should visit the flower of the 'correct' colour. If, however, it preferred to use spatial cues, it should visit the flower in the original location (the 'correct' spatial cue). We tested female rufous hummingbirds at a site in Canada and females of the white-eared hummingbird, *Hylocharis leucotis*, and of the magnificent hummingbird, *Eugenes fulgens*, at a site in Mexico. As we had the opportunity, we also tested male white-eared hummingbirds.

Our expectation was that if space use selects for a preference for using spatial cues, then like female mammals, the female hummingbirds should preferentially use feature information rather than spatial information when returning to a previously rewarded artificial flower. The male white-eared hummingbirds should, however, prefer to use spatial cues.

METHODS

Subjects and Field Site

Eleven female rufous hummingbirds were tested in free-flying field experiments along the Westcastle Valley in Alberta, Canada (49° 21′ N, 114° 25′ W). Individuals were identified by their unique throat feather patterns. Trials were run between 0700 and 1800 hours Mountain Standard Time from 13 to 24 July 2013. In Mexico, at the National Park 'La Malinche', Tlaxcala, in Central Mexico (19° 14′ N, 98° 58′ W with a 3000 m elevation) we tested eight males and three female white-eared hummingbirds and seven female magnificent hummingbirds. Individual birds in Mexico were identified by a detailed record of their visit rates to an artificial nectar feeder and identification of perch sites. To avoid retesting individuals only one bird of each species or sex was tested at a particular site. Trials in Mexico were run from 21 September to 11 November 2013.

The study was conducted with ethical permission from the University of St Andrews Ethical Committee, the University of Lethbridge Animal Welfare Committee, Alberta Sustainable Resource Development and Environmental Canada and with permission from the Scientific Station 'La Malinche' from the Universidad Autónoma de Tlaxcala.

Initial Training

In Canada, we put out feeders containing 14% sucrose solution along the Westcastle Valley during the third week of May. Each feeder had a red plastic base and the birds accessed the sucrose via a hole in a single yellow plastic flower that was secured to the base of the feeder. By the first week of July, females started to feed from the feeders regularly and to defend them.

During that time we trained those females that were defending feeders and had distinctive throat patterns to feed from artificial flowers. To do this we first lowered the feeder 20 cm at a time until it had reached a height of 60 cm above the ground and we then replaced the single yellow plastic flower on the feeder with another artificial 'flower'. This flower comprised a plastic vial full of 25% sucrose solution, which was surrounded by a yellow cardboard circle (2 cm in diameter). After the bird had fed from the cardboard 'flower' once, we replaced it with a larger one, also yellow (6 cm in diameter). Finally, after the bird fed from that flower, the feeder was removed and the experiment began. This training procedure ensured that the bird was exposed to both the spatial and colour cues the same number of times.

The hummingbirds tested in Mexico were trained following the same training protocol as described above. We first placed artificial feeders at locations within 1 km of La Malinche research station and waited for the hummingbirds to visit regularly. Then, birds were trained to feed from an artificial flower. At La Malinche both the white-eared hummingbird and the magnificent hummingbird are year-round residents with both males and females migrating altitudinally to match the blooming schedule of different flower species (Lara, 2006).

Experimental Trials

For the experiment we presented the bird with an array of four artificial flowers mounted on 60 cm high wooden sticks in an 80 cm square where only one flower was filled with 600 μl of 25% sucrose solution. The other three flowers were empty. The amount of sucrose solution in the rewarded flower was enough so that a single foraging bout was not sufficient for the birds to empty the flower. The rewarded flower was always the same colour as the feeder's plastic flower and was always placed in the same location as that where the bird had fed from the cardboard flower when it was still attached to the feeder. The other three flowers were each of one of three colours (possible colours were: yellow, red, pink and purple) and the location of these flowers within the array was assigned pseudorandomly.

Once the hummingbird had fed from the rewarded flower (Phase 1) and left the array, we switched the rewarded flower with one of the other flowers in the array so that its colour and its absolute location were in conflict (Fig. 1; Phase 2). We emptied all of the flowers and ensured that the birds did not return to the array for at least 5 min. When the bird returned to the array we recorded the first visit made. Visits were defined as a probe into a flower. Each bird was tested only once.

Statistical Analyses

We compared the distribution of observed first visits made to all flowers during Phase 2 to a distribution expected by chance with a chi-square goodness-of-fit test. Since the expected frequencies of the distribution of the visits were smaller than 5, a randomization