

Chapter 10

Perspectives on the Study of Field Hummingbird Cognition in the Neotropics



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10.1 Introduction

Cognitive abilities such as learning and memory are critical for the performance of behavioral traits strongly linked to fitness (Balda et al. 1998). In fact, many species depend on learning and memory abilities to perform mating displays which involve ritualized movements and songs, where the quality of this copy is directly related to the number of offspring (Araya-Salas and Wright 2013; Boogert et al. 2011). Furthermore, cognitive abilities could act as a buffer against environmental unpredictability, facilitating resource exploitation, and exploration of new resources (Pravosudov et al. 2015). For example, animals inhabiting harsh environments use their cognitive abilities seasonally to survive energetically demanding life cycles (Krebs et al. 1989). Every winter when the food is not abundantly available and also unpredictable, scatter-hoarding avian species rely on their memory abilities to retrieve as many as 100,000–500,000 individual items per year per individual which have been stored months ago (Sherry et al. 1989). Seasonal cognitive challenges, such as caching behavior, have been linked to seasonal reversible changes in brain structures associated with spatial memory, such as the avian hippocampal formation (hippocampus and parahippocampal area).

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Despite the relative success explaining the neural and proximate mechanisms associated with cognitive performance (Bolhuis and Gahr 2006; Sherry 2006), the selective regimes shaping the evolution of cognition have been less studied (Morand-Ferron et al. 2015). Comparative studies among taxa and populations have shed light on the forces driving the differences in cognition (Lefebvre et al. 2004; Dunbar and Shultz 2007; Dechmann and Safi 2009; Roth et al. 2010). It has been shown that environmental heterogeneity linked to abiotic factors such as social complexity (Domjan et al. 2002; Hansen and Slagsvold 2004), predation risk (Lönnerstedt et al. 2012), or foraging success (Healy and Hurly 2003), as well as to abiotic variables, as seasonality or the frequency and duration of unpredictable events (González-Gómez et al. 2015), can enhance cognitive abilities. These patterns have emerged as the study of free-living animals became more popular (Pravosudov and Clayton 2002; Pritchard et al. 2016). Although there are studies assessing the heritability of cognitive traits (Dukas 2004, 2008), our understanding of differences in individual cognitive performance is more limited, although extremely necessary to fully understand the evolutionary trajectory of cognitive abilities (Morand-Ferron et al. 2015). In this context, the environmental heterogeneity and biodiversity in the Neotropics present a compelling scenario where to study the functional and mechanistic links in the evolution of cognition.

10.2 Field Cognition in the Neotropics

For long time cognitive abilities were studied in laboratory animals, mainly rats and pigeons, through traditional approaches in experimental psychology (Brodin and Ekman 1994; Balda and Kamil 2006); however, in recent years many studies have focused on the adaptive role of cognition, and therefore taking the experimental study of cognitive abilities to the field (Pravosudov et al. 2015; Pritchard et al. 2016). Working in the free-living animals provides an insight of what animals actually do in their environment, and what kind of environmental challenges they face, including predators, competitors, mating opportunities, spatial and temporal variations of foraging resources. In summary, a number of variables, which are virtually impossible to reproduce in laboratory studies, which, as mentioned before, could have shaped the evolution of cognition.

Cognitive abilities in free-living birds have been relatively well described for North American species (Ten Cate and Healy 2017), but it has rarely been addressed in Central and South America despite the high biodiversity of birds in the Neotropics. The evolution of its highly endemic biota could be explained by the isolation of South America until the uplift of Central America, 3 million years ago, unlike North America, which was geographically connected to eastern Asia during the Pleistocene (50–60 MYA) (Simpson 1980; Ricklefs 2002). Thus, cognitive abilities, and their relation with resource availability, and environmental heterogeneity in the Northern and Southern hemispheres could have evolved in a completely different scenario of selective pressures; however, they are frequently treated as similar, and the findings

are usually extended to the other as generalizations among taxonomic groups. In our opinion, these findings should be viewed with some caution considering the evolutionary history of both regions. More efforts should be allocated to the development of long-term research programs in Neotropical birds where comparisons could explore historical divergence in patterns, and thus the selective landscape experienced by species in both regions, which possibly shaped cognitive abilities.

10.3 Studying Cognition in the Field: Cognitive Ecology in Hummingbirds

Hummingbirds are a particularly interesting group in which to examine cognitive performance, their energetic balance is the result of a complex interplay among foraging behaviors, cognitive performance, physiological constraints, and environmental conditions (Suarez and Gass 2002). Hummingbirds have the highest basal metabolic rate per gram in vertebrates, and the most expensive flight style known (Suarez and Gass 2002). In addition, during daily life, these birds do not store large amounts of energy—constraining their ability to face long periods without food. However, in migratory hummingbirds, the accumulation of large amounts of fat has been observed prior to departure (Suarez 2013). On the other hand, hummingbirds inhabit a variety of regions encompassing a gradient of environmental heterogeneity, which includes tropical and temperate environments (McGuire et al. 2014). This variability includes daily and seasonal variations which impact their thermoregulatory requirements, and food abundance, as their diet is mainly composed by nectar of flowers, which is temporally and spatially variable, as different plant species have different blooming schedules across the year (Suarez 2013). Furthermore, within the flowering season, nectar is dispersed among hundreds of flowers and varies in concentration, composition, and rate of renewal (Chalcoff et al. 2006). In addition, most of flowers pollinated by hummingbirds present flowers with long corollas, where nectar is enclosed inside of a nectar chamber, which makes nectar not visually detectable (Irwin 2000). Thus, and considering relatively poor olfactory capability of hummingbirds (Ioale and Papi 1989), they rely on cognitive abilities to keep track of, and harvest, the best sources of nectar (Healy and Hurly 2003).

10.4 Spatial Memory in Hummingbirds

Field studies in Neotropical hummingbirds have shown that they are able to recall the spatial location of the highest rewarding feeder among several poorer feeders (Healy and Hurly 1995; Hurly 1996; Henderson et al. 2001). The simplest protocol was initially carried out with territorial males of green-backed firecrown (*Sephanoides sephanioides*, 5.5 g), a migratory species that inhabits highly seasonal environments both at wintering and breeding grounds (González-Gómez and

Vasquez 2006). These hummingbirds were exposed to one nectar feeder among several feeders containing water. In the first phase of the experiment (i.e., search phase) the individual was allowed to explore the experimental grid and locate the nectar feeder. In the second phase (i.e., return phase), the hummingbird was allowed to return, and the number of feeders visited until finding the nectar source was recorded. If individuals are able to recall the location of the rewarding feeder, during the return phase of the experiment, they should visit the most rewarding feeder, ignoring the non-rewarding ones. As shown in Fig. 10.1a, most of green-backed firecrowns were able to return to the nectar feeder with no mistakes. In the second part of the experiment, and considering flowers vary in nectar quality, individuals were presented to a grid with one high-quality feeder and three low-quality feeders. Similarly to the first experiment, males recalled the best nectar source (Fig. 10.1b), although less accurately than in the first experiment (Fig. 10.1c).

In order to test the spatial memory in male of long-billed hermits (*Phaetornis longirostris*, 6 g), a tropical trapliner resident species, the protocol used with ter-

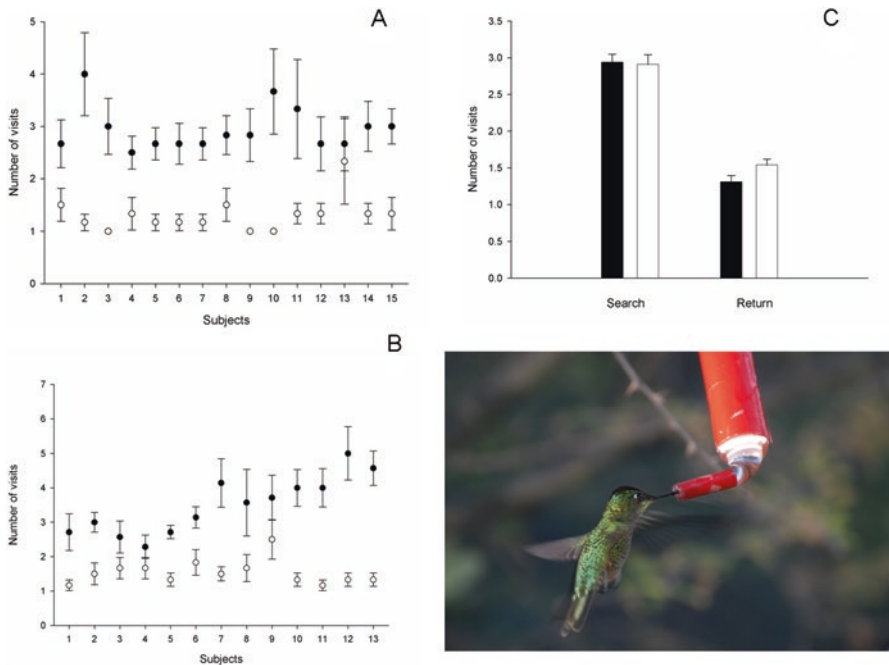


Fig. 10.1 Number of feeders visited by green-backed firecrown hummingbirds during the search (black dots) and return phases (white dots) during: (a) An experiment assessing the ability to recall the position of one rewarding feeder among non-rewarding feeders. (b) One high-rewarding feeder among several low-rewarding feeders (mean \pm SE, $n = 6$ trials for each subject). (c) Comparison of both experiments. During the search phase individuals visited the same number of feeders in both experiments (black bars); however, they visited significantly less feeders during the return phase of the first experiment, suggesting that it is easier to recall the location of a resource than the quality. Modified from González-Gómez and Vasquez (2006)

ritorial hummingbirds in temperate environments was modified (Araya-Salas et al. 2018). Considering that long-billed hermits do not defend feeding territories, we observed many individuals visiting the feeders in a short period of time, thus several individuals were tested simultaneously (i.e., with the same feeder setup during the same days). Similarly to the experiment with temperate hummingbirds, we carried out an experiment with two phases (search and return), where we registered the number of feeders visited in both phases. As many individuals were tested simultaneously, the feeder positions were not shuffled after each individual male has completed a trial, instead the position of the rewarding feeder was changed after most visiting individuals have completed the return phase and the experiment was run until most visiting marked individuals had completed at least 10 trials. Different from the study on *S. sephanoides*, spatial memory in long-billed hermits was compared with other traits related to territory ownership such as body size, bill tip length (used as weapon in agonistic interactions), load lifting, and singing. Spatial memory was also compared between “territorial” and “floater” males. In general, hummingbirds showed they were able to remember the most rewarding feeder. In comparison with other elements, although spatial memory and body size both positively affected the probability of lek territory ownership, the results suggest a stronger effect of spatial memory (Fig. 10.2). Bill tip length also showed a positive but smaller effect. Load lifting during vertical flight, a measure of physical performance relevant to agonistic interactions, had no effect on territory ownership. Finally, both body size and spatial memory were indicated in the structure of male song: body size negatively correlated with song lowest frequency, while spatial memory positively predicted song consistency. These findings lend support for cognition as a sexual selection target.

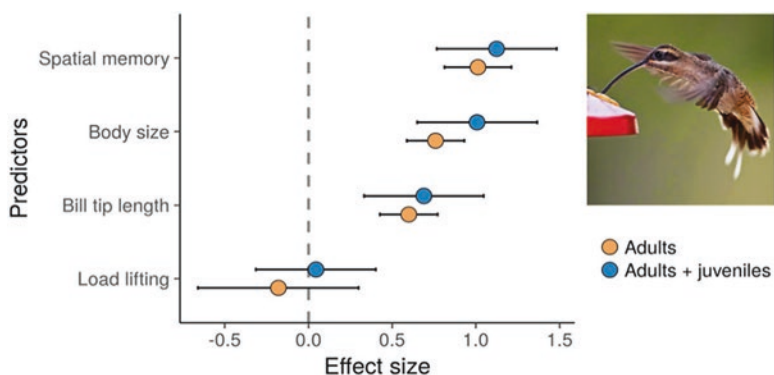


Fig. 10.2 Standardized effect sizes and 95 confidence interval traits related to territory acquisition in lekking long-billed hermit males. Effect sizes are shown for models on the complete data set, including juveniles ($n = 30$, blue markers) and the one on the subset of adult males ($n = 20$, orange markers). Effect sizes with confidence intervals that do not overlap with zero (highlighted by the vertical dashed line) were considered to have an effect on lek territory ownership. Photo (by David McDonald) shows a long-billed hermit visiting a feeder like those used in the spatial memory test. Figure from Araya-Salas et al. (2018)

10.5 Memory for Time and Location

In addition to variability in nectar quantity, quality, and location, plants replenish nectar several times a day, thus imposing the challenge to nectar renewal rate. As previously shown, hummingbirds can match their visits to renewal nectar rates, remembering when the nectar is available (Gass and Sutherland 1985; Sutherland and Gass 1995; Henderson et al. 2006). For example, Gill (1988) studied flower pattern visitation by long-tailed hermit hummingbirds (*Phaethornis superciliosus*), a species that exhibits traplining foraging strategies (i.e., regular foraging circuits). Hummingbirds visiting feeders that were refilled at fixed intervals established patterns matching nectar availability, often visiting before a scheduled refill. The ability to match visits to nectar renewal rate has also been observed in territorial hummingbirds inhabiting temperate environments, with similar results (Fig. 10.3).

In a more complex setting, Neotropical hummingbirds have been tested for their ability to recall time, location, and nectar quality at the same time. Free-living male green-backed firecrown hummingbirds (*Sephanoides sephaniodes*) were trained to defend feeders with different nectar quality and nectar renewal rates (González-Gómez et al. 2011a, b). After this training, individuals were presented with a similar grid than used for the spatial memory experiments, saving that the feeders contained a small amount of nectar, which was renewed every 10 min (high nectar quality) or 5 min (low nectar quality). The experiment was designed so if the individuals matched their visits with the low-rewarding feeders (and therefore visiting more often), they would gain the same energy amount than matching the high-rewarding feeders. Hummingbirds were successfully able to match their visits with the nectar schedules, although they preferred the high-quality reward, showing they can integrate time, location, and nectar renewal rates (Fig. 10.4).

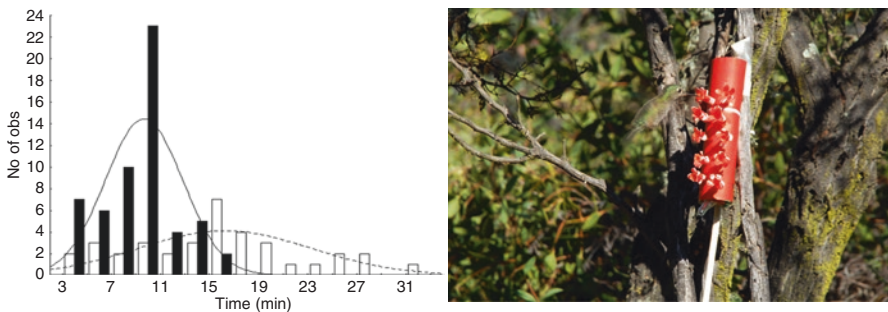


Fig. 10.3 (a) In order to measure the ability to recall nectar renewal schedules, free-living male green-backed firecrown hummingbirds were presented with two experimental groups of flowers with short (i.e., 10 min) and long (20 min) replenishment intervals. (b) The frequency distribution of visits to both, long (white bars, dashed line) and short interval (i.e., black bars, solid line), suggests that hummingbirds are able to recall nectar renewal times, and match their visits accordingly. Lines represent normal distribution adjustment. Modified from González-Gómez et al. (2011)

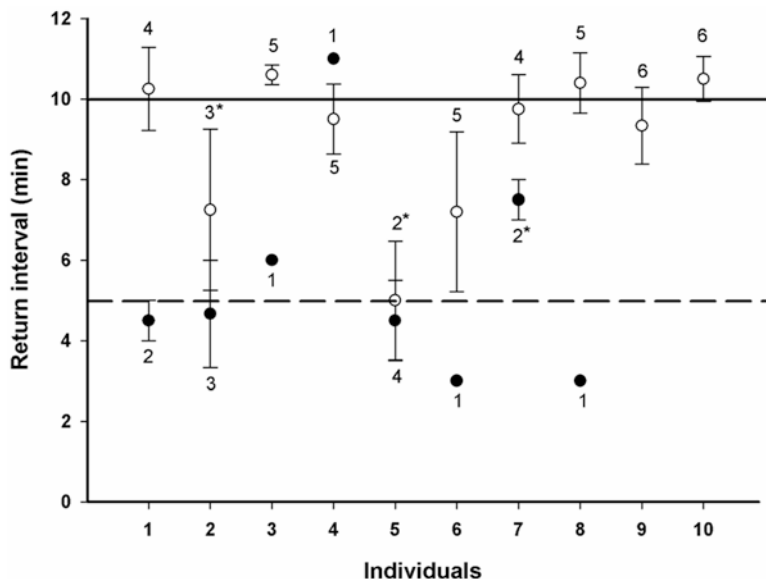


Fig. 10.4 Return intervals performed by individuals of green-backed firecrown hummingbirds to high-quality feeders (white dots, mean \pm SE) and low-quality feeders (black dots) between the search and return phase of the experiment. Number of visits to both nectar qualities is shown. Solid line shows the nectar renewal interval of high quality nectar feeders. Dashed line shows the renewal interval of low-quality nectar feeders. *Significantly different from the nectar renewal interval, 1000 bootstrap sampling (95% CI: 8.94–10.22 min). Birds 3, 4, 6, 8, 9, and 10 did not perform enough visits to low-quality feeders to analyze statistical differences from nectar renewal interval. In fact, individuals 9 and 10 did not visit the low-quality feeders in the return phase of the experiment. Modified from González-Gómez et al. (2011)

10.6 Role of Visual Cues, Observational Learning, and Competition in Cognitive Performance

Plant species which are pollinated by hummingbirds normally offer nectar enclosed in a nectar chamber, which is accessed through a long corolla (Fenster et al. 2004). This morphology implies that nectar is not visually detected. Thus, hummingbirds rely on cognitive abilities to recall several nectar characteristics such as nectar quantity, quality, and temporal availability within a plant species (Healy and Hurly 2003). However, among plant species, several visual cues are also relevant to maximize nectar harvesting. Plants vary their nectar composition (i.e., proportion of glucose, fructose, and sucrose), concentration, and production (Hornung-Leoni et al. 2013).

In this context, *visual cues* could be an important component of the foraging ecology of hummingbirds, facilitating information retrieval through association between visual and non-visual cues. Several experiments have tested the effect of visual cues on cognitive performance in Neotropical hummingbirds. For example, Perez et al. (2012) carried out a field experiment with white-eared hummingbirds.

Hylocharis leucotis, to assess their use of locations or visual cues when foraging on natural flowers *Penstemon roseus*. Their findings suggest that white-eared hummingbirds use both, visual cues and location, to visit unvisited rewarded flowers. Ornelas and Lara (2015) compared the role of color visual cues comparing four migratory (*Colibri thalassinus*, *Amazilia beryllina*, *Eugenes fulgens*, and *Selasphorus rufus*) and two non-migratory species (*Hylocharis leucotis* and *Lampornis amethystinus*), hypothesizing that migratory species would be more likely than resident to adjust their behavior to environmental change. As expected, migratory species visited more flowers and display more exploratory behaviors than resident species. Visual color cues were relevant for both, resident and migratory species, showing higher performance when red colors were used, which is coincident with the mainly red colors of hummingbird pollinated species (Chittka et al. 2001) and eye adaptations in hummingbirds (Herrera et al. 2008).

In a more complex setting, González-Gómez et al. (unpublished data) compared the performance of green-backed firecrown hummingbirds recalling time and location with and without visual cues. Using an experimental setting combining nectar availability schedule, location, and nectar quality, hummingbirds were presented with a grid in which all feeders were red (i.e., no visual cues) or a grid in that the high-rewarding feeder had black dots. Remarkably, the ability to recall location, which was related to nectar quality, significantly increased when using visual cues, unlike memory for time, which was the same using visual cues or not.

In addition to visual cues provided by plants, individuals also could obtain foraging information from conspecifics or heterospecifics exploiting the same resources. Lara et al. (2009) carried out a study to assess the role of *social learning* in hummingbirds with and without a knowledgeable tutor. Tutored hummingbirds were more successful in visiting the rewarding feeders than individuals without tutor. Furthermore, all tutored individuals only visited flowers of the color that had been previously visited by their tutors.

Although other individuals could provide valuable information about resources, they also could be an obstacle to exploitation. In fact, many hummingbird species defend foraging or reproductive territories by performing chases, vocalizations, direct attacks (Powers and McKee 1994; Camfield 2006; González-Gómez et al. 2011), and even escalated physical encounter that include stabbing opponents with a dagger-like structures at the tip of the bill (Rico-Guevara and Araya-Salas 2014). *Territorial status* may also be linked to cognitive performance. In both, tropical and temperate hummingbirds it has been observed that territorial individuals present higher cognitive performance than non-territorials (Rico-Guevara and Araya-Salas 2014), suggesting a competitive advantage of males related to more efficient foraging.

10.7 Energetics, Foraging, and Cognitive Performance

Environmental heterogeneity, and thus the frequency of unpredictable perturbation, is most likely a powerful variable in the development of cognitive traits (Roth et al. 2010; Sayol et al. 2016). During predictable events such as day/night, seasons, or

tides, animals carry out life cycles, such as breeding or migration which vary in energy cost (McEwen and Wingfield 2003). The initiation and duration of life cycles is mainly linked to the variation in local environmental cues, such as changes in environmental temperature or rainfall, and orchestrated by a series of changes in molecular and endocrine levels (Wingfield 2005). In contrast, during unpredictable perturbations of the environment, rapid changes in physiology and behavior, mediated by elevated levels of glucocorticoids, allow individuals to cope (Wingfield et al. 1998; Wingfield 2006). Thus, rapid mobilization of energy reserves via gluconeogenesis, increase of foraging behavior and immune response, among many other traits, to prioritize immediate survival (Wingfield et al. 1998; Landys et al. 2006), even interrupting the current life state (e.g., abandon breeding, interrupting molt), which detrimental effects on future fitness (Cornelius et al. 2011; Walker et al. 2015). Cognitive abilities can act as a buffer against environmental variation, helping individuals to explore new resources, and decreasing the uncertainty linked to environmental perturbations (Allman et al. 1993; Deaner et al. 2003; Sol 2009). In fact, González-Gómez et al. (2015) observed that avian species inhabiting highly variable environments showed better cognitive performance than species occurring in more stable habitats. Hummingbirds in particular showed more exploratory behaviors in more variable environments (González-Gómez et al. 2015).

10.8 Sexual Dimorphism in Cognitive Abilities

Many hummingbird species show sexual dimorphism in morphological and behavioral traits such as resource exploitation strategies (Temeles et al. 2005; González-Gómez and Estades 2009). In species where males are territorial and females are not, usually dominant males secure access to dense patches of nectar-rich flowers while subordinate females perform rapid intrusions into male territories to raid the good resources, or they are forced to forage in nectar-poor, scattered flowers (Kodric-Brown and Brown 1978). Thus, González-Gómez et al. (2014) hypothesized that territorial males should have higher demands on spatial abilities as a result of tracking nectar quality and availability in their territories. In contrast, females could be opportunistic foragers, guided mainly by visual cues about the presence/absence of flowers but without information about nectar quantity, quality, or availability (González-Gómez et al. 2014). Comparisons of cognitive performance between males and females of green-backed firecrown hummingbirds support this idea. González-Gómez et al. (2014) assessed the ability of males and females to recall position, quality, and nectar renewal schedule, where females show poorer cognitive performance than males (Fig. 10.5a).

According to the adaptive specialization hypothesis, natural selection may change behavior and its underlying neural mechanisms if such modifications enhance fitness (Krebs et al. 1989; Sherry et al. 1989; Sherry et al. 1992). Evidence supporting this hypothesis has been observed in several species in foraging and breeding contexts, where the group that performs behaviors which involve more

developed cognitive abilities shows larger hippocampal areas (Roth and Pravosudov 2009; Pravosudov et al. 2015). Hummingbirds have larger HF than other avian groups (Ward et al. 2012) (Fig. 10.5b). Nevertheless, González-Gómez et al. (2014) observed that despite females of greenbacked firecrown had lower cognitive performance than males, their HF was larger (Fig. 10.5c), which contradicts the adaptive specialization hypothesis. Possible explanations could be that females recall nectar characteristics at larger spatial scales, and therefore the experimental setup did not assessed their cognitive abilities. On the other hand, it could be that females remember social interactions; such males that display lower aggression levels. Nevertheless,

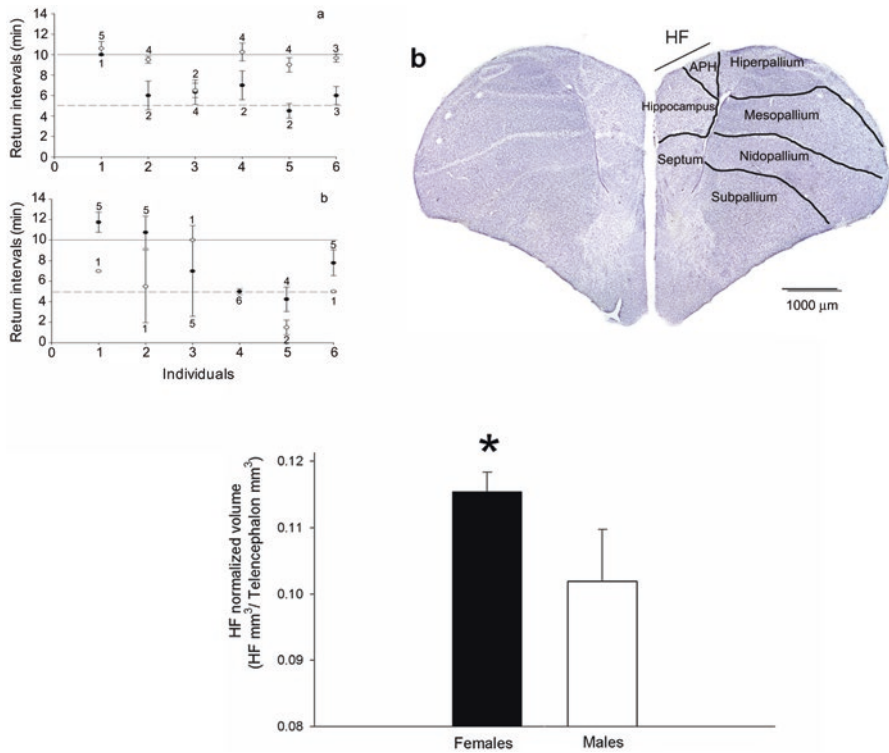


Fig. 10.5 (a) Return intervals of males (upper panel) and females (lower panel) to high-quality (white dots) and low-quality (black dots) feeders between the search and return phase of the experiment. Number of visits (mean \pm SE) to both nectar qualities is shown. Solid line: renewal interval of high-quality nectar feeders; dashed line: renewal interval of low-quality nectar feeders. *Return interval differed significantly from the nectar renewal interval, 1000 bootstrap sampling (high-quality nectar, 95% CI: 11.1–9.75 min, low-quality nectar, 95% CI: 6.15, 4.75 min). (b) Coronal section through the telencephalon of the green-backed firecrown hummingbird showing the hippocampal formation (i.e., hippocampus and area parahippocampalis (APH)) in the medial-dorsal aspect. Scale bar: 1000 μm . (c) The HF is significantly larger in females (13.96 \pm 0.81 mm³, mean \pm SE) than males (12.04 \pm 0.8) respect to the telencephalon volume (121.31 \pm 8.30, 117.81 \pm 5.36, respectively). Please note the statistical analysis was performed using telencephalon volume as a covariable. Data are presented as mean \pm SE. * $p < 0.05$. Modified from González-Gómez et al. (2014)

the study exemplifies the link between cognitive challenges of the environment and the structure of the underlying neural mechanisms.

10.9 Concluding Remarks

The Neotropics present extremely high habitat diversity with at least 10 bioregions, each of them with several ecoregions. Most likely, this environmental diversity promoted the high number of species occurring in this region, with a total of ~4750 species (Jenkins et al. 2013; Pimm et al. 2014). This contrasts with the number of species found in North America (1321) and Europe (552), where most of the studies in animal behavior, and in particular in animal cognition, are carried out. Overall, data in our revision showed that hummingbird species in the Neotropics present similar cognitive abilities than species at the Nearctic region. However, the diversity of environments in the Neotropical region allowed us to assess the role of environmental heterogeneity and resource exploitation strategies on learning and memory, although the lack of information in relation to the species richness is striking. Thus, our conclusions are limited by the few studies that have been carried out. Among different habitats, environmental heterogeneity seems to drive the development of cognitive abilities, however mediated by individual traits such as sex and social status. This could explain why, across all the studies, we observed important individual differences in cognitive performance, although more data are needed. Furthermore, inhabiting variable environments requires flexible adjustments in physiology and behavior to increase the chances of survival and reproduction. For example, in seasonal environments, animals are restricted in the initiation and duration of the different life history stages across the annual cycle. Thus, avoiding the overlap of expensive processes such as breeding and molt, and matching their cycles to resource availability. In this context, long-term integrative studies could be key to understand variations in cognitive performance, and how cognition acts to buffer environmental variability. In our opinion, the role of these variables should be further assessed integrating physiological traits, such as endocrine levels and energy balance. Thus, integrative and comparative studies in hummingbirds in the Neotropics could shed light on the different selective pressures that might have shaped the evolutionary trajectory of avian cognition.

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