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Does Environmental Heterogeneity Promote Cognitive Abilities?

Paulina L. González-Gómez,^{1,*} Pablo Razeto-Barry^{*†} Marcelo Araya-Salas[‡] and Cristian F. Estades[§]

^{*}Instituto de Filosofía y Ciencias de la Complejidad, Santiago, Chile; [†]Universidad Diego Portales, Vicerrectoría Académica, Santiago, Chile; [‡]Department of Biology, New Mexico State University, NM 88003, USA; [§]Facultad de Ciencias Forestales y de la Conservación de la Naturaleza, Universidad de Chile, Santiago, Chile

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¹E-mail: plgonzalezgomez@gmail.com

Synopsis In the context of global change the possible loss of biodiversity has been identified as a major concern. Biodiversity could be seriously threatened as a direct consequence of changes in availability of food, changing thermal conditions, and loss and fragmentation of habitat. Considering the magnitude of global change, an understanding of the mechanisms involved in coping with a changing environment is urgent. We explore the hypothesis that species and individuals experiencing highly variable environments are more likely to develop a wider range of responses to handle the different and unpredictable conditions imposed by global change. In the case of vertebrates, the responses to the challenges imposed by unpredictable perturbations ultimately are linked to cognitive abilities allowing the solving of problems, and the maximization of energy intake. Our models were hummingbirds, which offer a particularly compelling group in which to examine the functional and mechanistic links between behavioral and energetic strategies in individuals experiencing different degrees of social and environmental heterogeneity.

Introduction

In the context of global change the possible loss of biodiversity has been identified as a major concern (Wichmann et al. 2004). This effect could be, among other variables, a consequence of anthropic perturbations such as pollution, habitat destruction, application of pesticides, increasing temperatures, and changing patterns of rainfall (Rosenzweig et al. 2007). In some places like northern Chile, rainfall has declined roughly by 50% in the past 50 years (Gutiérrez et al. 2010). In addition, the El Niño Southern Oscillation has increased in frequency, duration, and magnitude (Wara et al. 2005). Thus, it is possible that current weather patterns reflect the combination of natural variability and a changing baseline (Gutiérrez et al. 2010). In turn, the alteration of this pattern may greatly affect the availability of food (Gutiérrez et al. 2010), and result in the loss and fragmentation of habitat (Thomas et al. 2004). Considering the magnitude of environmental changes, understanding the mechanisms involved in

how organisms cope with this phenomenon is urgent. Such mechanisms may shed considerable insight on why some individuals survive and others die (Wingfield 2008). In this context, populations in less predictable environments may be more likely to show a range of responses that cope with the different and irregular conditions imposed by global change (Wingfield 2008).

Natural selection may promote phenotypic changes depending on the degree of environmental variability (Razeto-Barry et al. 2011, 2012). As expected from an evolutionary point of view, the ability of animals to compensate for the environmental perturbations imposed by global change would depend ultimately on the individual degree of phenotypic flexibility (Korte et al. 2005). Recent studies have shown that highly seasonal (e.g., temperate) environments can promote a higher degree of flexibility in animals' responses in comparison with more stable environments (Wada et al. 2006). Cavieres and Sabat (2008) successfully correlated environmental variability and phenotypic

flexibility, showing that individuals from highly seasonal environments—such as Mediterranean regions—were able to adjust to new thermal conditions. In contrast, individuals from more stable environments were unable to change basal metabolic rates in response to new conditions. In this context, temperate-tropical comparisons have shown that highly seasonal, temperate environments promote a greater ability to respond to environmental changes than do equatorial regions where animals experience minimal variation in photoperiod and temperature (Wada et al. 2006). In addition to physiological traits, animals experiencing more heterogeneous environments show greater flexibility in behavioral traits and cognitive abilities, thereby promoting adaptation to new situations (Wright et al. 2010). One important variable that can be used to assess behavioral flexibility is exploratory behavior (Coppens et al. 2010). In this context, more exploratory behaviors should be expected in environments with high levels of heterogeneity (see below).

Learning, memory, and many other cognitive abilities are critical for the performance of behavioral traits strongly linked to fitness (Balda et al. 1998). For example, many animals in natural systems depend on cognitive abilities to learn and perform mating displays (Boogert et al. 2011), avoid predators (Brown et al. 2013), and search for food (González-Gómez et al. 2011c). In particular, problem-solving abilities and spatiotemporal memory, which allow individuals to recall time and location of items simultaneously, can be especially important for animals that rely on non-visual cues to retrieve food items. For example, scatter-hoarding avian species like some species of crows and parids, strongly depend on the ability to store and retrieve as many as 100,000–500,000 individual items per year per individual (Haftorn 1954), a direct result of strong spatial memory (Sherry et al. 1981). Animals inhabiting harsh natural environments with seasonal food resources are more prone to display “opportunistic foraging” (Temple 1996). For example kea (*Nestor notabilis*) who experience this kind of environment, show a wide variety of diet, feeding on more than one hundred species of plants (Clark 1970). In addition, very low threshold of neophobia, allowed kea to explore new resources (Huber et al. 2001; Gajdon et al. 2004). In particular, the ability to solve important environmental problems related to manipulating new resources is linked to causal reasoning (Emery and Clayton 2004). This cognitive ability allows some species, mostly vertebrates, to construct a series of mental representations resulting in the understanding of

events as being related in space and time. As well, there is some mediating force allows the subjects to predict or control those events (Hunt et al. 2006).

In this study, we explore the link between environmental heterogeneity and cognitive abilities at different levels of analysis. First, we searched the literature for data on spatial memory and problem solving in free-living birds in environments with different degrees of heterogeneity. Second, we compare exploratory behaviors in hummingbird species in environments with different degrees of heterogeneity. Third, we study spatial memory in two species of free-living hummingbirds experiencing tropical environments (i.e., with low environmental heterogeneity) and Mediterranean environments (i.e., with high environmental heterogeneity). Finally, we show an example of the application of cognitive studies as a tool for conservation biology.

Cognitive ecology and energetics of hummingbirds

Exploratory behaviors allow individuals to acquire information about their surrounding environment (Careau et al. 2009), and potentially include new items in their diets. This could be especially important for animals unable to store large amounts of energy or with relatively high energetic expenditures (Day et al. 1998). Hummingbirds (Family Trochilidae) offer a particularly compelling group in which to examine the functional and mechanistic link between cognitive abilities and environmental heterogeneity both in tropical and temperate environments. Hummingbirds inhabit a variety of regions encompassing a gradient of environmental heterogeneity from seasonal Mediterranean environments to one of the most aseasonal environments in the world, the Atacama Desert in Chile. In addition, the energetic balance in hummingbirds is the result of a complex interplay among foraging behaviors, cognitive performance, physiological constraints, and environmental conditions (Suarez and Gass 2002). In unpredictable environments, hummingbirds often face short-term fluctuations both in ambient temperature and in availability of food, and thus face extreme challenges in maintaining heat and energy balance (González-Gómez et al. 2011b). In contrast, hummingbirds living in more predictable environments experience the same degree of energetic cost but a relatively stable supply of food. In this context, hummingbirds inhabiting less predictable environments should display more exploratory feeding behaviors than do species inhabiting more stable ones.

In order to achieve energetic balance, hummingbirds use several cognitive abilities to keep track of, and harvest, the best sources of nectar (Healy and Hurly 2003). Hummingbirds experience patches of resources containing nectar with cues that are not visual (Irwin 2000). Nectar is dispersed among hundreds of flowers and varies in concentration, composition, and rate of renewal. Several studies have shown that free-living hummingbirds can recall the spatial location of high-quality resources (Blem et al. 2000; González-Gómez and Vásquez 2006), can match their visits to the rates at which nectar is renewed, remember when the nectar is available (Gill 1988; Henderson et al. 2006a; González-Gómez et al. 2011c), and simultaneously remember where and when the best resources are available, i.e., episodic-like memory (Gonzalez-Gomez et al. 2011a). As Henderson et al. (2006a) suggested, strong cognitive abilities should be a part of the daily life of a nectarivorous individual. From an evolutionary perspective, there should be an important fitness-mediated interplay between selective pressures and the development of complex cognitive abilities. In this study, we focus on the green-backed firecrown (*Sephanoides sephanioides*, 5.5 g), a territorial migratory species that inhabits highly seasonal environments both at wintering and breeding grounds (González-Gómez and Estades 2009), and the long-billed hermit (*Phaetornis longirostris*, 6 g), a non-migratory, resident species that occurs in tropical lowlands experiencing relatively low levels of environmental changes. We carried out two experiments in each group, assessing the subject's ability to recall the location of the most rewarding feeder among feeders with water (Experiment 1) or with low-quality nectar (Experiment 2).

From cognitive abilities to conservation biology

Within the framework of climatic change, one of the key questions of our time is how we apply the findings of research in basic science to conservation problems. In northern Chile, in the oases of the Atacama Desert, one of the most stable habitats in the world (Table 1), occurs the most threatened species of hummingbird in this country, the Chilean woodstar (*Eulidia yarrellii*, 2.6 g) (Estades et al. 2007; van Dongen et al. 2013). This endemic “bee” hummingbird, once very common, inhabited riparian areas with vegetation dominated by shrubs such as chañar (*Geoffroea decorticans*, Fabaceae), and pluchea (*Pluchea chingoyo*, Asteraceae), which provided nectar, and, presumably, pimienta boliviano (*Schinus molle*, Anacardiaceae) and pacama (*Morella pavanis*,

Myricaceae) as an alternative for nesting sites (Johnson and Goodall 1965). The causes of the population decline are multiple, but can be summarized as follows (Estades et al. 2007):

Habitat loss. The attractive stable climate in the region has resulted in growing pressure for developing industrial and agricultural activities. In the past 5–7 years we have observed an important change in land use (C. F. Estades, P. Munilla and M. A. Vukasovic, unpublished data). The replacement of small olive groves by farms massively producing seeds for corporations necessitated installation of extensive areas of nets for to protect the seed plants from aphids. Since olive trees were the most important sites for nesting, and because nets prevent birds access to sites for foraging, this development has dramatically reduced the habitat quality of the oases in the Atacama Desert (C. F. Estades, P. Munilla and M. A. Vukasovic, unpublished data). In addition, there is a growing use of river basins for vegetable plantations, thereby destroying the native vegetation.

Pollution and pesticides: During the early 1970s pesticides were aerially sprayed (Olalquiaga and Lobos 1993). Several chronicles reported numerous dead hummingbirds where these activities were carried out. Since then, the increase of agricultural activities has involved the systematic application of a variety of pesticides (Rázmilic 1982; Salazar and Araya 2001), presumably poisoning the nectar, and consequently, the birds.

Invasive species: Concurrent with the decline of the Chilean woodstar, the first observations of the Peruvian sheartail (*Thaumastura cora*, 2.6 g) were reported (Lavercombe and Hill 1972). This invasive species, a closely related bee hummingbird (McGuire et al. 2014), can hybridize with the Chilean woodstar (van Dongen et al. 2012, 2013) and their breeding season is at least twice as long as that of the completely overlapping native species (Lazzoni 2015), thereby representing a strong competitor both for resources and for reproductive opportunities. In this context, we assessed the sources of the native and exotic nectars used by the Chilean Woodstar, and its ability to explore new artificial sources. If hummingbirds can learn to feed consistently upon artificial nectar, provision of such nectar could lead to recovery of the population.

Methods

Relation between cognitive abilities and environmental heterogeneity in birds

We performed an extensive literature search looking for studies testing spatial memory or problem-solving abilities performed in the field by free-living birds (Table 1). In order to standardize the results,

Table 1 Localities, De Martone Index, and the species considered in this study

Locality	Coordinates	CV DMi	Species	Test	References
Arica, Chile	18°48'47.59"S, 70°09'11.34"W	0.0040	Chilean Woodstar Hummingbird (<i>Eulidia yarrellii</i>), Oasis Hummingbird (<i>Rodopis vesper</i>), Peruvian sheartail (<i>Thaumastura cora</i>)	EB	This study
Beaver Mines, Alberta, Canada	49°20'56.61"N, 114°24'38.49"W	3.1797	Rufous hummingbird (<i>Selasphorus rufus</i>)	SM	Flores-Abreu et al. (2012); Henderson et al. (2001, 2006b) Jelbert et al. (2014)
Chiloe, Chile	41°52'56.33"S, 73°39'49.52"W	3.5876	Green-backed firecrown (<i>Sephanoides sephaniodes</i>)	EB	This study
Cincinnati, OH, USA	39°08'56.83"N, 84°28'26.35"W	0.8978	Northern Mockingbirds (<i>Mimus polyglottos</i>)	PS	Farnsworth and Smolinski (2006)
Davis, CA, USA	38°33'36.05"N, 121°45'52.63"W	1.9759	Anna's Hummingbird (<i>Calypte anna</i>), Black-chinned Hummingbird (<i>Archilochus alexandri</i>)	EB	This study
Gotland, Sweden	57°44'33"N, 18°43'11"W	0.5945	Great tit (<i>Parus major</i>)	PS	Cauchard et al. (2013)
La Selva Biological Station, Costa Rica	10°25'25.35"N, 84°01'20.16"W	0.7144	Long-billed Hummingbird (<i>Phaethornis longirostris</i>)	SM	M. Araya-Salas, P. L. González-Gómez, K. Wojczulanis-Jakubas and T. Wright (unpublished data)
Mexico, Tlaxcala, Mexico	19°14'34"N, 98°1'28"W	2.6233	Magnificent hummingbird (<i>Eugenes fulgens</i>), White-eared hummingbird (<i>Hylocharis leucotis</i>)	SM	Tello-Ramos et al. (2014)
Mitlenatch Island, British Columbia, Canada	49°57'2"N, 125°0'7"W	3.0656	Northwestern crows (<i>Corvus caurinus</i>)	SM	Verbeek (1997)
Mount Cook Village, New Zealand	43°44'11.42"S, 170°05'58.56"E	0.0679	Kea (<i>Nestor notabilis</i>)	PS	Gajdon et al. (2004)
Rocky Mountains, Alberta, Canada	40°20'56.61"N, 114°24'38.49"W	15.519	Rufous hummingbird (<i>Selasphorus rufus</i>)	SM	Flores-Abreu et al. (2013)
San Carlos de Apoquindo, RM, Chile	33°24'59.13"S, 70°29'25.15"W	1.8132	Green-backed Firecrown Hummingbird (<i>Sephanoides sephaniodes</i>)	SM	González-Gómez et al. (2006, 2011a, 2011c)
Sarramea, New Caledonia	21°38'32.39"S, 165°50'46.15"E	0.3377	New Caledonian crow (<i>Corvus moneduloides</i>)	PS	Hunt (2000), Hunt et al. (2006)
Tabou and Taro Valleys, New Caledonia	21°33'S, 165°19'E	0.3378	New Caledonian crow (<i>Corvus moneduloides</i>)	PS	Bluff et al. (2010)
Taunton NP, Queensland, Australia	23°31'15.13"N, 149°13'0.840"W	0.4589	Spotted bowerbirds (<i>Ptilonorhynchus maculatus</i>)	PS	Isden et al. (2013)
Wallaby Creek NSW, Australia	28°28'S, 152°25'E	0.3232	Satin Bowerbird (<i>Ptilonorhynchus violaceus</i>)	PS	Keagy et al. (2009, 2011)
Westcastle Valley Alberta, Canada	49°21'N, 114°25'W	16.52	Rufous hummingbird (<i>Selasphorus rufus</i>)	SM	Tello-Ramos et al. (2014)
Wytham Woods Oxfordshire, UK	51°45'40"N, 1°14'47"W	0.4830	Great tit (<i>Parus major</i>), Blue tit (<i>Cyanistes caeruleus</i>)	PS	Morand-Ferron et al. (2011)

Notes: PS, problem solving test; SM, spatial memory; EB, exploratory behavior.

we scored cognitive ability as the number of individuals that performed the test successfully relative to the total number of individuals measured.

Environmental heterogeneity was considered as the coefficient of variation (hereafter CV) of the De Martone index ($Dmi = \sum P/T^\circ + 10$), where P is the monthly precipitation (mm) and T is the average monthly temperature ($^\circ\text{C}$) for each locality (Table 1) (Cavieres and Sabat 2008). We used the 30-year (1971–2000) average of climatic data collected by the World Meteorological Organization (WMO), and processed by the National Climatic Data Center and the National Oceanic and Atmospheric Administration (NOAA 2011). Data were accessed through Climate-charts. We tested the phylogenetic effect using the K parameter (Blomberg et al. 2003) and the R (version 3.1.2, 2014) package Phytools (Revell 2012). The molecular phylogenetic tree for all the taxa we considered in this study was built following Jetz et al. (2012) (Birdtree.org).

Cognitive abilities in hummingbirds

Exploratory behavior: ability to find new resources

Nectar feeders ($N=10$) were located for the first time in Davis, CA, USA; La Selva Biological Station, Costa Rica; Arica, Chile; Santiago, Chile; Senda Darwin Biological Station, Chile (Table 1). We recorded the number of days until the first hummingbird visited the feeders in each location. Because of the reduced sample size, we assigned each location to “high” (CV of $DMi > 1$, see above, Table 1) or “low” heterogeneity (CV of $DMi < 1$). We compared both categories using Student’s t -test.

Spatial memory in temperate hummingbirds

Subjects were green-backed firecrown hummingbirds, a species that inhabits central Chile during the non-breeding season. During the breeding season this species performs latitudinal and altitudinal migrations and experiences dramatic changes in temperature and rainfall, both daily and seasonally (González-Gómez et al. 2011b). The basic test for measuring spatial cognitive abilities in temperate hummingbirds has been extensively described in previous papers (González-Gómez and Vásquez 2006; González-Gómez et al. 2011a, 2011c). In short, the studies were carried out during the Austral winter in a field station located in the Andean foothills in central Chile ($33^\circ 23' 59.13''\text{S}$, $70^\circ 29' 25.15''\text{W}$, 1100 m above sea level). For the habituation period where hummingbirds learnt to feed from artificial feeders, we provided 25% sucrose (w/w in water) nectar *ad*

libitum. Feeders consisted of a 100-ml glass rodent’s water-dispenser wrapped with red paper. For the spatial memory task, we placed a 50×50 cm six-point grid where feeders were equally distributed. During the experiments four identical feeders were assigned to four randomly chosen points among the six points of the grid. The experiments were designed to assess the ability of birds to remember the position of a rewarding flower among non-rewarding flowers (Experiment 1) or low-rewarding flowers (Experiment 2) after a single learning experience (see below). At the beginning of each trial, each feeder contained 100 ml of a sucrose solution, in order to prevent the depletion 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 probed the feeders until it discovered the most rewarding feeder. A hummingbird was allowed to feed from it until the hummingbird stopped feeding spontaneously. After this, the observer did not allow re-visits to the grid, by staying close to the feeder and keeping the subject away from the feeders for 5 min. Birds were observed in their territories within this 5-min interval and they quickly returned to the experimental grid after the observer retreated to the hide. 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.

Spatial memory in tropical hummingbirds

Experiments were carried out at La Selva Biological station (M. Araya-Salas, P. L. González-Gómez, K. Wojczulanis-Jakubas and T. Wright, unpublished data) with long-billed hermit hummingbirds found in the tropical lowland rain forest. In general, this species experiences relatively low environmental variation, displays trap-line foraging, and does not consistently defend feeding territories, although males do defend small territories while they display in small leks to attract visiting females. Territorial males display at leks for 6–8 h per day for 8 months each year and establish intrasexual dominance hierarchies, maintain ownership of perches, and attract prospecting females while floater males aggressively try to acquire a position in the lek’s arena (Araya-Salas and Wright 2013; Ricco-Guevara and Araya-Salas 2015). All the individuals in the lek were captured with mist nets and marked for individual identification (see Ricco-Guevara and Araya-Salas 2015).

Since long-billed hummingbirds do not defend feeding territories, we had to modify our protocol in order to test spatial-memory abilities in the field. We offered three identical independent feeders separated by 2 cm containing 100 ml of nectar (Experiment 1). In the second experiment, we offered a modified feeder with three identical artificial flowers connected to three independent nectar reservoirs inside. Each nectar reservoir had 30 ml of liquid; two of them with water (Experiment 1) or low-quality nectar (Experiment 2) and one with high-quality nectar. Following the protocol described above for temperate hummingbirds, each trial had two phases: an exploratory one during which the hummingbirds could try all the feeders and discover the position of the most rewarding one (i.e., search phase), and a second phase during which animals visited the grid for the second time (i.e., return phase). In contrast to the protocol described for temperate hummingbirds, we did not control for the period of time between the two phases. We allowed all the hummingbirds to visit the feeder and we recorded individual visits and the time elapsed between the two phases for each individual bird. The trial ended when all the hummingbirds that performed the first phase had visited the grid again.

Data were analyzed using a nested ordinal logistic model with species, territorial condition nested in species, and individual nested in condition. The response variable was the success in finding the best nectar between feeders filled with water (Experiment 1) or with nectar of high quality (Experiment 2) immediately after they began the return phase of the experiments. Therefore, a subject visiting a low-quality feeder as a first choice during the second experimental phase was considered unsuccessful.

Evaluating nectar sources for the Chilean woodstar

To measure the volume and concentration of nectar available in chañar, the main nectar source for this hummingbird species, flowers were bagged for 14 h (1800–0800 h) with tulle bags to prevent access of visitors and to reduce evaporation. The total volume of nectar produced was assessed nondestructively by repeatedly inserting a 80- μ L microcapillary tube into the nectary of each flower until no further nectar could be extracted (Kearns and Inouye 1993). Flowers were sampled only once. We sampled 10 flowers on each of 20 trees. To estimate the concentration of sugar in the nectar, a temperature-compensated hand refractometer was used and concentration was expressed as grams of total sugar per 100 g of solution (mass percentage or conventional %w/w). To assess the preference of Chilean

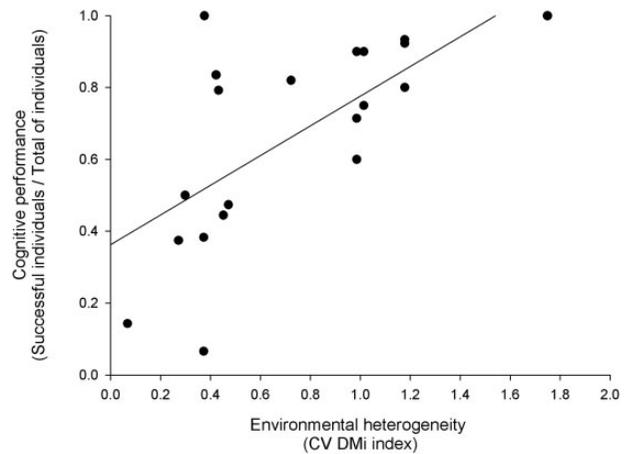


Fig. 1 Relation between environmental heterogeneity (CV DMI index) and cognitive performance (i.e., spatial memory and problem solving) in experiments carried out in the field with free-living birds.

woodstars for chañar trees we recorded the frequency of visits to both chañar and orange trees (*Citrus aurantinas*), a common crop in the area visited by hummingbirds (P. L. González-Gómez, personal observation). There were four non-consecutive observation periods of 15 min each at each of 16 individual trees of chañar and 20 of orange. We observed hummingbird visits between 7:30 and 11:00 am and we randomized the order in which each observation was carried out.

To assess the ability of hummingbirds to visit new sources of nectar we placed 12 vertical grids holding four nectar feeders (see above), two of them enveloped with red paper, one filled with 15% nectar, one with 30% nectar, and two wrapped with yellow paper and filled with 15% and 30% nectar. We recorded the rates of visits by Chilean woodstars.

Results

Relation between cognitive abilities and environmental heterogeneity in birds

We found 21 studies carried out in the field on 14 species in six families and four orders of free-living birds and that tested for spatial-memory abilities or for problem solving (Table 1). We did not find a significant phylogenetic signal in cognitive abilities at the species level ($K = 0.557$, $p = 0.08$). Environmental heterogeneity was positively related with cognitive abilities ($F_{(1,19)} = 18.07$, $p = 0.0004$, $r^2 = 0.48$, $N = 21$, Fig. 1).

Cognitive abilities of hummingbirds

Exploratory behavior: Ability to find new resources

We found eight species consistently feeding from our artificial feeders: black-chinned hummingbird

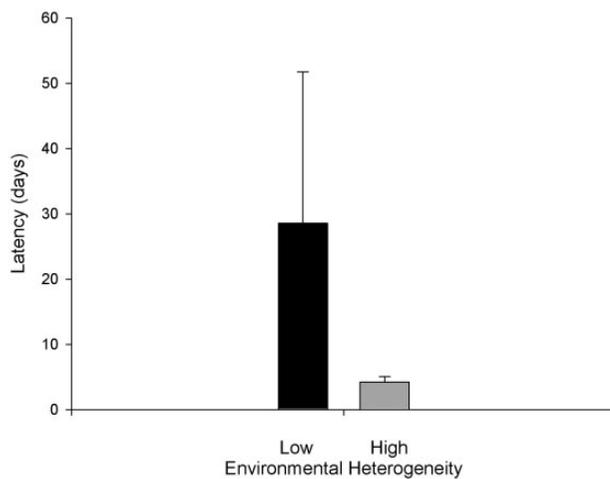


Fig. 2 Latency (number of days) to the first visit of a hummingbird to new feeders in environments with low heterogeneity (CV DMi index < 1) and high heterogeneity (CV DMi index > 1).

(*Archilochus alexandri*), Anna's hummingbird (*Calypte ana*) (Davis, CA, USA); long-billed hermit (*P. longirostris*), *Phaetornis striigularis* (stripe-throated hermit) (La Selva, Costa Rica); oasis hummingbird (*Rodopis vesper*), *Chilean woodstar* (*E. yarrellii*), Peruvian sheartail (*Thaumastura cora*) (Arica, Chile), and green-backed firecrown (*S. sephaniodes*) (Santiago, Chile) (Table 1). The number of days until we observed the first visit by a hummingbird (range: 2–60 days) was marginally lower in species inhabiting more heterogeneous environments than in more stable environments (t -test, $t_{1,7} = 2.26$, $P = 0.057$, Fig. 2).

Spatial memory in temperate and tropical hummingbirds

In the first experiment (hummingbirds had to remember the location of the nectar among feeders filled with water) we compared the performance of territorial ($N = 15$ green-backed firecrowns, $N = 11$ long-billed hermits) and non-territorial animals ($N = 6$ each species). Overall, green-backed firecrowns were able to remember more accurately the location of the artificial feeder holding nectar (nested ordinal logistic model, Chi-square = 69.086, $df = 37$, $P = 0.0011$, $AiCc = 629.825$, Fig. 3). We did not find differences in spatial memory among territorial individuals within each species (Chi-square = 5.9e-6, $df = 1$, $P = 0.99$). In contrast, non-territorial individuals of green-backed firecrowns were able to remember the location of nectar sources more accurately than long-billed hermits (Chi-square = 4.076, $df = 1$, $P = 0.0435$), although we found significant differences

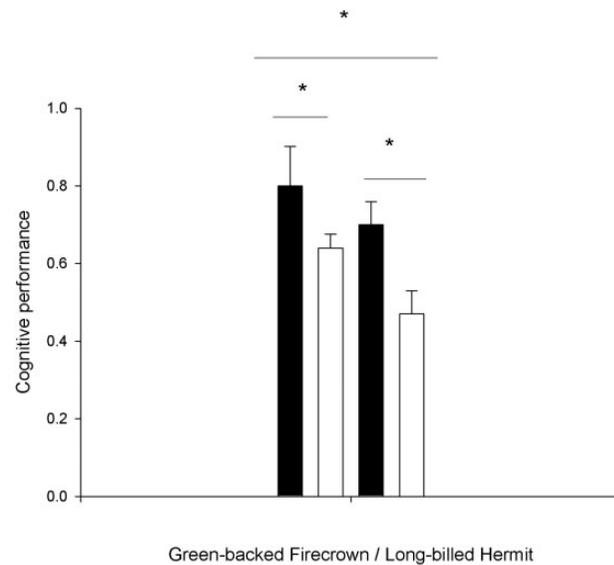


Fig. 3 Spatial memory in territorial (Black bars) and non-territorial (White bars) green-backed firecrowns and long-billed hermits. Both species inhabit environments with high and low levels of heterogeneity, respectively, as based on the CV DMi index (see text).

among individuals within a species (Chi-square = 25.47, $df = 10$, $P = 0.005$, Fig. 3).

In the second experiment (spatial task involved recalling the location of the feeder with high-quality nectar among feeders with poor-quality nectar), we observed the performance of territorial hummingbirds ($N = 13$ green-backed firecrowns, $N = 10$ long-billed hermits). We observed no significant differences in spatial memory between the two species (ordinal logistic model, Chi-square = 2.25, $df = 1$, $P = 0.13$), nor did we find differences among individuals in either species (Chi-square = 17.03, $df = 22$, $P = 0.76$).

Evaluating nectar sources for the Chilean woodstar

The rate of visits to Chañar (0.5 ± 0.10 visits/observation period) was higher than the rate of visits to orange trees (0.2 ± 0.11 visits/observation period, mean \pm SE, Mann-Whitney test, $Z = -2.03$, $P < 0.05$). The nectar in orange-tree flowers ($11.9 \pm 1.05 \mu\text{L}$) was more abundant than in chañar ($0.99 \pm 1.04 \mu\text{L}$, t -test, $t_{1,198} = -6.54$, $P \ll 0.001$); however, the latter species had more concentrated nectar ($42.59 \pm 18.96\%w/w$) than did orange trees ($16.26 \pm 4.27\%w/w$, $t_{1,126} = 10.83$, $P \ll 0.01$).

Although Chilean woodstars visited the sources of artificial nectar (0.12 ± 0.14 visits/period), they did it about four times less than in the case of sources of natural nectar, and it took them 18 days to start using artificial nectar. This species showed a strong

preference for feeders with 30% concentration of nectar (0.17 ± 0.01 visits/period) versus 15% concentration of nectar (0.06 ± 0.01 mean \pm SE visits/period, two-way ANOVA $F_{1,716} = 27.27$, $P < 0.001$). We did not find a preference for color (two-way ANOVA $F_{1,716} = 3.25$, $P = 0.08$) and we did not observe an interaction between color and nectar concentration (two-way ANOVA $F_{1,716} = 3.25$, $P = 0.08$).

Discussion

Environmental variability is a major cause of evolution by natural selection and determines the timing and magnitude of phenotypic changes (Razeto-Barry et al. 2011, 2012). One of the most relevant phenotypic changes in the context of global change is probably the development of cognitive abilities that allow animals to navigate, explore, exploit, and remember new environments (Reader and Laland 2003; Wright et al. 2010). The adoption of new behaviors could be more beneficial under new conditions in the same environment. Our results strongly suggest that in heterogeneous environments with relatively more dramatic changes in environmental temperature and availability water and, likely, of food, selection could have favored innovative responses, exploration of new sources, and manipulation of new tools to solve a variety of problems that ultimately allow individuals to adjust to unpredictable changes. Because food resources could be seasonally scarce, species inhabiting heterogeneous environments have to search for all kinds of seasonally available food. In this kind of environment extreme neophilia may have prompted animals to spend much time in exploration (Schloegl et al. 2009, but see Greenberg 2003; Brown et al. 2013). Therefore, the explorative behavior observed in many of the experiments found in our literature search might reflect a strategy that is adaptive to heterogeneous habitats. Consequently, in stable harsh environments, always adopting exploration could be too costly, which could have relaxed the pressure for developing this kind of traits. On the other hand, the ability to remember the location of nectar seems to be strongly linked to explorative abilities, at least in some animals. This trait represents a double benefit: greater opportunities for immediate exploitation (González-Gómez et al. 2011c) and the possibility of storing some items in anticipation of a time when food might be more difficult to find (Correia et al. 2007). Because our assessment of cognitive performance focused on the population level more than on the individual level, it could be seen as a measure of the degree of phenotypic

variability that exists in a particular population. It has been argued that behavioral flexibility can serve as an ecological buffering mechanism that enhances the survival of populations under global changes in the environment (Wichmann et al. 2004). However, our results suggest that this would be possible only if there are a critical number of individuals (enough to secure a viable population) expressing a combination of cognitive abilities such as exploration of new sources, memory to revisit them, and problem solving, as well as matching these cognitive traits with the limitations on energy imposed by the environment.

Hummingbirds' cognition in temperate and tropical environments

In terms of behavioral traits in birds, exploratory behaviors are documented to be linked to aggressiveness and boldness toward novel objects (Groothuis and Carere 2005). Because new information can be produced only if some environmental change occurs, in completely stable environments exploratory behaviors are unlikely to be adaptive (Mettke-Hoffmann et al. 2002). This idea is consistent with our results, showing that in more stable environments hummingbirds were less prone to visit new sources of nectar such as artificial feeders. Furthermore, in the most stable environment, the Atacama Desert, our focal species, the endangered Chilean woodstar, strongly prefers native vegetation over introduced plants even if the latter have high amounts of nectar (P. L. González-Gómez, personal observation). On the other hand, in extremely variable environments, exploratory behaviors could not be beneficial either (Mettke-Hoffmann et al. 2002). In this kind of environment the value of the new acquired information can decrease as rapidly as the environment changes. In addition, in stable, harsh environments exploratory behaviors could be energetically too expensive. In this sense, previous studies have shown that hummingbirds finely adjust their behavior accordingly to biotic conditions producing positive or negative energetic balance (González-Gómez et al. 2011b). Unfortunately, we do not have data on hummingbirds inhabiting the most changing or harsh environments year-round, but less exploration should be expected.

At the intraspecific individual level, the variation in behavioral profiles may explain variation in ecologically relevant behaviors such as foraging, dispersal, anti-predator behavior, and dominance, thereby allowing an individual to respond to environmental variability (McEwen and Wingfield 2003).

In our experiments on spatial memory both the temperate green-backed firecrown and the tropical long-billed hermit hummingbird could learn where sources of nectar were available and could match their foraging visits accordingly. These results are consistent with other field and laboratory tests of spatial memory in hummingbirds, showing that in the presence of identical visual cues, these birds revisited rewarding sites and avoided non-rewarding ones (Cole et al. 1982). Also, either they could distinguish among flowers that had been visited but were not totally depleted (Hurly 1996), or they paid more attention to spatial cues (Healy and Hurly 2003). Although in both species males visited a smaller number of flowers in the second phase of the experiments, showing that they could recall the spatial position of the best nectar, overall long-billed hermits inhabiting a more stable environment showed lower cognitive performance than did green-backed firecrowns that inhabited a more variable environment. This finding is consistent with the idea that environmental heterogeneity is positively related with cognitive performance (see above). Probably, heterogeneity by itself is a selective pressure for developing abilities that could help birds to respond appropriately under a variety of seasonal or unpredictable abiotic stimuli. In mountain chickadees (*Poecile gambeli*), for example, birds with less ability to explore new environments were significantly more likely to become dominant (Fox et al. 2009). These results suggest that behavioral profiles are related to the social status of individuals (Fox et al. 2009). Furthermore, the lower performance of the non-territorial individuals in both species in comparison with territorial individuals of their own species confirms this idea. When we compared only territorial males of the two species we found no significant difference in cognitive performance between the species. This finding supports the hypothesis that territorial males probably face a more variable environment, having to choose and acquire a territory first, and then, simultaneously having to defend the territory and display for females. In contrast, non-territorial males probably experience a constant, harsh, hostile environment. Not surprisingly, the ability of hummingbirds to remember and predict where and when nectar-rich flowers will be available results in higher energy rewards than would be obtained by subjects with poorer memory (González-Gómez et al. 2001a); therefore, the link between cognitive abilities and social status has no clear direction. If more dominant males have more energy available to them, they should perform better at defending territories. On the other hand, the challenges

involved in territorial defense and sexual display should stimulate the development of cognitive traits based solely on the more changing environment experienced by these birds. Therefore, the assessment of environmental heterogeneity should consider both biotic and abiotic conditions and more studies should be focused on the individual differences and on particular environments rather than having analyses focused on average performance.

Evaluating sources of nectar for Chilean woodstars

Chilean woodstars strongly preferred native nectar. This species was observed to be extremely reluctant to explore new sources of nectar and once it tried them, it reverted to the previous source (P. L. González-Gómez and C. F. Estades, personal observation). The poor exploratory abilities may be linked to the extremely stable environment in which this species occurs, where traditional sources of food are available year-round. In addition, variations in photoperiod, temperature, and precipitation at this site are extremely low. We speculate that in this environment the availability of new information (such as new sources of food or new environmental conditions) was so low that probably the pressure for developing exploratory behaviors relaxed. In this scenario, and knowing some of the cognitive traits on this species, we face the challenge of dealing with an endangered, behaviorally inflexible species. Our suggestions for strategies to be used in recovering this species include the restoration of the original habitat, and planting native plants. This scenario leads us to predict a critical situation in the coming years, mostly because the preferred native sources of nectar are slow-growing species. Globally, our conservation efforts should be focused on species inhabiting more stable environments, rather than on those living in changing ones.

Our results, at different levels of analysis strongly indicate the relevance of the environmental conditions in the development of cognitive traits such as spatial memory, problem solving, and exploratory behaviors. New findings could be obtained by carrying out cognitive studies in the field, using free-living animals that show what animals actually do in nature, instead of what they are able to do under artificial, controlled conditions. The field of cognitive ecology could greatly help to develop more efficient strategies for conservation biology.

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