A Field Study of Spatial Memory in Green-Backed Firecrown Hummingbirds (*Sephanoides sephaniodes*)

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Abstract

The foraging ecology of hummingbirds involves the exploitation of a high number of patchily distributed flowers. This scenario seems to have influenced capabilities related to learning and memory, which help to avoid recently visited flowers and to allocate exploitation to the most rewarding flowers, once learning has occurred. We carried out two field experiments with the green-backed firecrown hummingbird (*Sephanoides sephaniodes*, Trochilidae) in order to examine the ability of birds, first, to recall a nectar location, and secondly, to remember the location of the most rewarding flower among lower quality flowers. The first experiment showed that subjects were able to recall the location of nectar among flowers of identical appearance. In the second experiment, hummingbirds were also able to recall the location of the most rewarding nectar among less rewarding flowers with the same appearance. The results of this study suggest that *S. sephaniodes* can remember the location of the most rewarding patch, facilitating efficient exploitation of flowers in the absence of visual cues related to nectar quality.

Introduction

Cognitive abilities are pivotal to the performance of many behavioral traits in animals and hence they can have evolutionary impact through their effect on fitness. As a result of this, an ecologic and evolutionary perspective of animal cognition has gained considerable interest in recent years (Dukas 2004). However, most studies to date that have demonstrated the ability of species to remember spatial locations in absence of visual cues have been conducted in the laboratory under precise controlled conditions (see e.g. Mazur 1998). However, these laboratory studies do not necessarily reflect cognitive abilities of wild animals under natural conditions (Balda et al. 1998; Hurly & Healy 2003).

In the last decades the interest on evolutionary and ecologic aspects of cognition has prompted field research on animal learning and memory (Balda et al. 1998; Dukas 2004). Examples include food-storing animals, such as birds and mammals capable of remembering spatial locations of a large number of scattered caches (Sherry 1985; Kamil & Balda 1990; Shettleworth & Hampton 1998). However, in spite of these studies, there is still a lack of knowledge about how species cope with environmental information (see Vásquez et al. 2006), and about how animals learn and use resource patches under natural conditions (see Balda et al. 1998).

Research about cognitive abilities under field conditions provides insight about what animals can actually do in their natural habitats (Hurly & Healy 2003). Furthermore, field studies can improve our understanding of the fitness consequences of cognitive abilities by examining their influence on fitness-related traits, such as foraging success or timing of reproduction. Ideally, these studies should link cognitive abilities to fitness consequences via differential survival and/or reproduction (see Dukas 2004 for a recent review).

Hummingbirds might be expected to exhibit adaptive specializations in their spatial memory because of their foraging ecology (Healy & Hurly 1995; Hurly 1996). For example, hummingbirds hold and defend actively their food sources or territories. They perform many visits to flowers during a day of activity, and they can forage in different flowers separated by large distances (Feinsinger & Colwell 1978; Garrison & Gass 1999). The use of learning and memory can benefit hummingbirds because flowers are highly variable in many aspects, including shape, nectar quality and quantity, color, and nectar renewal rate, among others (Hurly & Healy 2003). In addition, the energetic cost of hovering demands the consumption of enormous amounts of nectar, which is scattered in hundred of flowers (Gass et al. 1999). A hummingbird returning to a recently emptied flower can experience a lower rate of energy gain than a bird landing in renewed flowers (Cole et al. 1982). Therefore, spatial memory is expected in hummingbirds in order to avoid depleted flowers (Cole et al. 1982; Hurly 1996). Moreover, hummingbirds use artificial feeders readily, allowing field observations with no apparent disturbance of their behavior, making them excellent subjects from an experimental viewpoint (Hurly & Healy 2003).

Hurly (1996) studied one trial associative learning in rufous hummingbirds *Selasphorus rufus* by assessing the ability of birds to recall the location of a reward after a single learning experience. In the present study, we carried out a similar field experiment with the green-backed firecrown hummingbird (*Sephanoides sephaniodes*), but we also went one step further. We first carried out an experiment similar to Hurly's (1996) study and evaluated the ability of hummingbirds to recall the spatial position of a previously experienced non-depleted reward, among rewarding and non-rewarding flowers. In a second experiment, we increased realism taking into account that at the study site, flower nectar varies up to fourfold in sugar concentration, and all flowers contain sugars in their nectars (Smith-Ramirez 1993). Therefore, in the second experiment we assessed the ability of hummingbirds to remember the best reward location (i.e. the flower with the highest concentrated nectar) among several less rewarding flowers (i.e. with less concentrated nectar), with identical visual cues among all feeders. We also compared the performance of birds between both experiments. If hummingbirds can retain the location of the best feeder, the number of visits needed to reach the best nectar in the second phase of each experiment should be significantly lower than the number of visits in the first phase of each experiment. On the other hand, if hummingbirds are equally efficient to retain the location of the best feeder either among water feeders or among feeders with less concentrated nectar, we expected no difference between the number of visits in the second phase of the experiments.

Methods

Species and Study Site

The study was carried out in July and August 2003 in a field site located in the Andean foothills within the Estación de Investigaciones Ecológicas Mediterráneas of the Pontificia Universidad Católica de Chile, San Carlos de Apoquindo, central Chile (33°23′S, 70°31′W, 1100 m a.s.l.), around 20 km east from Santiago. The study site is comprised by sclerophyllous vegetation known as matorral and physiognomically can be described as an evergreen scrub.

Subjects were free-living male green-backed firecrown hummingbirds, which had feeding territories in the study site (see below) and actively defended territories. We randomly selected 20 territories for our experiments. We could rely on their natural marks as well as their conspicuous territorial behavior to identify different subjects. The subjects that were used for the analysis were those birds that were visible all the time during the trials. As this species defend territories aggressively, and because territories are of small size (around 200 m^2), we decided to study a subject's behavior within a half-day of activity, and only when a subject could be followed entirely through his feeding territory by an observer. Therefore, trials were run between 8:00 and 12:00 hours. The aggressive display consisting of chases around the feeder accompanied with a distinctive shrill sound. Further, on a given day, we selected territories that were at least 40 m apart from each other. If during a trial, we lost track of a subject, we ended the trial and these data were not used in the analysis. Observations were carried out from hidden places (behind vegetation) at least 10 m from the feeder.

Initial Training

The experiments comprised a training period in which the subjects got used to the feeders, and defended them actively as part of their territories. For this, we placed training feeders that contained 200 ml of 25% sucrose in 20 different trees 5–15 m

high (tree species: *Quillaja saponaria*, *Litrea caustica*, *Eucalyptus globulus*) located in distinct territories where we had previously observed feeding hummingbirds. Nectar feeders where located at 1.5 m above the ground in a randomly selected branch. Within 2 d of training, males defended feeders actively as part of their territories; only one dominant male per feeder was observed. An artificial feeder consisting of a commercial 100 ml glass water dispenser for squirrels enveloped with red paper. Each feeder was filled twice a day in order to prevent for resource depletion and the eventual loss of territorial defense.

Experimental Protocol

For the spatial memory task, we constructed a 50×50 cm wooden frame with a middle vertical axis (Fig. 1). The six intersections of the wooden axes comprised a 6-point grid where feeders were located. The grid was placed vertically in a tree in the same position where we had observed a focal subject previously feeding from the training feeder. During the experiments, only four points in the grid had feeders. For each trial, four identical feeders were assigned to four randomly chosen points among the six points of the grid (see Fig. 1). Feeders had identical visual cues (i.e. color, size, material).
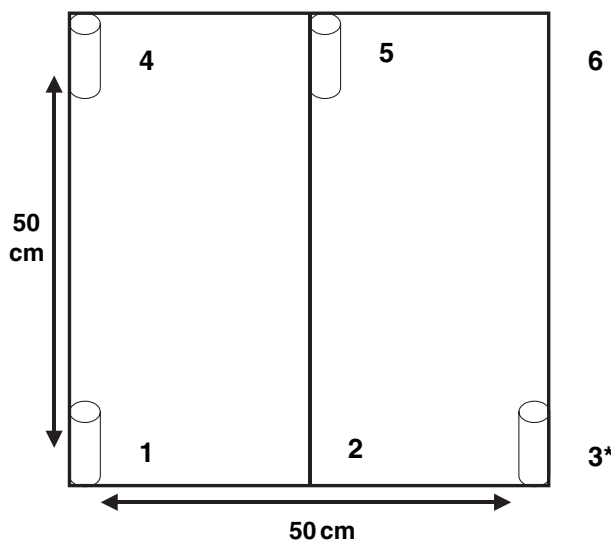

Fig. 1: Experimental vertical grid. Numbers indicate six feeder locations. Only four positions (i.e. four feeders) were used in each experiment [four feeders (tubes) are shown as an example]. *High quality nectar feeder

The experiments were designed to assess the ability of birds to remember the position of a rewarding flower among non-rewarding (first experiment) or low-rewarding (second experiment) flowers after a single learning experience (see below). At the beginning of each trial, each feeder contained 100 ml of sucrose liquid, in order to prevent for nectar depletion. A visit was defined as a subject inserting its bill in the feeder. We performed six trials with each subject during a given morning. A trial had two phases: in the first phase (search phase), the hummingbird probed the feeders until it discovered the most rewarding feeder. A hummingbird was allowed to feed from it until it stopped spontaneously. After this, the observer did not allow revisits to the grid, by staying nearby the feeder and maintaining the subject away from the feeders for 5 min. Animals were observed in the territory within this 5-min interval and they quickly return to the experimental grid after the observer left to the hide. In order to prevent that the bird could recognize the nectar feeder by some uncontrolled visual cue, the target feeder was changed by a similar one with the same sucrose concentration. In the second phase (returning phase), the hummingbird faced the same array of feeders, searching until it discovered the most rewarding feeder. After finishing the visit to the rewarding feeder, the trial was ended, and the following trial was initiated after 10 min. A new position for the rewarding feeder in the next trial was randomly selected.

In the first experiment conducted in July 2003, we examined the ability of each bird to find a rewarding feeder (25% w/w sucrose) among three non-rewarding feeders (filled with water). At the beginning of a trial, the four feeders were randomly located in the grid. In this experiment we used 15 subjects.

In the second experiment, conducted in August 2003, we used 13 subjects. This experiment was aimed to assessing individual and average performance of green-backed firecrown hummingbirds in a more realistic task, because subjects had to find and remember the location of the feeder with the best quality nectar among another three feeders with poorer quality nectar. In the experimental trials, one of the four randomly placed feeders had high quality nectar (30% w/w sucrose), and the other three feeders had poor quality nectar (10% w/w sucrose).

In both experiments, we also assessed the average (i.e. the mean of all individuals in each experiment) and the individual ability of hummingbirds to recall the position of the best feeder in the return phase of trials.

Data Analysis

Differences between the averages of individual number of visits in both phases of each experiment were assessed through a Friedman Test with multiple observations per cell (Zar 1998). The average performance between experiments was assessed through a Mann–Whitney test. Statistical analyses were performed using the software STATISTICA 6.0.

Results

In the first experiment, the number of visits carried out until the nectar feeder was found in the first phase of the experiment (i.e. search phase, 2.94 ± 0.10 visits, mean $\pm$ SE, n = 15) was significantly higher than the number of visits in the second phase of the experiment (i.e. return phase, 1.31 ± 0.08, n = 15; Friedman Test $\chi_r^2 = 32.75$, p < 0.001). At the individual level, 12 of 15 subjects performed lower number of visits in the return phase (Fig. 2). Some birds revisited flowers within trials, but only in the first phase of the experiment. These data were included in the analysis.

In the second experiment, the number of visits in the search phase (2.91 ± 0.13, mean $\pm$ SE, n = 13) was significantly higher than in the return phase (1.53 ± 0.09, n = 13, Friedman Test, Friedman's $\chi_r^2 = 27.328$, p < 0.01). Individually, in the return phase, eight of 13 subjects showed the ability to find
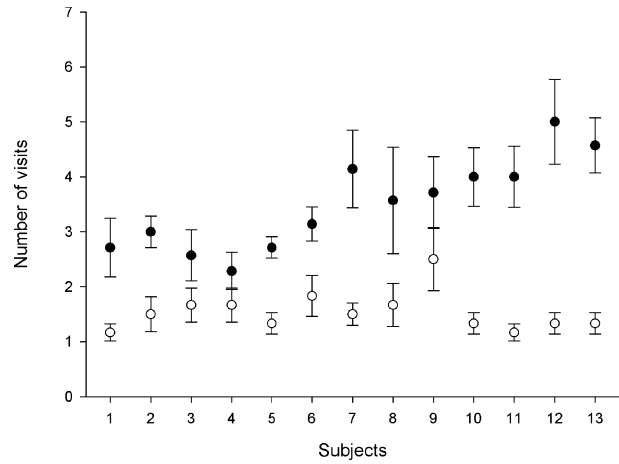

Fig. 3: Number of feeding visits performed by individuals of individual performance of green-backed firecrown hummingbirds in the second experiment. Black dots, search phase and white dots, return phase (mean $\pm$ SE, n = 6 trails for each subject)

the best nectar location in lower number of visits, in comparison with the search phase (Fig. 3).

On average, the number of visits performed by hummingbirds in the return phase of the first experiment was significantly lower than the number of visits in the return phase of the second experiment (Mann–Whitney test, U = 50, n = 28, p = 0.025; Fig. 4). We did not find significant differences between the performances of birds in the search phases of both experiments (Mann–Whitney test, U = 94, n = 28, p = 0.87; Fig. 4).
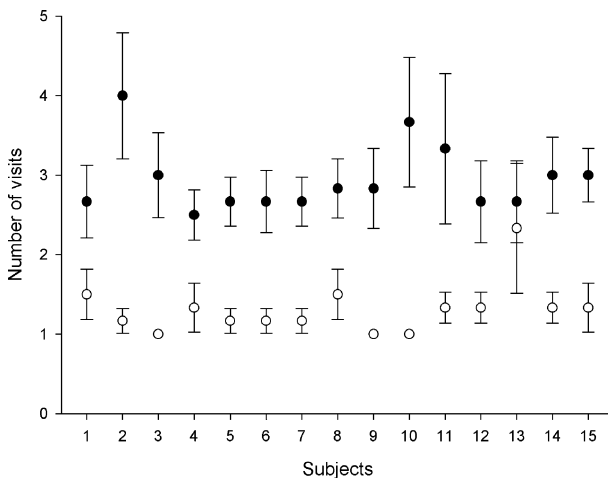

Fig. 2: Number of feeding visits performed by individuals of green-backed firecrown hummingbirds in the first experiment. Black dots, search phase and white dots, return phase (mean $\pm$ SE, n = 6 trials for each subject)
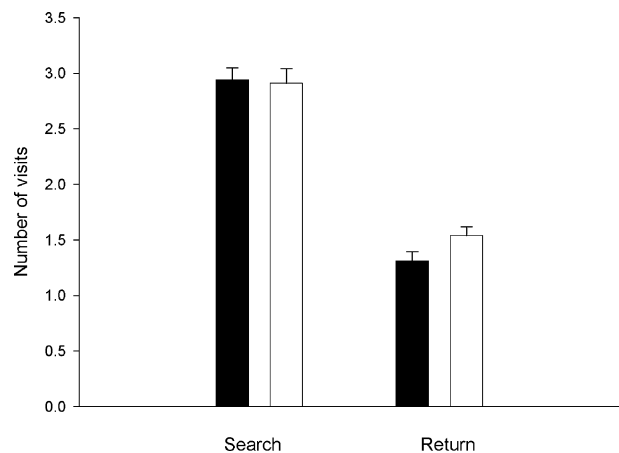

Fig. 4: Average performance per individual across experiments. The search phase between both experiments are not significantly different; however; the return phase in the first experiment (black bars) is significantly lower than in the second experiment (white bars; mean $\pm$ SE). See text for statistics (p < 0.05**)

Discussion

The smaller number of visits in the return phase of both experiments suggest that hummingbirds can recall the best nectar location among poorer flowers with identical visual cues. These results are consistent with other field and laboratory tests of spatial memory in hummingbirds. For instance, studies in Rufous hummingbirds (*S. rufus*) showed consistently that hummingbirds, in the presence of identical visual cues, revisited rewarding sites and avoided non-rewarding ones (Cole et al. 1982; Henderson et al. 2001) and distinguished among flowers that had been visited but were not totally depleted (Hurly & Healy 1996). Other studies have shown that even conspicuous changes to the visual aspect of artificial flowers do not affect the bird preference (Miller et al. 1985; Hurly & Healy 2002). The most consistent finding in hummingbirds foraging is that they pay much more attention to the spatial location of a flower rather than to visual cues (Healy & Hurly 1998; Hurly & Healy 2003). Therefore, available information suggests that hummingbirds use information gathered during previous visits (Pyke 1981; Wolf & Hainsworth 1990), rather than the automatic use of a visual attractor or a simple decision rule (Hurly & Healy 2003). This may be the result of the relative familiarity of spatial location in the presence of identical visual cues (Braithwaite & Newman 1994; Burt et al. 1997). The relative location of the feeder may be used to relocate the best resource instead of the feeder itself. In addition, because the last feeder visited in the search phase prior to the retention interval is the most rewarding feeder, in terms of time elapsed, the rewarded feeder is the relatively most familiar one. This suggests that relative familiarity could be an important factor guiding the spatial behavior of hummingbirds.

On the other hand, studies in food-storing birds reveal that they can recall information about the spatial location as well as the content (quality) of cache sites (Sherry 1985; Clayton & Dickinson 1999; Clayton et al. 2001). The average performance observed in the second experiment suggests that hummingbirds can recall a preferred option among several less rewarding options; however, less efficiently. Territorial intrusions cannot explain the differences in foraging efficiency observed between the first and the second experiment because we observed these territorial challenges during both experiments. Results suggest, however, that the poorer performance in finding the most rewarding nectar is observed when birds face different patch qualities.

In standard learning protocols such as the radial arm maze, animals are submitted to deprivation before the beginning, and subjects are allowed to probe all the rewarded sites before the initiation of the experimental trials (see e.g. Olson & Samuelson 1976). Furthermore, in laboratory experiments, most animals have no other activities that can interfere with their memory for rewarding sites. Field experiments differ in all these conditions. In fact, during the experiments, hummingbirds were involved in several other activities such as territorial defense, antipredator vigilance, foraging in natural patches, among others. Previous field tests of spatial memory have examined the performance of individuals facing rewarding vs. non-rewarding patches only (e.g. Hurly 1996). In the second experiment of our study with more realistic conditions, where only the quality of the resource was variable but all patches were rewarding to some level and visually identical, the efficiency to find the most rewarding resource decreased. However, the most rewarding patches were still preferred showing that *S. sephaniodes* can remember the location of the most rewarding patch in an experiment in the field. This demonstrates that spatial memories can facilitate efficient exploitation of flowers in the absence of visual cues related to nectar quality.

Acknowledgements

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