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# Elements of episodic-like memory in free-living hummingbirds, energetic consequences

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Episodic memory has been described as the ability to recall personal past events, involving what, where and when an event has been experienced. Cognitive abilities like learning and memory are pivotal to the performance of many behavioural traits such as food procurement. Nectar, the primary food of hummingbirds, is dispersed in hundreds of flowers and varies in concentration and renewal rate. Therefore, a hummingbird that can remember elements of episodic-like memory such as what, where and when the nectar becomes available will have a higher energy rate of intake when compared to random foraging. We conducted a field experiment with green-backed firecrown hummingbirds, *Sephanoides sephaniodes*. We assessed the ability to recall the location, nectar quality and renewal rate of the most rewarding flowers among several less rewarding flowers with identical visual cues. Hummingbirds were able to remember the most profitable nectar sources and flower position and adjust their visits to nectar renewal interval. Cognitive performance varied among individuals, implying up to 6.3-fold differences in energy gain. Our results strongly suggest that hummingbirds use cognitive abilities to exploit nectar sources efficiently and, therefore, that cognitive abilities are potentially tied to survival probability.

Episodic memory has been described as the ability to recall personal past events, involving what, where and when an individual event has been experienced (Tulving 1972, 2002). The integrated representation of these elements implies that when one element is recalled (e.g. when), the other elements (what and where) are also brought to the present and must be flexible to the acquisition via learning of new information in novel situations (Schwartz & Evans 2001; Clayton et al. 2003). Clayton & Dickinson (1998) provided the first evidence of elements of episodic memory in nonhuman animals, showing that scrub-jays, *Aphelocoma coerulescens*, storing different food items have the ability to remember what (food type), where (location in the tray) and when (time of caching and recovery). In later experiments those authors demonstrated that scrub-jays have a detailed representation of these elements (Clayton & Dickinson 1998, 1999a, b; Clayton et al. 2001, 2003). As nonhuman animals are unable to verbally express subjective experiences, the concept of ‘episodic-like memory’ was introduced (Clayton & Dickinson 1998) to emphasize that behavioural criteria do not assess subjective experiences; instead, the concept is focused on the content of memory (i.e. knowledge of what, where and when a unique event occurred; see Crystal 2009).

The ecology of diverse species strongly suggests that elements of episodic memory should be present and tied to foraging or reproductive necessities (Clayton & Dickinson 1998; Emery & Clayton 2001). Nectarivorous animals such as hummingbirds experience patches of resources containing nectar with different characteristics that are not assessable through visual cues (Irwin 2000). Nectar is dispersed in hundreds of flowers and varies in concentration, composition and renewal rate. In addition, hummingbirds are excellent candidates to possess episodic-like memory because of the complex energetic scenario that they experience. The high energetic cost of hovering demands the consumption of relatively large amounts of nectar, which is scattered among hundreds of flowers (Gass et al. 1999). Therefore, a nectarivorous animal should remember where and when the best nectar (i.e., what) will be available to forage most efficiently (Henderson et al. 2006). This means performing the lowest number of visits to decrease the travel

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cost, decrease predation risk and simultaneously obtain the highest energy reward. A hummingbird returning to a recently emptied flower can experience a lower rate of energy gain compared to that of exploiting a renewed flower (Henderson et al. 2006). Consequently, cognitive abilities are expected in hummingbirds in order to avoid visiting depleted flowers (Cole et al. 1982; Hurly 1996).

Preliminary studies showed that hummingbirds can recall the highest sucrose concentration among energetically poorer nectar resources (Blem et al. 2000; González-Gómez & Vásquez 2006). These studies suggest that hummingbirds are capable of remembering what was consumed. In addition, hummingbirds consistently visit locations that offer a reward and avoid nonrewarding sites (Cole et al. 1982; Gass & Sutherland 1985; Healy & Hurly 1998), distinguishing between visited and not totally drained flowers (Hurly & Healy 1996) (i.e. hummingbirds are able to remember where to forage). Moreover, hummingbirds can match their visits to renewal nectar rates, remembering when the nectar is available (Gill 1988; Henderson et al. 2006; González-Gómez et al. 2011). Thus, different studies suggest that hummingbirds could accomplish the three aspects of learning that fulfil a general definition of episodic-like memory (Henderson et al. 2006).

In the present study we conducted a field experiment with free-living nonreproductive males of the green-backed firecrown hummingbird, *Sephanoides sephaniodes*. We evaluated cognitive performance as the ability to remember the information acquired in past individual events (i.e. training period) and to apply it to novel situations (i.e. experimental trials). We assessed their ability to remember the location, nectar quality and renewal interval of the most rewarding artificial flower (i.e. the flower with the highest nectar concentration) among several less rewarding artificial flowers (i.e. less concentrated nectar) with identical visual cues. If hummingbirds can remember the location of the best flower, the number of visits needed to reach the best nectar in repeated trials (return phase of experiments) should be significantly lower than the number of visits in novel trials (search phase of each experiment). Thus, they should visit the high-quality nectar feeders when nectar is available. If cognitive performance has energetic consequences, hummingbirds that can recall the best nectar location and renewal interval should obtain a higher rate of energy gain than individuals with poorer performance.

## METHODS

### Study Site and Subjects

The study was conducted during the Austral winter (2008) in a field station 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 elevation). Subjects were free-living male green-backed firecrown hummingbirds (mean ± SE mass = 6.3 ± 0.08 g), which had feeding territories in the study site (see below) and actively defended territories against males and females. We randomly selected 12 territories for our experiments. We identified individuals mainly by their conspicuous territorial behaviour. Green-backed firecrown hummingbirds are extremely aggressive, performing notorious chases against other males and females in the nonreproductive season (González-Gómez & Vásquez 2006; González-Gómez & Estades 2009). Males defend territories of up to 200 m$^2$ and use two to three perches within their territory near the defended main resource (i.e. feeder; P. L. González-Gómez, personal observation). Differences in crown feathers were also visible on two males in this study (i.e. one or two lost feathers). The subjects used for the analysis were those birds that were visible continuously during and between the trials. If we lost track of a subject during a trial, we ended the trial and excluded the subject's data from the analysis. Trials were run between 0800 and 1300 hours. Observations were conducted from hidden places (behind vegetation) at least 10 m from the feeder.

### Initial Training

The experiments began with a training period in which the subjects got used to the feeders and defended them actively as part of their territories. We placed training feeders in 12 trees (*Quillaja saponaria*, *Lithrea caustica*, *Eucalyptus globulus*) 5–15 m high located in distinct territories where we had previously observed feeding hummingbirds. Nectar feeders were hung 1.5 m above the ground from a randomly selected branch. Within 2 days of training, males defended feeders actively as part of their territories; only one dominant male per feeder was observed. An artificial feeder consisted of a commercial 100 ml glass water dispenser for squirrels surrounded with red paper. Each feeder was filled with 100 ml of 20% (weight/weight) sucrose twice per day to prevent resource depletion and the consequent eventual loss of territorial defence (González-Gómez & Vásquez 2006).

#### Nectar quality training

On the day of the experiment, to show to the focal subject that there were two nectar qualities in its territory, we replaced the training feeder with a vertical grid with two feeders (Fig. 1a), one of them filled with 100 ml of 15% weight/weight sucrose (low quality) and the other one filled with 100 ml of 30% w/w sucrose (high quality). The quality of each feeder was randomly selected. The feeders were identical to training feeders. The grid consisted of a 50 × 50 cm wooden frame with a middle vertical axis. We maintained this array for 30 min or until the grid was defended as a part of the territory and the subject had visited both feeders.

#### Temporal training

Following the nectar quality training we presented hummingbirds with nectar schedules associated with nectar quality, by replacing the previously used grid with an identical vertical grid but with one artificial flower in the bottom of each of the two feeders (Fig. 1b). The addition of one artificial flower allowed us to present hummingbirds with quantities of nectar small enough to be consumed in one visit. Each artificial flower was an orange syringe tip with red paper petals mounted horizontally in an empty training feeder (Fig. 1c). The flower contained 60 μl of nectar. The high-quality flower (i.e. 30% sucrose) was refilled every 10 min after it was drained. The low-quality flower (i.e. 15% sucrose) was refilled every 5 min. Artificial flowers were filled manually. To prevent hummingbirds from using the filling bouts as a visual cue of nectar renewal interval, we randomly performed five pretence fillings per hour. During pretence fillings, the observer went through the motions of refilling the flowers without actually doing so at time points inconsistent with the assigned nectar replenishment schedule. A visit was defined as a focal individual inserting its bill into the artificial flower. We maintained the temporal training for 1 h or until the last three visit intervals of the subject did not differ from the nectar replenishment interval (see below).

### Experimental Protocol: Testing Elements of What, Where and When

The experiment was designed to assess the ability of birds to remember the position and renewal interval of a high-rewarding flower among low-rewarding flowers after a single learning experience (i.e. search phase, see below). The subject had to combine information acquired during the training about nectar renewal intervals associated with nectar quality and apply these memories

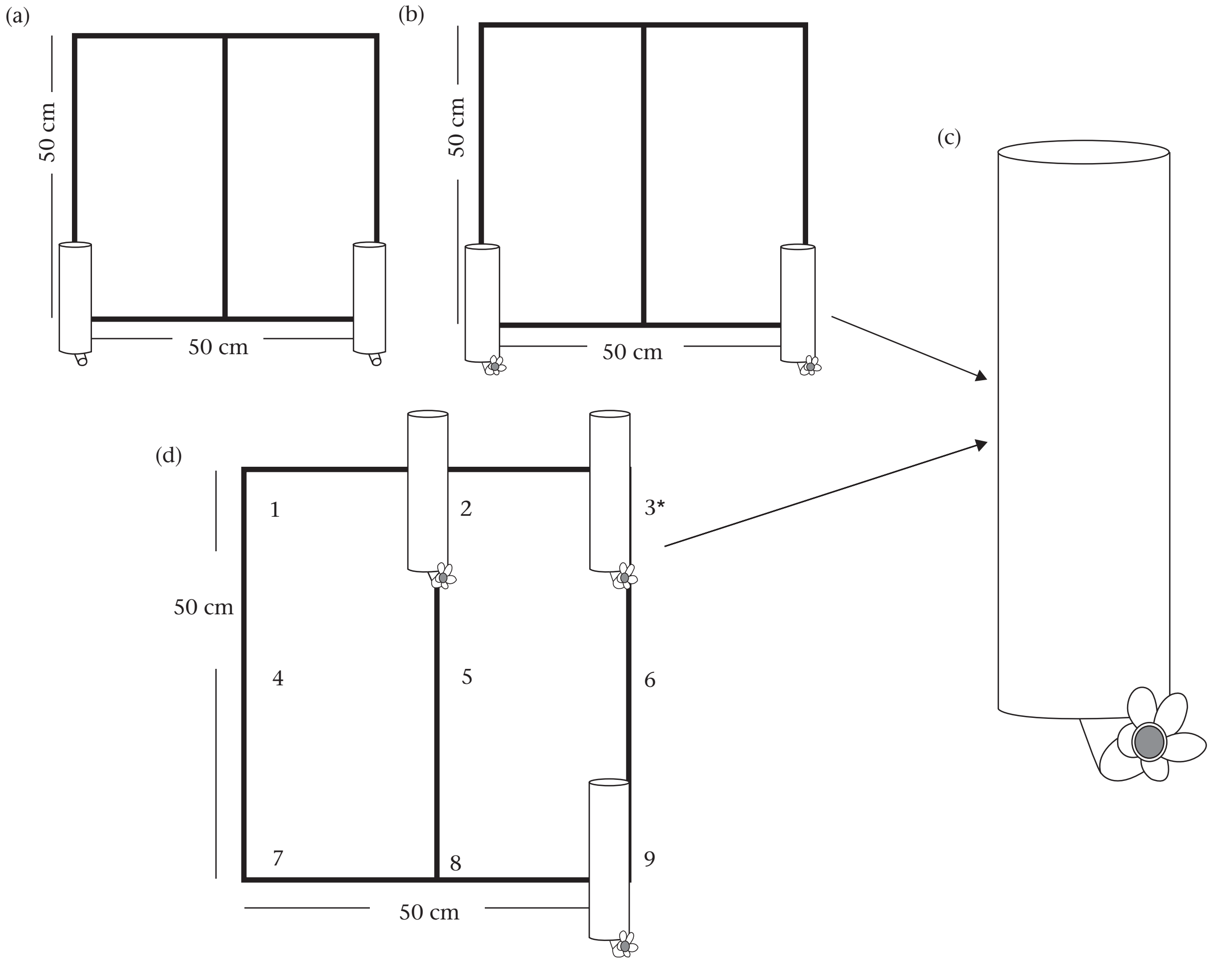

**Figure 1.** (a) Diagram of the experimental set-up used in the nectar quality training. Each feeder contained 100 ml of high- or low-nectar quality. (b) Diagram of the experimental set-up used in temporal training. Two artificial flowers, mounted on empty feeders, with different nectar qualities and different nectar renewal intervals were attached to the experimental grid. (c) Enlarged image of artificial flowers used in the temporal training and in the test of elements of what, where and when memory. (d) Diagram of the experimental set-up used to test the ability of hummingbirds to recall where and when the best nectar (what) was available. Numbers indicate nine flower locations. Only three positions (i.e. three flowers mounted on empty feeders) were used in each experiment (three flowers are shown as an example). *Indicates position of high-quality artificial flower.

to a new situation (i.e. return phase, see below). Following the temporal training we replaced the grid with a new 50 × 50 cm wooden frame with a middle vertical axis (Fig. 1d). We identified nine points in the new grid where artificial flowers could be located. The artificial flowers consisted of an orange syringe tip with red paper petals mounted horizontally in an empty training feeder (Fig. 1c). The flower contained 60 μl of nectar. We performed six trials with each subject during a given morning. A trial had two phases; in the first phase (search phase), the hummingbird was free to visit the flowers until it fed from the most rewarding flower and left the grid. In the second phase (return phase), the hummingbird faced the same array of feeders. The second phase started when the hummingbird visited the grid again and ended when the bird left the grid. For each trial, three flowers were assigned to three randomly chosen points among the nine points of the grid (i.e. only three points in the grid had flowers). At the beginning of each trial, every flower contained 60 μl of sucrose liquid. One of the flowers was randomly chosen as the high-quality nectar flower (i.e. 30% sucrose) and was refilled every 10 min after it was drained. The others two flowers were low-quality nectar flowers (i.e. 15% sucrose) and were refilled every 5 min. Artificial flowers were filled manually. To prevent hummingbirds from using the filling bouts as a visual cue of nectar renewal interval, we performed the same procedure described above at least three times during the trials.

For each trial we recorded the number, position and quality of visited feeders and the time elapsed between both phases of the experiment (i.e. revisit time). After finishing the return phase, the trial was ended and the following trial was initiated after 10 min. A new position for all flowers was randomly selected.

### *Ethical Note*

All protocols were conducted according to Chilean laws, legal permits and the ethical committees of our Universities.

## RESULTS

We lost track of two subjects during trials; therefore, we ended the trial and excluded the data from the analysis. All subjects ($N = 10$) were successful in the territory defence. In each trial, the territorial male was the only subject that consumed the nectar.

During temporal training, each subject visited the low-quality feeder (mean $\pm$ SE $= 6.1 \pm 0.42$ visits, range 5–8 visits) and the high-quality feeder ($8.2 \pm 0.34$ visits, range 7–10 visits). To compare the inter-meal interval among the high- and low-quality feeders, we calculated the time between the last three visits in which the low-yield flower was visited and compared this value to the time between the last three visits in which the high-yield flower was visited. The mean inter-meal interval of the last three visits was significantly longer when subjects were visiting the high-quality feeder (mean ± SE = 10.33 ± 0.26 min, $N = 30$) than when were visiting low-quality feeders (5.7 ± 0.96 min, $N = 30$, repeated measures ANOVA: $F_{1,18} = 55.27$, $P < 0.001$). Performance did not differ significantly between individuals (repeated measures ANOVA: $F_{2,36} = 0.50$, $P = 0.61$). The time intervals of the three last visits to the high-quality feeder and to the low-quality feeder did not differ significantly from the respective replenishment intervals of the feeders (one-sample $t$ test against 10 min: high-quality feeder: $t_9 = 1.98$, $P = 0.07$; one-sample $t$ test against 5 min: low-quality feeder: $t_9 = 1.66$, $P = 0.13$).

During testing, we evaluated each hummingbird's ability to recall the component 'where' (the location where the best nectar was available) by comparing the averages of the number of feeders visited by each individual in both phases of the experiment. Hummingbirds visited significantly more feeders in the search phase (mean ± SE = 2.33 ± 0.14 feeders, $N = 10$) than in the return phase (1.1 ± 0.05, $N = 10$; Friedman test: $\chi^2_{r,\ 1,9} = 18.03$, $P < 0.001$). Individually, 8 of 10 subjects found the best nectar location in fewer visits during the return phase than during the search phase (Fig. 2).

During the return phase of the experiment, hummingbirds made significantly more visits to the feeder containing high-quality nectar as a first option (one-sample proportion $z$ test against 0.5: $z = 7.86$, $N = 46$, $P < 0.01$) than they did to feeders containing low-quality nectar (one-sample proportion $z$ test against 0.5: $z = 9.26$, $N = 14$, $P < 0.01$). Mean revisit time to high-quality feeders was significantly longer than that to low-quality feeders in the return phase (mean ± SE = 8.97 ± 0.59 min versus 5.52 ± 0.94 min; repeated measures ANOVA: $F_{2,8} = 110$, $P < 0.01$; Fig. 3). Revisit intervals of eight individuals to high-quality feeders did not differ significantly from the high-quality renewal interval (Fig. 3). Similarly, revisit intervals of two individuals to low-quality feeders did not differ significantly from the low-quality renewal interval (Fig. 3), suggesting that individuals that successfully remembered the nectar quality and location also accurately recalled the nectar availability schedule. We assessed within-bird variability of visits to feeders of high and low quality by subtracting the return times for each bird to each type of feeder from the respective feeder renewal intervals (10 min and 5 min, respectively). We took the absolute values of these differences and averaged them together. We then paired these values with the number of trials in which the high-quality feeder or the low-quality feeder was visited as a first option in the return phase. The absolute difference between the return visit time of each bird to the nectar renewal interval (i.e. 10 or 5 min) was marginally related to the number of times in which the quality (high or low) was chosen as the first option in the return phase by every subject (simple regression: $R^2 = 0.2$, $F_{1,16} = 3.70$, $P = 0.072$), suggesting that individuals that visited one feeder quality more frequently tended to remember more exactly the time when this nectar quality was available.

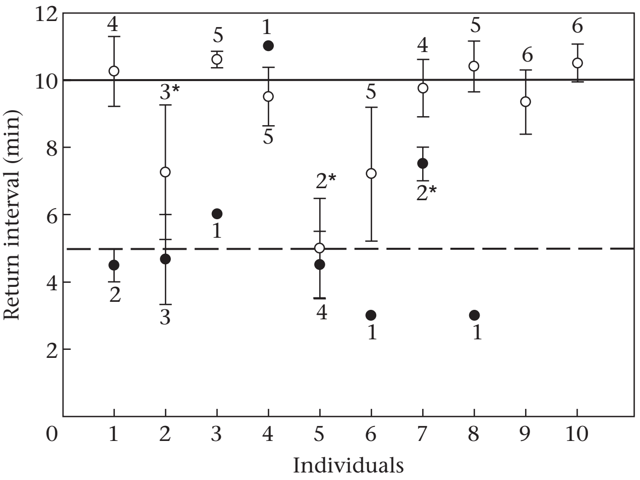

**Figure 3.** Mean ± SE return intervals of green-backed firecrown hummingbirds to high-quality (○) and low-quality (●) feeders between the search and return phase of the experiment. Number of visits to both nectar qualities is shown. Solid line: renewal interval of high-quality nectar feeders; dashed line: renewal interval of low-quality nectar feeders. *Return interval differed significantly from the nectar renewal interval, 1000 bootstrap sampling (95% CI: 8.94–10.22 min). Birds 3, 4, 6, 8, 9 and 10 made too few visits to low-quality feeders for comparison with the nectar renewal interval. Individuals 9 and 10 did not visit the low-quality feeders in the return phase of the experiment.

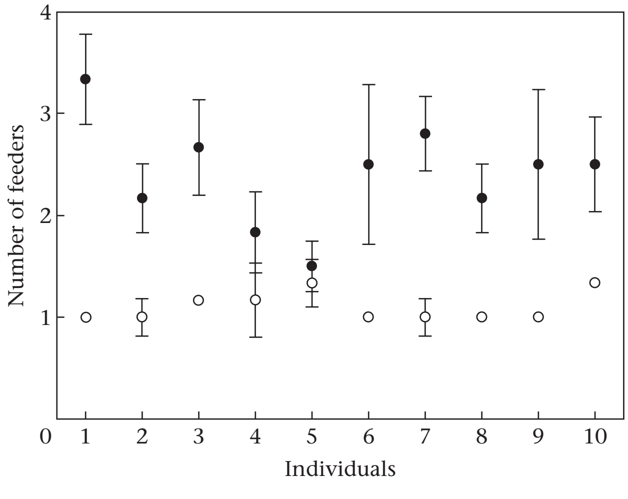

**Figure 2.** Mean ± SE number of feeders visited in the search phase (●) and in the return phase (○) of the experiment testing the ability of green-backed firecrown hummingbirds to recall what, where and when ($N = 6$ trials).

The sum of nectar obtained in the return phase, transformed to energy units (joules, hereafter, J), was 2.98 times higher in individuals that made return visits to the high-quality nectar resources in the time when nectar was available (mean ± SE = 1435.05 ± 135.33 J, $N = 8$) compared to individuals that were not able to track the best-quality nectar location and availability (481.5 ± 167.1 J, $N = 2$, individuals 2 and 5; Mann–Whitney $U$ test: $U = 0.00$, $P < 0.05$; Fig. 4).

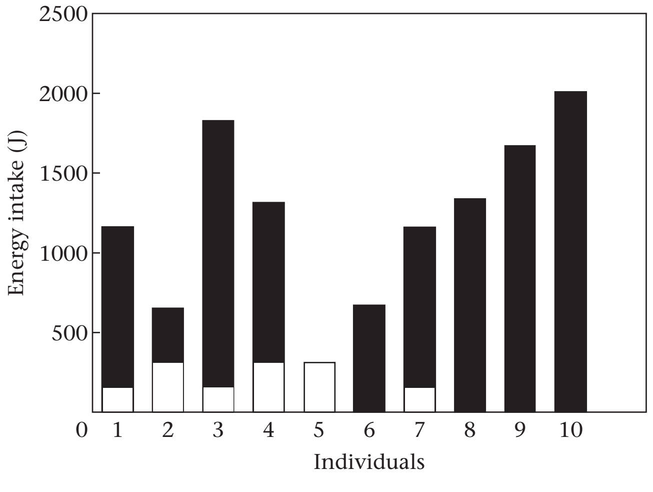

**Figure 4.** Total energy obtained (J) by green-backed hummingbirds in the return phase of the experiment (sum, $N = 6$ trials for each subject). Individuals were assigned to one of two groups depending on their ability to match their return visits to the nectar replenishment schedule (see text). □: energy obtained from low-quality nectar; ■: energy obtained from high-quality nectar.

Furthermore, the individual that had the best performance (individual number 10; see Fig. 4) obtained 6.3 times more energy than the individual with the poorest performance (individual number 5).

## DISCUSSION

Free-living hummingbirds showed the ability to recall where and when the best nectar sources (i.e. what) were available and match their foraging visits accordingly. Both the smaller number of flowers visited in the second phases of the experiments and the coincidence between foraging visit intervals and nectar renewal intervals strongly suggest that hummingbirds use cognitive abilities to exploit nectar sources efficiently. As far as we know, this is the first demonstration that free-living hummingbirds can remember in a single experiment three main elements of episodic memory. Although we cannot ascribe autonoetic consciousness (i.e. conscious experience of self) to hummingbirds, since they do not have the ability to express their experience verbally (Tulving & Markowitsch 1998), our results show that hummingbirds can remember elements of what, where and when something has occurred (Schwartz & Evans 2001; Clayton et al. 2003).

Our experiment resembled conditions that hummingbirds experience in natural environments. For example, if nectar is not eaten, it is reabsorbed by the flower (Nicolson 1995) or consumed by an intruder. We avoided testing artificial situations such as degraded nectar, which is mostly nonexistent in nature, despite losing accuracy to detect the internal mechanism acting in the memory process. On the other hand, we could not control the strengthening of semantic memory when we tested the ‘what’ component. Under ideal conditions the animal is presented with two kinds of food having the same energetic value but different tastes, and both food types are equally liked. The animal is pre-fed with one type. If the animal can remember ‘what’, then it will choose the not-pre-fed food (Clayton & Dickinson 1999a, b). In nature, it is possible to find different nectars having the same energetic value but different tastes; however, this characteristic is linked with nectar composition (Nicolson & Fleming 2003; Fleming et al. 2004). Flowers pollinated by hummingbirds produce sucrose-enriched nectars, and hummingbirds strongly prefer this kind of food over fructose-enriched nectars (Martínez del Río 1990; Fleming et al. 2004). Therefore, it is not possible to find two equally preferred foods of different tastes to test the strength of semantic memory under natural conditions. Instead, we tested the ‘what’ component with different nectar qualities, a well-known component of hummingbird-pollinated plants.

The strongest argument for episodic-like memory is that the average return time was longer (across birds) when hummingbirds visited the high-quality feeder first. Since the feeders were randomly arranged in every trial, it is possible that just one feeder (i.e. the high-quality feeder) was visited, and therefore, that the search phase ended before the low-quality feeders had been visited. In this case, birds that returned early would have visited the feeder that they knew would still contain food, because they had not emptied it yet.

The ‘just one visit’ case in the search phase occurred in 13 of 60 trials. However, in nine cases, the subjects visited just one feeder in the return phase: the high-quality feeder. In two trials, the subjects visited one of the untouched low-quality feeders and then the high-quality feeder, and in just two trials, the subject visited the high-quality feeder in the search phase and one of the untouched low-quality feeders in the return phase.

As Henderson et al. (2006) suggested, episodic-like memory should be a part of the daily life of a nectarivorous territorial individual. It is supposed that nectarivorous animals should be able to keep track of the best nectar sources and remember the location and nectar availability schedules in order to increase the rate of energy gain. In fact, our results integrate into a single study numerous previous experiments showing that hummingbirds can recall the nectar quality (Blem et al. 2000), location (Hurly & Healy 1996) and more recently, nectar renewal rates (Gill 1988; Henderson et al. 2006).

We found an important variability in spatial and temporal cognitive abilities among individuals. This variability did not differ from that previously reported by González-Gómez and Vásquez (2006) and González-Gómez et al. (2011). In both studies, approximately 20% of individuals performed worse than the rest of the studied birds. One possible explanation is the existence of different strategies in the population. Risk aversion, territory defence costs and/or the number of competitors could influence individual foraging performance, but these factors were not assessed in those studies. Because cognitive ability is strongly tied to nectar reward in hummingbird foraging ecology (Gass & Sutherland 1985; Healy & Hurly 2003), differences in cognitive ability may be closely related to differential fitness. In hummingbirds, foraging success is vital because of the extremely high mass specific rates of aerobic metabolism (Suarez 1992; Suarez & Gass 2002). In addition, green-backed firecrowns experience winter temperatures below −5 °C, at which the cost of thermoregulation is roughly 5.2 times basal metabolic rate (López-Calleja & Bozinovic 1995), representing a challenging energetic scenario. Although hummingbirds could use strategies to save energy (e.g. through torpor), the ability to maintain body mass could be a trait directly related to fitness (e.g. affecting survival), especially during periods of high energetic demand and high thermoregulatory costs (Hainsworth 1978). If territorial males have the ability to recall sugar content and the location of flowers and they have the ability to predict when a flower will offer the maximum quantity of nectar, they will increase their foraging opportunities and, therefore, their chances of surviving a harsh winter.

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