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**CONSECUENCIAS ENERGÉTICAS DEL DESEMPEÑO DE
RASGOS COGNITIVOS**

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"I took much pleasure in watching the habits of birds, and even made notes on the subject. In my simplicity I remember wondering why every gentleman did not become an ornithologist" - Darwin



PAULINA L. GONZÁLEZ GÓMEZ

Ingresa al Magíster EBE, Facultad de Ciencias (Universidad de Chile) en 2002, proveniente del mundo de las humanidades. Es Cientista Político, Pontificia Universidad Católica de Chile (2000) y Administrador Público, Universidad de Chile (2000). Estuvo a punto de tener una vida profundamente miserable vestida de traje de dos piezas y tacos altos hasta que milagrosamente, y mas temprano que tarde, descubrió su verdadera vocación de bióloga - ornitóloga. Comenzó su carrera científica, su vida cambió radicalmente y ahora es infinitamente feliz. Su línea de investigación es fisiología ecológica y evolutiva y ecología cognitiva.

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RESUMEN

En el ámbito del forrajeo, los beneficios de las habilidades cognitivas están relacionados con la retención de información acerca de la calidad de los recursos disponibles, presentándose la oportunidad de sesgar el forrajeo a la explotación de parches de más alta calidad y por más tiempo, maximizando la energía neta ganada. Sin embargo, tanto la variación individual en retención de información a cerca del ambiente como las consecuencias de las variaciones en el desempeño de rasgos cognitivos como memoria y aprendizaje, sobre el balance energético de los individuos, han sido aspectos poco estudiados. Consecuentemente, el objetivo de este estudio es evaluar si existen diferencias intraespecíficas tanto intra como intersexuales en la retención cognitiva de relaciones espacio-temporales y si estas tienen efecto sobre el balance energético de *Sephanoides sephaniodes*, el modelo de estudio de esta tesis. Los experimentos para determinar la flexibilidad en la conducta de forrajeo de *S. sephaniodes* muestran que los picaflores pueden modular, al menos parcialmente la frecuencia de forrajeo para maximizar la energía obtenida. Por otra parte, machos territoriales fueron capaces de recordar el tiempo en que se encuentra disponible el mayor néctar acumulado, la calidad de éste y su ubicación espacial (i.e., memoria episódica), lo que es la primera evidencia sobre habilidades cognitivas complejas en nectarívoros. Se encontró una importante variabilidad a nivel individual en las habilidades espaciales y temporales lo que se tradujo en la energía obtenida por cada sujeto, lo que podría afectar la posibilidad de sobrevivencia y por lo tanto, la adecuación

biológica de los individuos.

En el picaflor chico, machos y hembras resultaron tener diferentes estrategias de forrajeo. Las hembras tienen una estrategia de forrajeo principalmente oportunista, presentando rasgos morfológicos sujetos a selección fenotípica que les confieren ventajas dada esta estrategia. El dimorfismo sexual también se manifestó en habilidades cognitivas. Los machos tuvieron significativamente mejor desempeño que las hembras lo que parece cercanamente relacionado a diferencias en la estrategia de explotación de recursos y presiones selectivas diferenciales actuando sobre machos y hembras. Estas diferencias se tradujeron en diferencias altamente significativas en energía ganada. El desarrollo de habilidades cognitivas complejas hasta ahora solo había sido descrito para pocos organismos. A través de los experimentos desarrollados, se propone un contexto microevolutivo para explicar la aparición de la memoria episódica y el desempeño cognitivo diferencial tanto intra como intersexualmente.

SUMMARY

In the foraging context cognitive abilities are pivotal. Higher abilities to remember the quality of food sources allow to bias the foraging trials to the richer patches and to avoid the poorer ones, maximizing the energy gained. Nevertheless, the variation in cognitive individual performance, and their consequences of the energy balance of individuals have been scarcely studied. In this context, the objective of this study is to assess intra and interspecific differences in cognitive performance and its energetic consequences at individual level in *Sephaniodes sephaniodes*, the study model of this thesis. My experiments to evaluate the foraging flexibility in green-backed firecrown hummingbird strongly suggest that hummingbirds can modulate at least partially their feeding frequency using cognitive abilities to match their visits to nectar replenishment rates in order to maximize the gained energy. On the other hand, territorial males were able to remember the nectar renewal rates, position and quality of nectar in flowers (i.e., episodic memory). I found an important variability in individual performances and consequently differences in energy gained by different subjects.

In *S. sephaniodes*, males and females had different resource exploitation strategies. Females had mainly an opportunistic strategy. Their morphological traits were subjects of phenotypic selection rendering an advantage given this strategy. I also found sexual dimorphism in cognitive abilities. The significantly higher cognitive performance observed in males appears to be closely related both to different resource exploitation strategies

and to different selective pressures acting upon males and females. The different cognitive performance observed among individuals and sexes produced dramatic differences in the energy gained. The development of complex cognitive abilities had been just described for a few of organisms. Through the experiments of this thesis I propose a microevolutionary framework to explain the development of episodic memory and differential cognitive performance as much intra as inter sexually.

INTRODUCCIÓN

Fenómenos tan disímiles como selección de hábitat y de presas, evasión de depredadores o selección de pareja entre otros, involucran el uso de capacidades cognitivas, permitiendo a los animales ajustar su conducta para responder de forma adaptativa a situaciones ecológicas cambiantes (Balda & Kamil 1998). Los beneficios en adecuación biológica de rasgos como memoria y aprendizaje han sido ampliamente documentados (véase Dukas 2004). En el ámbito del forrajeo, los beneficios de las habilidades cognitivas están relacionados con la retención de información acerca de la calidad de los recursos disponibles (Stephens 1991, Vásquez et al. 2006). Un individuo enfrentado a un ambiente donde los recursos se distribuyen parchosamente tiene la oportunidad de sesgar su forrajeo a explotar los parches de más alta calidad y por más tiempo (Valone & Brown 1989). Sin embargo, tanto los modelos primarios de forrajeo óptimo como de selección de hábitat (Fretwell & Lucas 1970, Charnov 1976) suponían que los individuos ya poseen plena información a cerca del ambiente que los rodea, pese a que un hecho notable dentro de los estudios de habilidades cognitivas es que no todos los individuos son capaces de retener información con la misma eficiencia (e.g., Hurly 1996). Poco se ha tratado por una parte, la variación individual en retención de información a cerca del ambiente y por otra, las consecuencias

de las variaciones en el desempeño de rasgos cognitivos como memoria y aprendizaje, sobre el balance energético de los individuos. El entendimiento de estos fenómenos es fundamental para comprender bajo qué condiciones, en qué sistemas y cuándo estas habilidades habrían evolucionado (Dukas 1999).

La selección natural favorece las conductas de forrajeo que tienden a maximizar la energía neta ganada, en el sentido de mantener un balance energético suficiente para cubrir las necesidades presentes de un individuo y acumular la energía para la reproducción futura, es decir, aumentar la adecuación biológica del individuo (Wolf & Hainsworth 1980, Stephens & Krebs 1986, Krebs & Kacelnik 1991). Con el fin de maximizar la energía neta ganada, la conducta de forrajeo puede ser vista como un proceso que se organiza en la siguiente secuencia: necesidad de alimento - búsqueda - detección - captura y manipulación - ingesta - digestión y asimilación. En cada etapa del proceso, el individuo debe enfrentar una serie de decisiones a cerca del esfuerzo de forrajeo, en el sentido de maximizar la diferencia entre beneficios y costos por unidad de tiempo (Hainsworth 1981, Houston & Krakauer 1993). Algunas de estas decisiones están asociadas a aspectos internos relacionados a la ingesta, tales como restricciones intestinales y de absorción del alimento y otras involucran factores externos a cerca de dónde forrajear, cuándo y por cuánto tiempo, sin embargo, las decisiones en cada una de las etapas se encuentran estrechamente ligadas (Hughes 1993). Por esta razón, este proyecto considerará aspectos que unen estas etapas, divididas en dos grandes secciones: (i) búsqueda, detección, captura y (ii)

manipulación e ingesta, digesta y asimilación. Ambas secciones contribuirán a explicar el efecto de las variaciones en el desempeño cognitivo sobre el balance energético de los individuos.

En las etapas de búsqueda, detección y captura del alimento, un individuo se ve enfrentado comúnmente a la elección de una estrategia de forrajeo relacionada básicamente con defender o no activamente un territorio (Carpenter 1987, Hixon 1987). En los picafloros, por ejemplo, un gran número de especies presenta la defensa activa de un territorio (Cody 1968, Stiles & Wolf 1970). Sin embargo, ello es válido para los machos de estas especies, dado que normalmente, las hembras son desplazadas de los territorios con los recursos de mejor calidad y más densos tendiendo a una técnica de forrajeo no territorial en parches más pobres y menos densos (Kodric-Brown & Brown 1978, Carpenter et al 1991, Temeles et al. 2005). Esta diferencia sexual en la ecología del forrajeo se encuentra cercanamente relacionada con diferencias morfológicas entre machos y hembras, presentando los primeros mayores masas corporales y largos de pico menores (Temeles et al. 2000, Temeles & Kress 2003). Este fenómeno sugiere que las decisiones en la cadena de organización de la conducta de forrajeo son diferentes entre machos y hembras, debido probablemente a un patrón de explotación de recursos diferentes entre ambos sexos. Sin embargo, este fenómeno ha sido largamente ignorado en la literatura debido a que tradicionalmente los estudios se han sesgado hacia la conducta y fisiología de los machos (e.g. Lopez-Calleja & Bozinovic 1995, Hurly 1996, Hurly & Oseen 1999, Hiebert et al. 2000, Hurly & Healy 2002, Lopez-Calleja

& Bozinovic 2003).

Una vez definida la estrategia de explotación de los recursos, estos deben ser detectados, lo que involucra información acerca de la distribución y la calidad de cada uno de los parches en los que se encuentran (e.g., Vásquez et al. 2006). La determinación del valor relativo de los recursos puede obtenerse a través de información obtenida durante el proceso de explotación, captando señales visuales (Marshall & Cooper 2004), olfativas (Schatz et al. 2003) o químicas (Hoefler et al. 2002). Sin embargo, existen ciertos recursos que no presentan diferencias en estos aspectos y donde la única fuente de información acerca de la calidad o disponibilidad de los recursos para el forrajeador es la información obtenida en visitas previas al parche, es decir, la propia experiencia retenida a través de la capacidad de memoria (Valone 1991, Hurly & Healy 1996, Vásquez et al. 2006). La memoria respecto de experiencias individuales pasadas (i.e., memoria episódica, *sensu* Tulving 1972, 2002) a diferencia de la memoria semántica que consiste en hechos a cerca del ambiente que rodea al individuo (i.e., vocabulario, geografía, operaciones matemáticas, entre otros), involucra la representación integrada de tres elementos fundamentales: qué, dónde y cuándo ocurrió un evento experimentado individualmente, tal que al recordar una característica de un episodio (e.g., cuándo ocurrió), automáticamente se recuerdan las otras (i.e., dónde y qué ocurrió), siendo la memoria episódica flexible a la adquisición de información en nuevas situaciones (Schwartz and Evans 2001, Clayton et al. 2003, Crystal 2009). Se ha sugerido memoria episódica para córvidos, ya que éstos son capaces de recuperar presas

almacenadas recordando con exactitud la ubicación, el tiempo de almacenamiento y calidad del alimento, incorporando nueva información acerca de la calidad de las presas y del contexto social en el que ellas fueron almacenadas (Clayton & Dickinson 1998, Emery & Clayton 2001).

La ecología de diversas especies sugiere que el fenómeno de la memoria episódica debiera presentarse frecuentemente ligado a necesidades reproductivas (i.e., parásitos de nidada o especies de sistema de apareamiento polígamo), mantención de jerarquías sociales y vigilancia de territorios, así como almacenamiento de presas (Clayton et al. 2001). La biología de animales que realizan secuencias de forrajeo tales como los picaflores (Wolf & Hainsworth 1990), sugiere fuertemente la presencia de los tres elementos de memoria episódica (Hendersson et al 2006, Healy et al. 2009). Los picaflores experimentan parches que presentan una disposición espacial variable de las flores que forrajean, es decir deben recordar dónde forrajear (Hurly & Healy 1996). En segundo lugar, las flores contienen néctar en concentraciones variables, siendo las de más alta concentración de sacarosa de más alta calidad, lo que favorece recordar qué es lo que se consume (Blem et al. 1999), y por último, la tasa de producción de néctar, es decir, el intervalo al cuál el néctar está disponible en las flores impone la necesidad de retener relaciones temporales, involucrando recordar cuándo se debiera visitar una flor para obtener la mayor cantidad de néctar entre las flores que componen los parches que son defendidos (Wolf & Hainsworth 1983, Valone 1991). En este contexto, la memoria es un importante elemento de la conducta de forrajeo en picaflores tanto entre parches de

flores (Gass & Sutherland 1985), como dentro de ellos para evitar recursos recientemente agotados (Wolf & Hainsworth 1991, Healy & Hurly 1995, Hurly & Healy 2002). Estudios preliminares han determinado la habilidad de estas aves de recordar la más alta concentración de sacarosa entre otras fuentes más pobres energéticamente (Blem et al. 2000), es decir, qué se ha consumido. Además, los picaflores son capaces de visitar consistentemente sitios que ofrecen recompensa y evitar los que no la ofrecen (Cole et al. 1982, Healy & Hearly 1998), y distinguir entre flores que han sido visitadas, pero no completamente agotadas (Hurly & Healy 1996), es decir son capaces de retener dónde forrajear. Por otra parte, los picaflores presentan la capacidad de ajustar las visitas de forrajeo a un determinado cronograma de producción de néctar (Gill 1988, Hendersson et al. 2006), lo que indica que recuerdan cuándo es conveniente realizar una visita. Pese a que la evidencia sugiere que los picaflores debieran presentar memoria episódica, no se ha realizado una evaluación integrada, en un mismo estudio, de los tres elementos que componen este fenómeno.

Las variaciones en la tasa neta de energía ganada como consecuencia de las variaciones individuales en el desempeño de la memoria en picaflores serían esperables dado el escenario energético que enfrenta este grupo. Este escenario sugiere fuertemente que existiría una ventaja selectiva en aquellos individuos que optimizan la ingesta de alimento debido a que los picaflores presentan (i) una dieta casi exclusivamente nectarívora que demanda el consumo de enormes montos de néctar repartido entre cientos de flores (Gass et al. 1999), (ii) la más alta tasa

masa-específica de metabolismo aeróbico (V_{O_2}/Mb) conocida entre vertebrados (Suarez et al 1991, Suarez 1992), (iii) vuelo de tipo estacionario con costos estimados en 14 veces el metabolismo basal, a lo que se suma (iv) la pérdida de calor por convección, efecto que además es incrementado por (v) un pequeño tamaño que aumenta la relación masa-unidad de superficie (Bicudo 1996, Gass et al. 1999, Fernandez et al. 2002). Se suman restricciones fisiológicas como (vi) baja capacidad de almacenamiento de grasas (Bicudo 1996, Suarez & Gass 2002) y (vii) una triple limitación (véase más adelante) que impone el proceso digestivo a la ingesta de alimento (Diamond et al. 1986, McWorther et al. 2005). Los mecanismos de ahorro energético tales como la disminución significativa en la actividad ante el aumento en los requerimientos energéticos y la capacidad de entrar en sopor, entre otros mecanismos, no son suficientes para compensar la necesidad de ingesta continua de alimento (Hiebert 1990, López-Callejas et al. 1997, McWorther et al. 2003, McKechnie & Wolf 2004).

La ingesta del alimento, como parte de la cadena de etapas de la conducta de forrajeo, involucra, por una parte, la energía contenida en el alimento, lo que determina el monto de alimento consumido y por otra parte, el número de eventos de forrajeo, lo que se traduce en la frecuencia de alimentación (Lopez-Calleja et al. 1997). Sin embargo, este proceso de decisión acerca de qué comer y cuán frecuentemente hacerlo, se encuentra íntimamente relacionado con el proceso de digestión-asimilación (Diamond et al. 1986). En este contexto, una pregunta habitual ha sido por qué los picaflores gastan solamente cerca del 20% de su tiempo despiertos

alimentándose, mientras el resto del tiempo se encuentran perchados (Stiles 1971, Hainsworth & Wolf 1972). La hipótesis es que la asimilación de energía en picaflores se encuentra más limitada por el proceso digestivo que por la capacidad de coleccionar alimento (Diamond et al. 1986, McWorther & Martínez del Río 2000). La morfología y cinética de un intestino tal como el de los nectarívoros impone una triple limitación a la ingesta de alimento. Primero, el tiempo de vaciado del buche puede limitar la frecuencia de alimentación (Diamond et al. 1986, Karasov et al. 1986). Segundo, la tasa de hidrólisis de sacarosa es cercana al máximo teórico, imponiendo límites a la asimilación de azúcar (McWorther & Martínez del Río 2000), y tercero, al mismo tiempo que la concentración de glucosa en el néctar incrementa también lo hace el tiempo de retención, reforzando la limitación de la frecuencia de alimentación (Lopez-Calleja et al. 1997, McWorther et al. 2005).

Aunque hay varios mecanismos fisiológicos que limitan el proceso de digesta-asimilación del alimento, los nectarívoros, como ya se mencionó, presentan capacidades cognitivas que facilitan la explotación eficiente del alimento (Gill 1988, Henderson 2006). Pese a lo anterior, no hay estudios acerca de la capacidad conductual de modular, al menos parcialmente, la tasa de ingesta de acuerdo a condiciones fisiológicas y ecológicas, forzando la ingesta al consumo del néctar de más alta calidad, aunque el tiempo transcurrido no haya sido suficiente para terminar completamente la absorción de la ingesta anterior, pero logrando así ajustar el intervalo de visitas a las fuentes más ricas de néctar.

En el contexto mencionado de las dos grandes secciones de etapas contenidas en el proceso de forrajeo se encuentran aspectos conductuales, fisiológicos y ecológicos que sugieren fuertemente que, por una parte, los picaflores debieran recordar relaciones espacio-temporales y que las diferencias en las capacidades de memoria debieran explicar diferencias en el balance energético de los individuos, considerado éste, como una medida indirecta de la adecuación biológica.

Objetivos

Objetivo General:

El objetivo de este estudio es evaluar el efecto potencial de la retención cognitiva de relaciones espacio-temporales sobre el balance energético de *Sephanoides sephaniodes*.

Objetivos específicos:

1. Evaluar la capacidad de *S. sephaniodes* de modular conductualmente la digestión de néctar para acoplar las visitas a intervalos de renovación de néctar.
2. Evaluar la capacidad de *S. sephaniodes* de recordar relaciones espaciales incluyendo la calidad de los recursos involucrados.
3. Evaluar integralmente la capacidad de *S. sephaniodes* de retener relaciones espacio-temporales (i.e., memoria episódica).
4. Describir el grado de dimorfismo sexual en las estrategias de forrajeo *S. sephaniodes* y el escenario de presiones selectivas en que se presenta.

5. Caracterizar el grado de variación intraespecífica en el desempeño de la memoria en un contexto de forrajeo y determinar si este es un rasgo con dimorfismo sexual.
6. Establecer los efectos de las diferencias intraespecíficas en la memoria episódica sobre el balance energético individual tanto en machos como en hembras de *Sephanoides sephaniodes*.

Hipótesis y predicciones

Hipótesis general

Dado que la ecología del forrajeo de los picaflores involucra como principal recurso al néctar producido por las plantas que se distribuyen heterogéneamente en el espacio, las presiones selectivas favorecerán a los individuos que son capaces de explotar más eficientemente este recurso recordando qué, dónde y cuándo el néctar se encuentra disponible, logrando así mayor energía neta ganada y por lo tanto regulando su balance energético.

Predicción 1. Los picaflores son capaces de recordar la ubicación del mejor recurso, tanto en una situación donde otras flores (parches) ofrecen ausencia de recompensa como entre flores que ofrecen recompensas de menor calidad.

Predicción 2: Los picaflores al enfrentar dos calidades de néctar con la misma tasa de renovación, son capaces de ajustar las visitas a la fuente más rica de néctar, sesgando sus visitas a ésta, aunque el tiempo teórico para la absorción de la ingesta anterior no haya transcurrido completamente.

Predicción 3: Si la variabilidad en el desempeño de rasgos cognitivos es

un rasgo con dimorfismo sexual en *S. sephaniodes*, entonces se espera que la variabilidad en la retención de relaciones espaciales y espacio-temporales se significativa a nivel intersexual.

Predicción 4: Si existen consecuencias energéticas del desempeño de rasgos cognitivos y variabilidad intraespecífica en dichos rasgos, entonces se espera que los individuos menos eficientes en la retención de relaciones espaciales y espacio-temporales, disminuyan significativamente tanto su éxito de forrajeo como su retorno energético en relación a aquellos individuos más eficientes.

Esta tesis se organiza de la siguiente manera. El objetivo 1, se explora en el manuscrito titulado "Flexibility of foraging behavior in hummingbirds, the role of cognitive abilities". En el se muestran los resultados de tres experimentos determinando cuál es la capacidad del picaflor chico de modular al menos parcialmente la tasa de ingesta de néctar.

En el capítulo 2 titulado "A field study of spatial memory in green-backed firecrown hummingbirds (*Sephanoides sephaniodes*)" investigamos la capacidad de estas aves de recordar la ubicación de la mejor fuente de alimento en ausencia de pistas visuales, el segundo objetivo planteado para esta tesis.

En el tercer capítulo ("Energetic consequences of episodic like memory in free-living hummingbirds") se muestran los resultados de experimentos en los que se determinó la capacidad de los picaflores para recordar la ubicación, temporalidad y calidad del néctar, tercer objetivo de la tesis.

El objetivo 4 de esta tesis se explora en el cuarto capítulo ("Is natural selection promoting sexual dimorphism in the Green-backed Firecrown Hummingbird (*Sephanoides Sephaniodes*)?"). En esta sección se muestran las diferencias intersexuales en los rasgos relacionados a las estrategias de explotación de recursos.

Por último, los objetivos 5 y 6 de esta tesis se desarrollan en el capítulo 5 ("Energetic consequences of sexual dimorphism in cognitive abilities") donde se evalúan y comparan tanto las habilidades cognitivas de machos y hembras de *Sephanoides sephaniodes* como las consecuencias energéticas de este desempeño.

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CAPÍTULO I

FLEXIBILITY OF FORAGING BEHAVIOR IN HUMMINGBIRDS, THE ROLE OF COGNITIVE ABILITIES.

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SUMMARY

It is generally agreed that physiology modulates foraging behavior. However, it has been less studied how much foraging preferences and cognitive performance influence foraging frequencies and how flexible is foraging behavior. Firstly, we evaluated digestive processing time and *ad libitum* nectar consumption of different nectar concentrations in green-backed firecrown hummingbirds (*Sephanoides sephaniodes*). Then, we carried out a field experiment to assess the ability to recall the nectar renewal rates between two groups of flowers with the same nectar concentration in absence of visual cues. In a second experiment, we recorded the ability of hummingbirds to remember different nectar renewal rates in flowers with different nectar concentration, with identical visual cues among all flowers. The results of this study suggest that *S. sephaniodes* can recall different nectar renewal rates and to adjust the rate of visits to them. When birds were confronted with two nectar qualities tied with different nectar renewal rates, they were able to integrate concentration and renewal rates to choose feeders that maximize the average rate of energy harvest, nevertheless, less successfully. Despite the physiological constraints, our results strongly suggests hummingbirds can modulate at least partially their feeding frequency using cognitive abilities to match their visits to nectar replenishment rates in order to maximize the gained energy.

Keywords: behavioral ecology, ecological physiology, energetics, individual performance.

INTRODUCTION

It is generally agreed that physiology modulates foraging behaviour, through different mechanisms. For example, enzymatic activity and intestinal processing time can limit foraging choices, dietary items, and foraging frequency (Diamond et al. 1986, Martínez del Río and Stevens 1989, Martínez del Río and Karasov 1990). Less obvious however, is how much foraging preferences and cognitive performance influence these aspects of foraging ecology and how flexible is the foraging behaviour. Hummingbirds which inhabit temperate zones are excellent models to study the role of cognitive abilities on feeding frequency and foraging choices mainly because in their foraging ecology converges diverse factors, like exceptionally high metabolic demands due to low environmental temperatures , and physiological and ecological constraints to food harvesting (Fernandez et al. 2002). The complex energetic interplay among a small body size, an energy expensive flight style and a nectarivorous diet demands the consumption of enormous amounts of nectar (Gass et al. 1999, Suarez and Gass 2002). However, physiological evidence indicates that energy assimilation in hummingbirds is limited by the crop emptying time and the digestive process rather than by food collection (Diamond et al. 1986, Karasov et al. 1986, McWhorter and Martínez del Río 2000). On the other hand, flowers, as a source of food, may impose relevant constraints to food harvesting (Stephens et al. 2007). Natural nectar replenishment rates impose that nectar availability varies throughout the day (McDade and Weeks 2004), and when nectar is available, the flowers pollinated by hummingbirds offer nectar which might fluctuate more

than 9 times in concentration and over 300 times in quantity (P. L. González-Gómez *un-published data*).

In order to facilitate efficient exploitation of nectar sources, hummingbirds are able to use their memory to recall the highest sucrose concentration sources among sources of different concentration (Tamm and Gass 1989, González-Gómez and Vásquez 2006). Moreover, they are able to adjust their visits in order to match nectar renewal schedules (Gill 1988, Henderson et al. 2006). In this context, the aim of this study was to evaluate the flexibility of feeding frequency of hummingbirds and the adjustment of the feeding frequency nectar renewal rates in order to maximize net energy gain. Henderson (2006) studied timing in free-living rufous hummingbirds *Selasphorus rufus* by assessing the ability of birds to recall two nectar renewal rates in the field. In the present study we carried out a similar field experiment with the green-backed firecrown hummingbird (*Sephanoides sephaniodes*), but we also went one step further. Firstly, we evaluated digestive processing time and nectar consumption of high and low nectar concentration. Then, we carried out an experiment similar to Henderson's (2006) study and evaluated the ability of hummingbirds to recall the nectar availability between two groups of flowers in the field. In a second experiment, we increased realism taking into account that at the study site, flower nectar varies up to four-fold in sugar concentration, and all flowers contain sugars in their nectars (Smith-Ramirez 1993). We also assessed under semi-natural conditions the ability of hummingbirds to remember different nectar renewal rates of flowers with high and low nectar concentration, with identical

visual cues among all feeders. Thus, if hummingbirds can match their flower visits to nectar replenishment schedules, we expect that the frequency of visits to the group of flowers with short nectar replenishment intervals is significantly higher than the frequency of visits to the second group of flowers with longer nectar replenishment schedules. If hummingbirds can modulate at least partially the feeding frequency when they are confronted with different qualities of nectar and different renewal rates, we predicted that hummingbirds will adjust the number of visits to higher quality nectar sources even when these nectar renewal rates could be lower than the necessary time to digest the previously consumed nectar.

METHODS

Study site

The study was carried out during fall and winter 2007-2008 in a site in the Andean foothills within the Estación de Investigaciones Ecológicas Mediterráneas of the Pontificia Universidad Católica de Chile, San Carlos de Apoquindo, central Chile (33°23'S, 70°31'W, 1100 m a.s.l.), about 20 km east of Santiago. The study site is comprised of sclerophyllous vegetation known as matorral which physiognomically can be described as an evergreen scrub. Between March and August, temperatures can fluctuate notoriously from over 30°C to minus 5°C. Climate and habitat are described in detail at www.bio.puc.cl/sca/.

Feeding rate and Time Processing Index (PTI)

Subjects were 6 male green-backed firecrown hummingbirds (5.97 ± 0.89 g) captured in the site 12 hours before the experiments. Trials were run between 8:00-12:00 h. Birds were maintained in individual 1.0x1.0x1.0 m cages with *ad libitum* 25% sucrose and supplemental fruit flies. Water was available *ad libitum*. Birds were released after the experiments were finished.

To assess the effect of sugar concentration on the interval between feeding bouts, we offered on consecutive days a 30% or 15% sucrose w/w solution to 6 hummingbirds. We recorded both intermeal intervals and the volume of consumed nectar. Volumetric food consumption was assessed using a graduated syringe enveloped with red paper as a feeder, inclined at a 45° angle. Intervals between feeding bouts were recorded with a video camera (Sony Handycam VHi8 CCD-TR818) for 2 hours (from 9:00-11:00).

To assess meal retention time of the two nectar qualities, we used a processing time index (PTI, Lopez-Calleja et al. 1997). Because birds mix both urine and feces in the cloaca, the apparent assimilated mass coefficient (AMC*, Karasov 1990) underestimates true assimilation time. As an indirect measurement of meal retention time we used PTI, which is the reciprocal of the excretion rate (see, Penry and Jumars 1986, Martínez del Río 1990). Birds were deprived of fruit flies for 48 hrs before the experiments. Additionally, they were fasted beginning one hour after sunset, previously to the experimentation day. To obtain excretion rates, we offered on consecutive days a 30% or 15% sucrose weight/weight solution to 6 hummingbirds. The order of presentation of

different nectar qualities was homogenized. After three hours of ingestion, a plastic sheet in the bottom of cages was removed to collect and measure the excreta at 5 min periods for two hours.

One nectar quality, two nectar renewal rates

Subjects were 6 free living male green-backed firecrown hummingbirds, which had feeding territories in the study site and actively defended territories. We randomly selected 6 territories for our experiments. In order to identify the subjects we could rely on their natural marks as well as their conspicuous territorial behavior. The subjects that were used for the analysis were those birds that were visible all the time during the trials. Since this species defend territories aggressively, and because territories are of small size (around 200 square meters), we decided to study a subject's behavior within a half-day of activity, and only when a subject could be followed entirely through his feeding territory by an observer (González-Gómez and Vásquez 2006). Therefore, trials were run between 7:30-12:00 h. Further, on a given day, we selected territories that were at least 40 m apart from each other. If during a trial, we lost track of a subject, we ended the trial and these data were not used in the analysis. Observations were carried out from hidden places (behind vegetation) at least 10 m from the feeder.

Initial Training

The experiments comprised a training period in which the subjects got used to the feeders, and defended them actively as part of their territories. We placed training feeders that contained 200 ml of 20% (weight/weight) sucrose in 20 different trees 5-15 m high (Tree species: *Quillaja saponaria*, *Litrea caustica*, *Eucalyptus globulus*) located in distinct territories where we had previously observed feeding hummingbirds. Nectar feeders were located at 1.5 m above the ground in a randomly selected branch. Within two 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 enveloped with red paper. Each feeder was filled twice a day in order to prevent for resource depletion and the eventual loss of territorial defense (González-Gómez and Vásquez 2006).

Experimental protocol

To present hummingbirds with nectar schedules we replaced the training feeders for two feeders with two groups of ten artificial flowers each (N=20). All the flowers contained the same sucrose concentration, 22.5% w/w. An artificial flower was an orange syringe tip with red paper petals mounted horizontally in an empty training feeder. Each flower was capable of holding 10 μ L. Both groups of flowers were located in a 50x50 cm wood vertical grid. The grid was hung 1.5 m from the ground from a branch within the subject territory. In every territory we randomly selected one group of flowers to be refilled every 10 min after the flowers were drained, hereafter, short interval flowers. The other group was refilled every 20 min, long interval flowers. We maintained the temporal schedule for two hours and we recorded the rate of visits to the flowers. A visit was defined as a subject inserting its bill in the feeder.

Two nectar qualities, two nectar renewal rates

In order to perform a more precise assessment of the ability to remember nectar qualities associated to nectar renewal rates, the experiment was carried out in a 6.0x6.0x5.0 m aviary exposed to field temperatures. Air temperatures during the experiments (5.57 ± 0.6 °C, mean \pm s.e.) were recorded using three data loggers (StopAway Tidbit Data Logger; <http://www.microdaq.com/occ/underwater/tidbit.php>). Temperatures were similar to

field temperatures. Subjects were 6 male green-backed firecrown hummingbirds (5.97 ± 0.89 g). The experiment included a 12 h training period in which the subjects became accustomed to use the feeders. The nectar dispensation system is composed of a solenoid valve connected to a recipient of nectar (500cc) and to four hoses (2 mm interior diameter each). Each hose dispensed nectar in a feeder. Nectar feeders consisted of a medicine dropper enveloped in red paper. The system was connected to a computer in order to automate the quantity and timing of nectar dispensation. To avoid nectar accumulation in the feeder between periods (see below), we inserted another hose into the feeder that expelled air and caused the nectar in the droppers to fall out, if not consumed. Each portion of nectar remained available for 60 s until it was consumed or expelled out. Feeders with identical visual cues (i.e., colour, size, material) were located in a 150 x 100 cm plastic grid, which was placed horizontally in the aviary, at 2 m of height.

To test the ability of hummingbirds to match the schedule of meals, we offered 8 identical feeders with equal quantities of nectar (60 ± 0.01 μ l/portion, mean \pm s.e.), half of them with 15% sucrose w/w (i.e., low quality) and the remainder with 30% sucrose w/w (i.e., high quality). Low quality and high quality nectar were dispensed at 3 and 6 min intervals, respectively. These nectar renewal rates are 50% lower than the theoretical inter-meal interval necessary to process 30% and 15% sucrose w/w nectar, respectively (see López-Calleja et al. 1997). A visit was defined as a subject inserting its bill into the feeder. We recorded the number of visits, nectar consumption, and the schedule of visits to the feeders during 4 hours (from 7:30-11:30 h).

RESULTS

Feeding rate and Time Processing Index (PTI)

Hummingbirds fed with 30% nectar *ad libitum* showed an intermeal interval (6.57 ± 1.13 min, mean \pm s.e., N=6) 5.8 times greater than individuals fed with 15% nectar (1.46 ± 0.15 min, mean \pm s.e., repeated-measures ANOVA $F_{0.05(1), 1,6}=35.25$, $p<0.001$). The meal retention time, assessed as PTI, was 2.8 times higher when hummingbirds were fed with 30% sucrose w/w nectar (0.207 ± 0.026 min* μl^{-1} , mean \pm se) than when they were fed with 15% sucrose w/w nectar (0.056 ± 0.008 min* μl^{-1} , mean \pm se; Two-way nested ANOVA $W_{1,13}=123.54$, $p<0.001$).

One nectar quality, two nectar renewal rates

Because the rate of visits among free-living hummingbirds was not significantly different (Table 1), we combined the data of the subjects for the analysis. Individuals visited short interval flowers significantly more frequently (9.19 ± 0.45 min, mean \pm se) than long interval flowers (16.17 ± 1.18 min, Table 1, Figure 1), however the ten minute flowers were not, visited twice as often as 20 min flowers (ratio of visits to 10:20 min flowers: 1: 1.76).

	Wald Chi-Square	df	P
Individual	1.938	5	0.86
Rate of visits	50.767	6	0.000

Table 1. Effect of nectar renewal rate (i.e., short or long interval flowers) in the rate of visits in *S. sephaniodes* (Nested ANOVA).

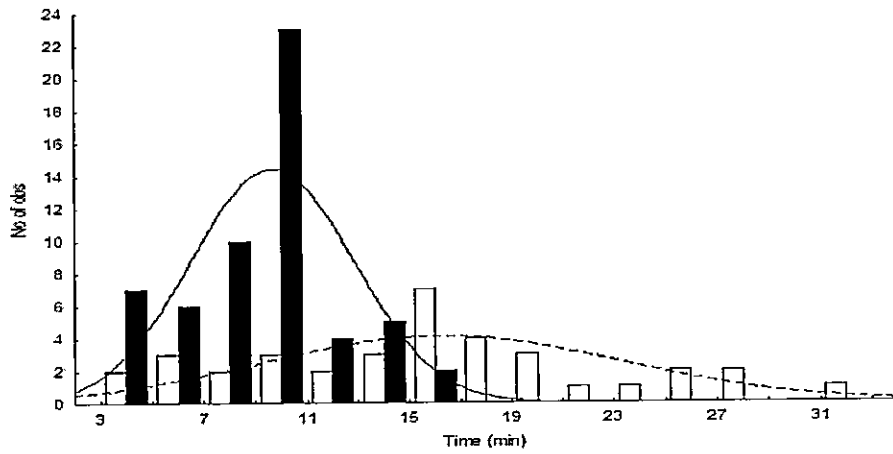


Fig 1. Frequency distribution of visits to long (i.e., 20 min, black bars) and short interval (i.e., 10 min, white bars) by *S. sephaniodes*.

Two nectar qualities, two nectar renewal rates

Four out of six individuals memorized successfully the availability of the best nectar, showing that some individuals have the ability to recall nectar renewal rates and to match the inter-meal interval to the best nectar availability (Figure 2).

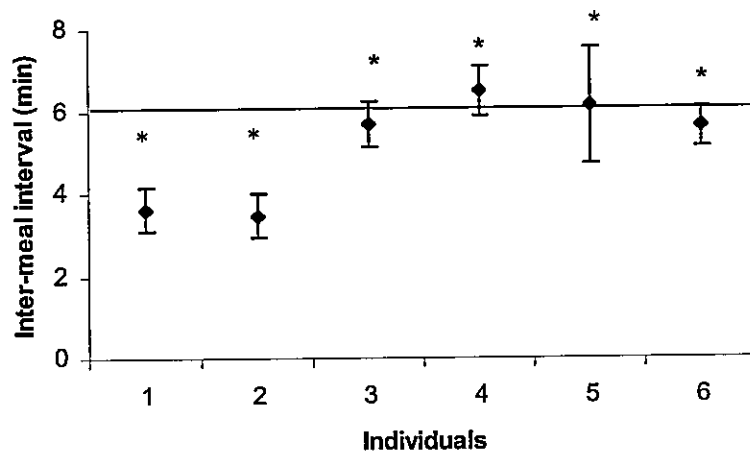


Fig 2. Individual matching of green-backed firecrown hummingbirds to the best nectar availability interval (mean \pm s.e). (*) Non significant differences from best nectar availability (i.e., 6 min, t test, $p < 0.05$).

Because the successful visits were positively correlated with energy intake, mean of energy intake differed significantly among individuals (One-way ANOVA $F_{5,98}=219.36$ $p < 0.001$, Figure 3).

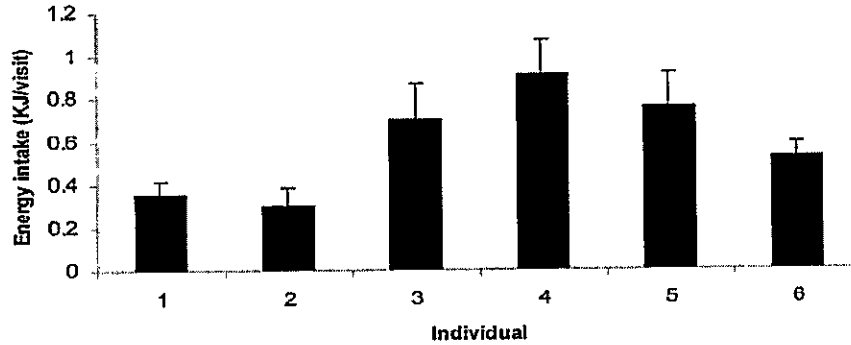


Fig 3. Energy intake per individual per visit (mean \pm s.e.) among individuals. Subjects 1 and 2 obtained significantly less energy than other individuals (Tukey multiple comparisons (Honest Significant Differences), for unequal sample size, (*) Significant differences, $P < 0.05$).

DISCUSSION

Free-living hummingbirds were able to recall different nectar renewal rates and to adjust the rate of visits to them in the absence of visual cues. Those results are coincident with previous studies demonstrating the ability of hummingbirds to match their visits to nectar renewal rates and more accurately to shorter intervals (Gill 1998, Brodbeck et al. 1998, Henderson et al. 2006). Higher variance in memorized distributions of longer intervals is consistent with scalar expectancy theory (Gibbon et al. 1977) which showed that the variance of memorized distributions increases with the magnitude of intervals between rewards. Because hummingbirds are tied to floral nectar dynamics, it is expectable that cognitive abilities facilitate efficient nectar exploitation (Cole et al. 1982, Wolf and Hainsworth 1990). In this context, the ability to establish temporal associations to find the higher quantity of accumulated nectar in the flowers is a central ability in the

foraging ecology of nectarivorous animals (Healy and Hurly 2004). However, an animal using flowers as food resource needs to remember more elements (i.e., quality and location) and to link them in one piece of information to be successful (Henderson 2006). Nevertheless, subjects were less successful in more complex tasks. Most of the birds confronted to two nectar qualities tied to two different nectar renewal rates were able to discriminate and select higher quality nectar sources; however two individuals failed in to remember the period in that the best nectar was available. One possible explanation is that some subjects take more time to acquire the information about the environment (Groothuis & Carere 2005, Elmore et al. 2009, Minderman et al. 2009).

Differences in individual performance, which are translated into total energy obtained per individual suggest that differences in information use, possibly via differences in individual cognitive abilities, could explain fitness differences in an energetically demanding context. Hummingbird species inhabiting temperate zones, such as *S. sephaniodes* in central and southern Chile, experience a wide range of temperatures and consequently, their thermoregulatory costs and foraging demands vary largely (Lopez-Calleja and Bozinovic 1995, Fernández et al. 2002). In this context, the increment of net energy gain rate is imperative because high metabolic rates make more difficult energy storage in hummingbirds (Hainsworth 1978). Territorial males may increase their foraging opportunities and therefore the chances to survive to a hard winter, if they have the capacity to recall the sugar content and location of a flower and to predict the time when the flower has the maximum quantity of nectar.

An important question in this context is about the margin in those behavioral aspects like preferences or the knowledge about the environment can be expressed given a physiological constraints scenario. In hummingbird foraging ecology, physiological aspects could explain some variability in feeding frequencies. At the same sugar concentrations, feeding frequencies shown by hummingbirds were almost 60% higher and PTI at 30% w/w were 0.35 times lower than frequencies previously reported for *S. sephaniodes* (López-Calleja et al. 1997, López-Calleja and Bozinovic 2003). The differences may hold the hypothesis that crop emptying rate and feeding rate may vary with ambient temperature and sugar concentration of the meal, among other factors (Karasov et al. 1986, Hainsworth 1989, Fernández et al. 2002). Despite the physiological constraints, our results strongly suggests hummingbirds can modulate at least partially their feeding frequency using cognitive abilities to match their visits to nectar replenishment rates in order to maximize the gained energy, when they confront a demanding environment (i.e., low ambient temperatures).

Although hummingbirds are excellent models to test the interplay between cognitive and physiological constraints in the resource exploitation strategies, the generality of our findings needs to be tested in organisms with different cognitive abilities and diverse resource exploitation strategies if we aspire to have a global picture about the relationship between physiological constraints and behavior.

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

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Abstract

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

Introduction

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

In the last decades the interest on evolutionary and ecologic aspects of cognition has prompted field research on animal learning and memory (Balda et al. 1998; Dukas 2004). Examples include food-

storing animals, such as birds and mammals capable of remembering spatial locations of a large number of scattered caches (Sherry 1985; Kamil & Balda 1990; Shettleworth & Hampton 1998). However, in spite of these studies, there is still a lack of knowledge about how species cope with environmental information (see Vásquez et al. 2006), and about how animals learn and use resource patches under natural conditions (see Balda et al. 1998).

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

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

Hurly (1996) studied one trial associative learning in rufous hummingbirds *Selasphorus rufus* by assessing the ability of birds to recall the location of a reward after a single learning experience. In the present study, we carried out a similar field experiment with the green-backed firecrown hummingbird (*Sephanoides sephanioides*), but we also went one step further. We first carried out an experiment similar to Hurly's (1996) study and evaluated the ability of hummingbirds to recall the spatial position of a previously experienced non-depleted reward, among rewarding and non-rewarding flowers. In a second experiment, we increased realism taking into account that at the study site, flower nectar varies up to fourfold in sugar concentration, and all flowers contain sugars in their nectars (Smith-Ramirez 1993). Therefore, in the second experiment we assessed the ability of hummingbirds to remember the best reward location (i.e. the flower with the highest concentrated nectar) among several less rewarding flowers (i.e. with less concentrated nectar), with identical visual cues among all feeders. We also compared the performance of birds between both experiments. If hummingbirds can retain the location of the best feeder, the number of visits needed to reach the best nectar in the second phase of each experiment should be significantly lower than

the number of visits in the first phase of each experiment. On the other hand, if hummingbirds are equally efficient to retain the location of the best feeder either among water feeders or among feeders with less concentrated nectar, we expected no difference between the number of visits in the second phase of the experiments.

Methods

Species and Study Site

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

Subjects were free-living male green-backed firecrown hummingbirds, which had feeding territories in the study site (see below) and actively defended territories. We randomly selected 20 territories for our experiments. We could rely on their natural marks as well as their conspicuous territorial behavior to identify different subjects. The subjects that were used for the analysis were those birds that were visible all the time during the trials. As this species defend territories aggressively, and because territories are of small size (around 200 m²), we decided to study a subject's behavior within a half-day of activity, and only when a subject could be followed entirely through his feeding territory by an observer. Therefore, trials were run between 8:00 and 12:00 hours. The aggressive display consisting of chases around the feeder accompanied with a distinctive shrill sound. Further, on a given day, we selected territories that were at least 40 m apart from each other. If during a trial, we lost track of a subject, we ended the trial and these data were not used in the analysis. Observations were carried out from hidden places (behind vegetation) at least 10 m from the feeder.

Initial Training

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

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

Experimental Protocol

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

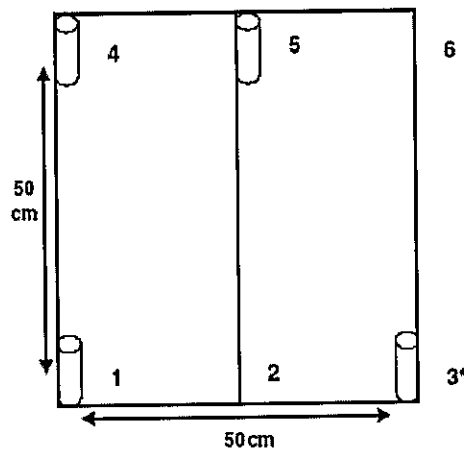


Fig. 1. Experimental vertical grid. Numbers indicate six feeder locations. Only four positions (i.e. four feeders) were used in each experiment (four feeders (tubes) are shown as an example). *High quality nectar feeder

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

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

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

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

Data Analysis

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

Results

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

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

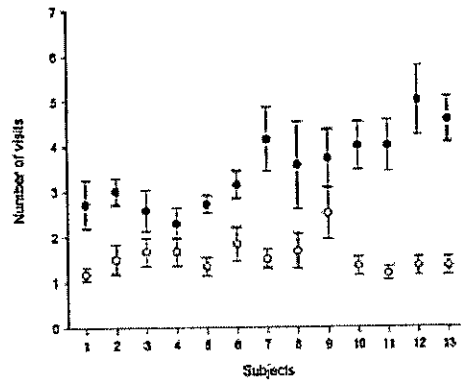


Fig. 3: Number of feeding visits performed by individuals of individual performance of green-backed firecrown hummingbirds in the second experiment. Black dots, search phase and white dots, return phase (mean \pm SE, $n = 6$ trials for each subject)

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

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

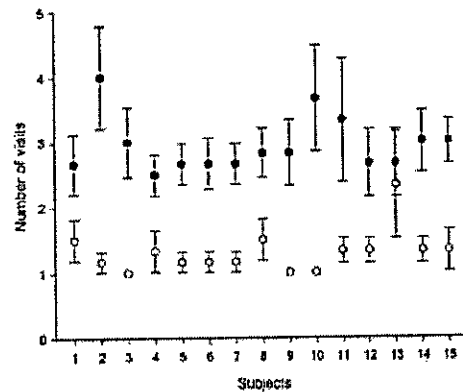


Fig. 2: Number of feeding visits performed by individuals of green-backed firecrown hummingbirds in the first experiment. Black dots, search phase and white dots, return phase (mean \pm SE, $n = 6$ trials for each subject)

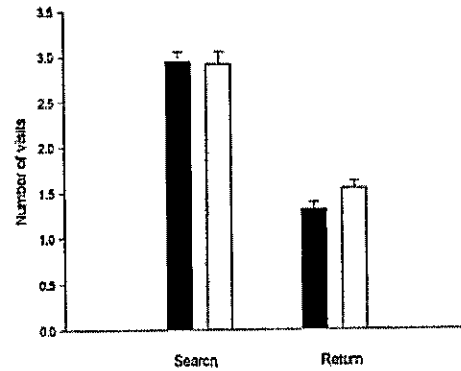


Fig. 4: Average performance per individual across experiments. The search phase between both experiments are not significantly different; however, the return phase in the first experiment (black bars) is significantly lower than in the second experiment (white bars; mean \pm SE). See text for statistics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

Discussion

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

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

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

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CAPÍTULO III

ENERGETIC CONSEQUENCES OF EPISODIC LIKE MEMORY IN FREE-LIVING HUMMINGBIRDS

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MANUSCRITO EN FORMATO PARA SER ENVIADO A ANIMAL BEHAVIOUR

ABSTRACT

Episodic memory has been described as the ability to recall personal past events, involving what, where and when an event has been experienced. Through learning animals acquire new information shaping episodic memory for novel situations such as food procurement. Nectar, the primary food of hummingbirds, is dispersed in hundreds of flowers and it varies in concentration and renewal rate. Therefore, a hummingbird that remembers what, where and when the nectar becomes available will have higher energy intake when compared to random foraging. We carried out a field experiment with green-backed firecrown hummingbirds (*Sephanoides sephaniodes*) (n=10). We evaluated the ability to recall, in novel situations, the location, nectar quality and renewal rate of the most rewarding flowers among several less rewarding flowers with identical visual cues.

Our results identify a novel behavioural strategy in hummingbirds, which were able to remember the most profitable nectar sources and flower position and to adjust their visits to nectar renewal rate. Cognitive performance varied among individuals implying up to 1.5-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.

INTRODUCTION

Episodic memory has been described as the ability to recall personal past events, involving what, when and where an individual event has been experienced (Tulving 1972; Tulving 2002). The integrated representation of its elements implies that when one element is recalled (e.g., when), the other elements (what and where) are also brought to the present, and it must be flexible to the acquisition via learning of new information in novel situations (Schwartz and Evans 2001; Clayton et al. 2003).

Cognitive abilities are pivotal to the performance of many behavioral traits in animals and hence they could have evolutionary impact through their effect on fitness. In this context, the ecology of diverse species strongly suggests that episodic memory should be present frequently, tied to foraging or reproductive necessities (Clayton and Dickinson 1998; Emery and Clayton 2001).

Nectarivorous animals, like 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 it varies in concentration and renewal rate. Therefore, a hummingbird should remember where, what and when the best nectar will be available in order to forage most efficiently. It means to perform the lowest number of visits in order to decrease the travel cost and predation risk and simultaneously to obtain the highest energy reward. Preliminary studies have determined that hummingbirds can recall the highest sucrose concentration among energetically poorer resources (i.e., what it was consumed, Blem et al. 2000; González-Gómez and Vásquez

2006). Hummingbirds are able to visit consistently the locations that offer a reward and to avoid non-rewarding sites (Cole et al. 1982; Healy and Hurly 1998), and to distinguish between visited but not totally drained flowers (Hurly and Healy 1996)(i.e., hummingbirds are able to remember where to forage). Moreover, hummingbirds can adjust the visits to a determined renewal nectar schedule relatively independent of the digestive constraints (Gill 1988; Hendersson et al. 2006) . Therefore they can remember when the nectar is available. Thus, different studies suggest that hummingbirds accomplish the three aspects of learning that fulfill a general definition of episodic memory (Hendersson et al. 2006).

In addition, hummingbirds are excellent candidates to possess episodic-like memory due to the complex energetic scenario that they experience. The energetic cost of hovering demands the consumption of enormous amounts of nectar, which is scattered among hundreds of flowers (Gass et al. 1999). A hummingbird returning to a recently emptied flower can experience a lower rate of energy gain compared to exploiting a renewed flower (Cole et al. 1982). Consequently, cognitive abilities are expected in hummingbirds in order to avoid depleted flowers (Cole et al. 1982; Hurly 1996).

In the present study we carried out a field experiment with males of the green-backed firecrown hummingbird (*Sephanoides sephaniodes*). We evaluated the ability to recall, in novel situations, the location, nectar quality and renewal rate of the most rewarding flower (i.e., the flower with the highest nectar concentration) among several less rewarding flowers (i.e., less concentrated

nectar) with identical visual cues. If hummingbirds can recall 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), and they should visit the flower position during the period when nectar is available. If memory has energetic consequences, hummingbirds that can recall the best nectar location and schedule, should have a higher rate of energy gain than individuals with poorer performance.

MATERIALS AND METHODS

Study site and subjects

The study was carried out 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 a.s.l.). Subjects were free living male green-backed firecrown hummingbirds, which had feeding territories in the study site (see below) and actively defended territories. We randomly selected 20 territories for our experiments. We identified individuals from plumage differences as well as their conspicuous territorial behavior. Trials were run between 8:00-13:00 h. The subjects used for the analysis were those birds that were visible continuously during the trials. If we lost track of a subject during a trial, we ended the trial and these data were excluded from the analysis.

Observations were carried out from hidden places (behind vegetation) at least 10 m from the feeder.

Initial Training

The experiments comprised a training period in which the subjects got used to the feeders, and defended them actively as part of their territories. For the training period, we placed one feeder containing 200 ml of 25% sucrose in each of the 20 different territories. Feeders were located 1.5 m above the ground on a randomly selected branch. Within two 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 enveloped with red paper. Each feeder was filled twice a day in order to prevent for resource depletion and the eventual loss of territorial defense.

Nectar quality training

On the day of the experiment, we replaced the training feeder for a vertical grid (see below) with two feeders, one of them with 15% weight/weight sucrose (low quality) and the other one with 30% w/w sucrose (high quality). The feeders were visually identical to training feeders. 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

To present hummingbirds with nectar schedules associated with nectar quality, following the initial training, we replaced the feeders for two feeders with two

artificial flowers in the bottom. An artificial flower was an orange syringe tip with red paper petals mounted horizontally in an empty training feeder. Each flower was capable of holding 30 μ L. The quality nectar flowers (i.e., 30% sucrose) were refilled every 10 min after the flowers were drained. Low quality flowers (i.e., 15% sucrose) were refilled every 5 min. We maintained the temporal training for one hour or until the subject adjusted the visits to the best nectar schedule.

Episodic memory protocol

The experiments were designed to assess the ability of birds to remember the position and renewal schedule of a rewarding flower among low-rewarding flowers after a single learning experience (see below). We constructed a 50 x 50 cm wooden frame with a middle vertical axis. We identified nine points in the grid where feeders were located. During the experiments, only three points in the grid had feeders. At the beginning of each trial, each flower contained 30 μ L of sucrose liquid. For each trial, three feeders were assigned to three randomly chosen points among the nine points of the grid. One of them was refilled with high quality nectar each 10 min and the others were refilled with low quality nectar each 5 min.

We performed 6 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 drained the most rewarding feeder. In order to prevent the bird

from recognizing the best flower by some uncontrolled visual cue, the target flower was changed to a similar one with the same sucrose concentration between phases. In the second phase (returning phase), the hummingbird faced the same array of feeders. We recorded the position and the time in which feeders were revisited. After finishing the revisit to the grid, the trial was ended, and the following trial was initiated after 10 minutes. A new position for the rewarding feeder in the next trial was randomly selected. In order to prevent that the subject could recognize the observer as a visual cue of nectar availability, we pretended to refill the flowers randomly at least three times during the trials.

Data analysis

To assess spatial memory we evaluated the differences between the averages of individual number of visits in both phases of the experiment through a Friedman test with multiple observations per cell (Zar 1999). To evaluate the temporal memory performance, we compared the individual means of intermeal interval with the best nectar schedule through a t test. To integrate the ability to remember the time (when), the spatial location (where), and the content of the feeder or nectar quality (what), we performed a Spearman correlation between the identity of the first feeder (i.e., 15% or 30%) visited in the second phase of the experiment, independently of the presence of the reward and the intermeal time of the visit. To evaluate the energetic consequences of the ability to track

nectar quality of best sources, we transformed the mean of nectar obtained in the second phase of the experiment to energy units (joules, hereafter, j). The individuals were assigned to one of three groups depending on the energy gained in the trials. To assess the differences among group, we performed a nested analysis of variance for unbalanced samples (Sokal and Rohlf 1995). Data were tested for autocorrelation and they met the assumptions for each test.

RESULTS

The number of visits in the search phase (2.33 ± 0.14 , mean \pm SE, $n = 10$) was significantly higher than in the return phase (1.1 ± 0.05 , $n = 10$, Friedman Test, Friedman's $\chi^2_r = 18.03$ $p < 0.001$). Individually, in the return phase, eight out of ten subjects showed the ability to find the best nectar location in fewer visits, in comparison to the search phase (Fig. 1).

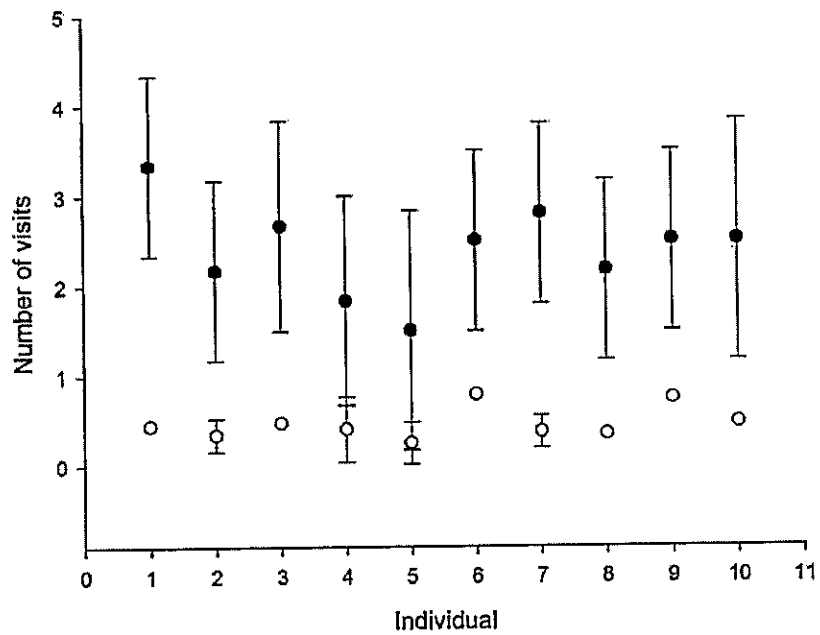


Figure 1. Number of feeding visits performed by individuals of *S. sephaniodes*. Black dots, search phase and white dots, return phase (mean \pm SE, $n=6$ trials for each subject).

The intermeal interval did not differ significantly from nectar interval for the best nectar for the same eight individuals (Fig. 2).

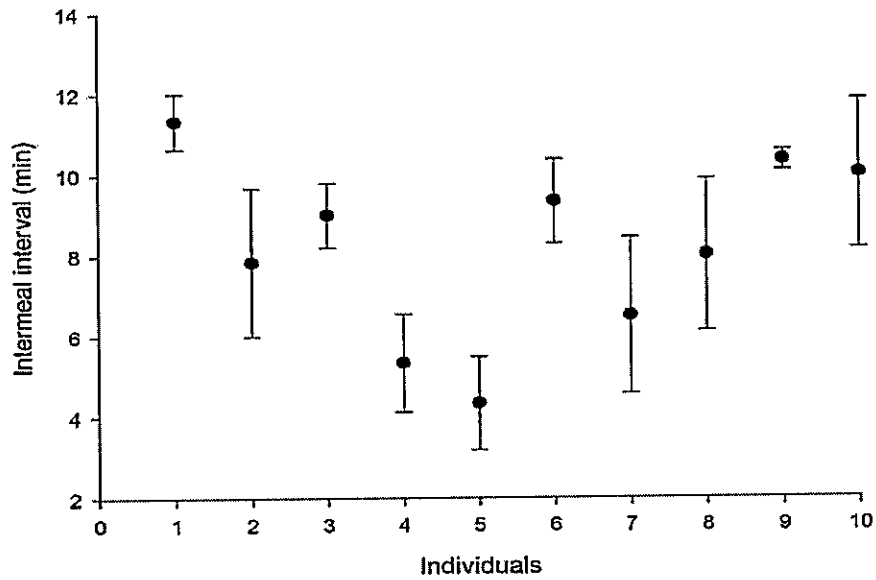


Figure 2. Adjustment of green-backed firecrown hummingbirds to nectar schedules of the best nectar source (mean \pm SE, n= 6 trials for each subject). Line interval of the best nectar source. * Significantly differences from the interval of the best nectar source, t test, $p < 0.05$.

There is a significant positive association between spatial and temporal memory (Spearman correlation $t_s = 3.38$, Spearman $R = 0.60$, $p < 0.05$), suggesting that the individuals that successfully remember the nectar quality and location can accurately recall the nectar availability schedule as well (Fig. 3).

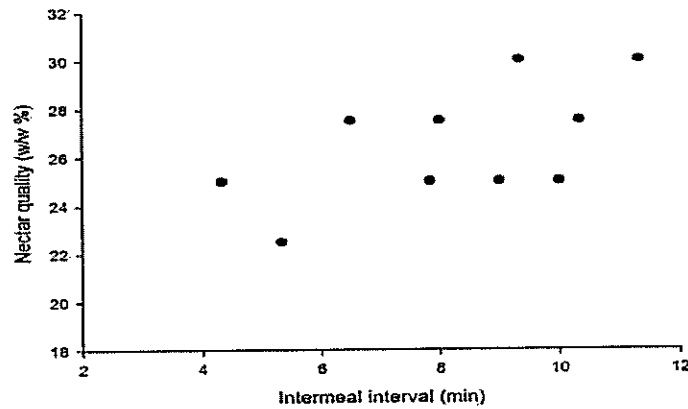


Figure 3. Association between spatial and temporal memory of *S. sephaniodes* (N=10).

The energy intake was 1.37 times higher in individuals (N=4) that could remember the location, quality and nectar schedules compared to individuals (N= 2) that were not able track those characteristics (Table 1).

Source of variation	SS	df	MS	F
Energy intake	635	2	317,5	29.633***
Individuals	75	7	10,714	0.122
Error	4383,333	50	87,667	

Table 1. Effect of cognitive ability in energy reward of *S. sephaniodes*. Nested ANOVA. ***
p<0.001.

Furthermore, the individual who had the best performance (individual number 6, see Fig. 4) obtained 1.5 times more energy than the individual with the poorest performance (individual number 4, Fig. 4).

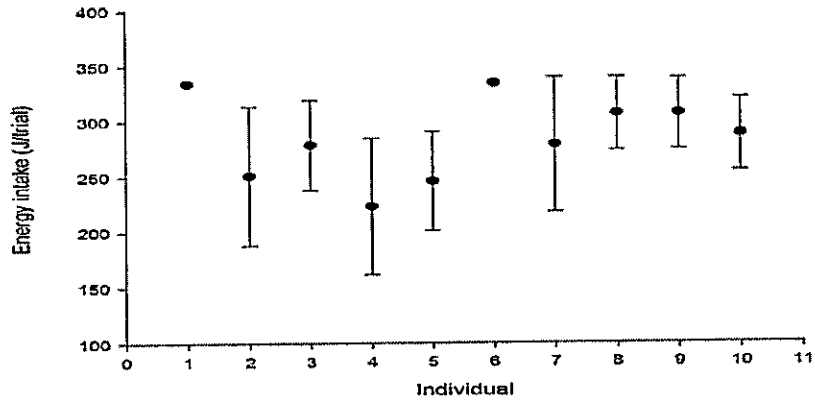


Figure 4. Energy reward obtained by individuals of green-backed hummingbirds as a result of the combination of the performance of spatial and temporal memory (mean \pm SE, $n=6$ trials for each subject). Numbers and lines identify three groups of individuals in ascendant order of performance.

DISCUSSION

The smaller number of visits in the second phase of the experiment and the adjustment to nectar schedules; strongly suggest that hummingbirds use cognitive abilities in order to exploit nectar sources efficiently. As far as we know, this is the first demonstration that free-living hummingbirds can remember in a single study, the three components of episodic-like memory. Although we cannot describe autothetic consciousness (i.e., conscious experience of self), since hummingbirds do not have the ability to express their experience verbally (Tulving and Markowitsch 1998), we showed that hummingbirds can remember

what, where and when something happened and, more important, that they can apply this knowledge to new situations like different experiment trails (Schwartz and Evans 2001; Clayton et al. 2003). Our experiment resembled natural conditions which hummingbirds experience in natural environments. For example, if nectar was not eaten, it is reabsorbed by the flower (Nicolson 1995) or consumed by an intruder. We avoided testing artificial situations like degraded nectar which is mostly nonexistent in nature, despite losing accuracy in order to detect the internal mechanism acting in the memory process.

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

We found an important variability in spatial and temporal cognitive abilities among individuals. Because in hummingbird foraging ecology these capacities are strongly tied to nectar rewards (Gass and Sutherland 1985; Healy and Hurly 2003), we suggest that differences in cognitive abilities could be closely related with differential fitness. Green-backed firecrowns experience winter temperatures below -5°C , representing an extremely challenging

energetic scenario. In hummingbirds, foraging success is imperative because, among vertebrates, these birds display the highest mass specific rates of aerobic metabolism (Suarez 1992; Suarez and Gass 2002). High metabolic rates likely make it difficult for hummingbirds to store energy (Hiebert 1993). Although hummingbirds have the possibility to use strategies to save energy (e.g., through torpor), the ability to maintain or increase the body mass is a trait directly related to fitness, because it can directly affect their survival, especially in periods of high energetic demand and high thermoregulatory costs (Hainsworth 1978). If territorial males have the ability to recall the sugar content and location of rich flowers, and the ability to predict the time when the flower will offer the maximum quantity of nectar, they will increase their foraging opportunities and therefore the chances to surviving a hard winter.

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CAPÍTULO IV

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ORIGINAL ARTICLE

Is natural selection promoting sexual dimorphism in the Green-backed Firecrown Hummingbird (*Sephanoides Sephaniodes*)?

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Abstract In many hummingbird species there is an opposite pattern of sexual dimorphism in bill length and other morphometric measures of body size. These differences seem to be closely related with differences in foraging ecology directly associated with a different resource exploitation strategy. The aim of this study was to assess if natural selection is acting on wing length and bill size in hummingbird males and females with different resource exploitation strategies (i.e., territorial males and non-territorial females). If competition for resources promotes sexual dimorphism as a selective pressure, males should be subjected to negative directional selection pressure for wing length and no selection pressure over bill size, while females should undergo positive directional selection pressure for both bill size and wing length. The morphometric data we collected suggests that there is no selection for wing length and bill size in male hummingbirds. In contrast, our females exhibited positive directional selection for both wing length and bill size. Although we cannot reject sexual selection acting on sexually dimorphic

traits, this study suggests that natural selection may promote sexual dimorphism in traits that are closely related with hummingbird foraging ecology and resource exploitation strategies.

Keywords Hummingbirds · Phenotypic selection · Sexual dimorphism

Introduction

In species that exhibit behavioral and morphological sexual dimorphism associated to different resource exploitation strategies, it is expected that natural selection will act differentially in each sex, promoting those key traits of the resource exploitation strategy that increase competitive abilities and, consequently, the fitness of the individuals. In many hummingbird (Trochilidae) species there is an opposite pattern of sexual dimorphism in bill length and other morphometric measures, such as body mass and size (Bleiweiss 1999). These differences seem to be closely related to differences in foraging ecology and resource exploitation strategies (Temeles et al. 2000; Temeles and Kress 2003). In species where males are territorial and females are not, dominant males usually secure access to dense patches of nectar-rich flowers, while subordinate females either perform rapid intrusions into male territories to raid the good resources or are forced to forage in nectar-poor, scattered resources (Kodric-Brown and Brown 1978; Temeles et al. 2005).

An alternative hypothesis, that of wing disc loading (see below), suggests that territorial hummingbird species (or sexes) tend to have shorter wings than non-territorial species or sexes (Feisinger and Chaplin 1975; Feisinger and Colwell 1978; Kodric-Brown and Brown 1978; Carpenter

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et al. 1993a). Wing disc loading is defined as the ratio between body mass and a disc whose diameter is the wing span. The relatively shorter wings of territorial birds (i.e., higher wing disc loading) likely confer higher maneuverability, acceleration, and speed. Simultaneously, the power output required to hover increases with the increment in wing disc loading (Feinsinger et al. 1979). Therefore, territorial individuals spend more energy in hovering than non-territorial birds, but they compensate the higher energetic cost of territory defense with a better access to nectar-rich resources.

Territorial behavior likely causes the relaxation of the handling time because of the relatively unlimited access to the floral resources contained in territories. In contrast to territorial birds, non-territorial individuals have developed traits that increase resource exploitation, such as longer bills. Laboratory experiments have shown that individuals with longer bills are more efficient in exploiting floral resources (Temeles and Roberts 1993). These longer-billed individuals have shorter handling times and higher maximum extraction depths than birds with shorter bills at flowers having longer corollas (Temeles 1996; Temeles et al. 2002).

In hummingbirds, foraging success is imperative because these birds display the highest mass specific rates of aerobic metabolism among the vertebrates (Suarez et al. 1991; Suarez 1992). High metabolic rates likely make it difficult for hummingbirds to store energy (Hainsworth 1978). The allometric prediction of the daytime fat storage for a 3- to 5-g hummingbird is just about 5% of its body mass (Calder 1974), which is roughly equivalent to the amount needed to meet their nighttime metabolic demands if they remain normothermic (Powers et al. 2003). Although hummingbirds have the possibility to use strategies to save energy (e.g., torpor), the ability to maintain or increase body mass (assessed as body condition) is a trait directly related to fitness, because it implies the probability to survive, especially during periods of high energetic demand, such as high thermoregulatory costs or the pre-migration stage (Carpenter et al. 1993b; Hiebert 1993).

Sephanoides sephanioides (Green-backed Firecrown Hummingbird) is a species that lives in central and southern Chile, where they can experience field winter temperatures below -5°C . This temperature represents an extremely challenging scenario for hummingbirds. This species exhibits morphological and behavioral sexual dimorphism. Males have a significantly greater body mass and body size and a smaller bill size than females. Male hummingbirds of this species also actively defend feeding territories, while females do not (González-Gómez and Vásquez 2006); in an experiment with 28 artificial nectar feeders, male birds actively defended the feeders while females did not. The same pattern seems to occur under

natural conditions (authors, personal observations). In addition, the foraging behavior of females consists of in fast intrusions into male territories until they are aggressively chased by the male territory owner (P. L. González-Gómez, unpublished data). An indirect source of evidence indicating that female *S. sephanioides* may be much more mobile than males comes from the capture rates for both sexes in mist nets. When nets were distributed in the landscape in a pattern unrelated to the location of flowers, females were captured in a much higher proportion than males (approximately 3:1; see sample sizes in Methods). This difference can be partially explained by the fact that more mobile birds have a higher probability of being captured in mist nets (Rensen and Good 1996). In contrast, when the nets were placed close to flowering patches in order to maximize the chances of capturing Firecrowns (i.e., for student training), the captures of males significantly outnumbered those of females (C.F. Estades, personal observation).

The aim of the study reported here was to analyze whether morphometric data indicate the presence of differential phenotypic selection pressure on wing length and bill size for female and male *S. sephanioides*. We tested the prediction that, if competition for resources promotes sexual dimorphism as a selective pressure, males should be under negative directional selection for wing length and show no selection for bill size, while females should undergo positive directional selection for bill size and wing length. In our analysis we used body condition as a fitness proxy.

Methods

We worked with *S. sephanioides* in the coastal Maulino forest region of central Chile from 1999 until 2006. We caught birds using mist nets as part of a larger project aimed at studying the entire avifauna of the area. For each bird, we measured folded wing length (distance from carpal joint to the tip of the longest primary), bill length (i.e., exposed culmen), tarsus length, total length, tail length, and body weight. We sampled a total of 106 males and 344 females. Folded wing length was measured to the nearest millimeter with a ruler, while bill and tarsus length were measured to the nearest 0.1 mm with Vernier calipers. Wing disc loading and power hovering were calculated following Feinsinger and Chaplin (1975). Differences between males and females were assessed through a *t*-test.

Assessment of phenotypic selection

The ideal approach to assessing phenotypic selection is the use of a direct measure of fitness, such as reproduction or

survival. However, testing the association of wing and bill length and direct measures of fitness in free-living Green-backed Firecrews is a formidable task due to their migratory character, non-variable clutch size, and polygamous reproductive system with no participation of males in rearing tasks, among others. Therefore, we used a body condition index as a surrogate for individual fitness due to the close relation between the probability of surviving high thermoregulatory demands and the body conditions of individuals.

To avoid the sampling bias due to interannual variation in selective pressures, we performed a phenotypic selection analysis on wing length and bill size for males ($n = 47$) and females ($n = 150$) using data from January 1999 until November 2000. To evaluate the potential of the traits (i.e., wing and bill length) to evolve under selection, we used multivariate statistical techniques, estimating the linear and nonlinear selection coefficients by following the methodology of Lande and Arnold (1983). Multiple selection analyses enabled us to estimate direct linear and nonlinear selection gradients as a measure of direct selection acting on a trait, while holding the effects of other traits constant. This provides information on the strength, direction, and form of the within-generation selection surface (Lande and Arnold 1983; Lynch and Walsh 1998).

To describe the direct force of selection acting on the phenotypic character I , excluding indirect selection, we applied the multivariate model of Lande and Arnold (1983):

$$\omega = \alpha + \sum_{i=1}^n \beta_i z_i + \varepsilon \tag{1}$$

where α is a constant, β_i represents the average slope of the selection surface in the plane of the character I , and ε is an error term. In Eq. 1, the linear gradient of selection, β_i , provides information on the direction and magnitude of the change expected after current selection. The nonlinear selection gradients, γ (Eq. 2), describe the nature of selection on quadratic deviations from the mean for both single and pairwise combinations of characters. Nonlinear gradients were estimated from the second-order coefficients of the following model:

$$\omega = \alpha + \sum_{i=1}^n \beta_i z_i + \frac{1}{2} \sum_{i=1}^n \gamma_{ii} z_i^2 + \sum_{i=1}^n \sum_{j < i}^n \gamma_{ij} z_i z_j + \varepsilon \tag{2}$$

where γ_{ii} represents the curvature of the relationship between the character I and relative fitness. A value of $\gamma_{ii} < 0$ implies downward concavity and stabilizing selection acting upon the character, while $\gamma_{ii} > 0$, reflects upward concavity, implying disruptive selection. The correlational selection gradient, γ_{ij} , reflects the extent to which selection acts upon the correlation of traits I and j . The significance of

β and γ in Eqs. 1 and 2, respectively, was determined directly from the regression coefficients after the effects of all other parameters had been removed (Medel et al. 2003). Individual measures of fitness (body condition index—i.e., body mass/tarsus length) were converted to relative fitness, with a mean value of 1 within a population. Wing length and bill size were standardized to a mean of zero and unit variance. Thus, the selection coefficients presented here are standardized selection coefficients.

Results

Morphometric data

Total body length and wing length were significantly higher for males (males were 1.25-fold heavier than females; Table 1). In contrast, females had bills 1.11-fold longer than those of males. Tarsus length was independent of other morphological measures, such as total body length and body mass for males ($R^2 = 0.020$, $F_{2,44} = 0.46$, $P = 0.64$) and females ($R^2 = 0.019$, $F_{2,147} = 1.46$, $P = 0.24$). Wing disc loading and power hovering were significantly higher in males than in females (Table 1).

Selection analysis

For females, the multiple linear regression model of relative body condition index on wing length and bill size, including the interactions between the traits, was significant, suggesting that at least one of the traits might be significantly related to fitness ($F_{5,144} = 3.701$, $P = 0.003$, $R^2 = 0.11$). The linear selection gradient was positive and significant for wing length and culmen size (Table 2, Fig. 1). The multiple non-linear regression model of relative fitness (body condition index) on wing and bill length was not significant, indicating that there is no evidence of stabilizing, disruptive or correlational selection on the traits. In this context,

Table 1 Morphometric data from males and females of *Sephanoides sephanoides*

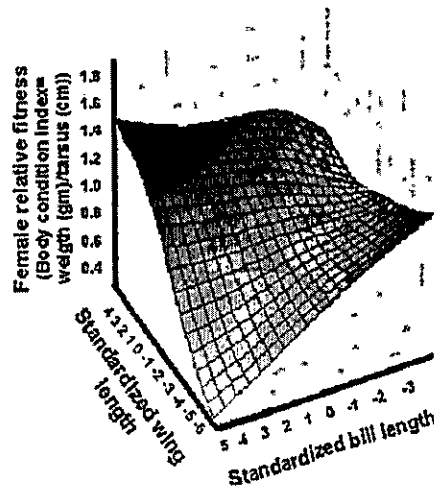
Measure	Males (n = 106)	Females (n = 344)	$t_{(448)}$
Weight (g)	5.925 ± 0.068	4.736 ± 0.033	-16.99***
Body size (cm)	10.152 ± 0.028	9.754 ± 0.018	-11.33***
Wing length (cm)	6.229 ± 0.025	5.670 ± 0.015	-18.72***
Bill length (cm)	1.426 ± 0.016	1.577 ± 0.008	7.817***
Tarsus length (cm)	0.691 ± 0.010	0.669 ± 0.018	-0.658
Wing disc loading	0.031 ± 0.000	0.030 ± 0.000	-2.221*
Power hovering	12.348 ± 0.089	12.128 ± 0.048	-2.226*

* $P < 0.05$; *** $P < 0.001$

Values are the mean ± standard error (SE)

Table 2 Linear ($\beta_i \pm SE$), nonlinear ($\gamma_{ii} \pm SE$), and correlational ($\gamma_{ij} \pm SE$) selection gradients on wing length and bill size in males ($n = 47$) and females ($n = 150$) hummingbirds

Traits i	$\beta_i \pm SE$	P	$\gamma_{ii} \pm SE$	P	$\gamma_{ij} \pm SE$	P
Females						
Wing length	0.260 \pm 0.084	0.002*	0.033 \pm 0.084	0.687	0.067 \pm 0.081	0.403
Bill length	0.228 \pm 0.083	0.006*	0.033 \pm 0.083	0.687		
Males						
Wing length	-0.053 \pm 0.166	0.752	0.266 \pm 0.52	0.088	0.023 \pm 0.187	0.9
Bill length	0.126 \pm 0.182	0.491	-0.314 \pm 0.169	0.071		

Significant at * $P < 0.05$ **Fig. 1** Surface of selection of relative body index condition (i.e., fitness) on wing and culmen length in hummingbird females

females with longer bills and wings have higher a body condition index (Table 2), our surrogate for fitness.

For males, although the model of relative fitness on wing and bill size was significant ($F_{5,41} = 2.49$, $P = 0.05$, $R^2 = 0.23$), the linear selection gradient model was neither significant for wing length or culmen size nor for their interactions, suggesting that directional selection pressure is not acting on these traits (Table 2). Nonlinear selection gradients on wing and culmen size and their interactions were also nonsignificant, suggesting that stabilizing, disruptive, and correlational selection pressures are not acting on wing and bill length in males (Table 2).

Discussion

Natural selection should favor phenotypes that increase the abilities of individuals to exploit resources efficiently given

a determined foraging strategy. In fact, for female hummingbirds (i.e., non-territorial), the results of our phenotypic selection analysis showed that wing and bill length are subjected to positive directional selection pressure. Longer bills in female hummingbirds imply shorter handling times and higher maximum nectar extraction depths (Temeles and Roberts 1993; Temeles 1996; Temeles et al. 2002). Thus, because of their longer bills, females have the potential to feed from longer flowers than males, and can do so more quickly (Temeles and Roberts 1993). Taking into consideration the fact that females frequently are intruders in male territories, longer bills represent an advantageous trait. In contrast, the positive directional selection on wing length in females could be explained by the positive effect of longer wings on energy saving during the long trips between different male territories. Additionally, *S. septentrioides* is a partially migratory species, moving northwards during the austral winter (Ortiz-Crespo 1986). Natural selection tends to favor long wings, thereby reducing the energetic costs of the long trips of migratory species (Hainsworth and Wolf 1972; Feisinger and Chaplin 1975). Thus, there may be two selective forces acting in the same direction (i.e., competition and migration). This fact could explain why beta gradients are significantly higher for wing length than bill length ($t_{296} = 260$, $P \ll 0.01$). The latter sheds light on why there are areas, in the selective landscape, where we found females with long bills, short wings, and low fitness values, indicating that wing length is a more preponderant factor for female fitness.

In contrast, in males, neither bill nor wing lengths were subject to selection. Territorial behavior likely causes the relaxation of the handling time as a selective pressure on males because of the relatively unlimited access that they have to the floral resources contained in their territories. On the other hand, we had expected to find evidence of a negative selective pressure on male wing length due to the importance of acceleration power on the ability to defend the territory by chasing and fighting intruders. We suggest two possible explanations for the lack of such an effect. Altshuler and his colleagues (2004) conducted a pooled analysis with broad taxonomic sampling through an elevational range of

3500 m and concluded that wing disc loading is a poor predictor of the competitive ability of hummingbirds at high elevations; however, at low elevations, this conclusion is less absolute (Altschuler et al. 2004; Altschuler 2006). For two species of territorial hummingbirds in the Colorado Rockies, success at dominating the preferred resource shifted across elevations. Long-winged *S. platycercus* males were subordinate to short-winged *S. rufus* males at low elevations but were dominant at high elevations (Altschuler 2006). Therefore, the fact that natural selection does not favor proportionately shorter wings in *S. sephaniodes* could confirm that wing disc loading is not a good indicator of competitive ability, even at low altitudes. Second, as mentioned earlier, natural selection tends to favor long wings in migratory species (Feisinger and Chaplin 1975; Hainsworth and Wolf 1972). Therefore, the absence of phenotypic selection on male wing length could be the result of two opposite selective pressures (negative effect of competition and positive effect of migration) acting on this trait.

Since the time of Darwin, sexual selection has been considered as one of the main forces promoting sexual dimorphism, either through mate competition or mate choice (Darwin 1871). We cannot reject sexual selection acting on sexually dimorphic traits in *S. sephaniodes*; nevertheless, if our assumption that a body condition index is a good surrogate variable for fitness, this study strongly suggests that natural selection may be promoting sexual dimorphism in traits that are closely related to foraging ecology and resource exploitation strategy in order to optimize the resource exploitation and diminish the costs of direct competition.

Zusammenfassung

Fördert natürliche Selektion Geschlechtsdimorphismus beim Chilekolibri?

Bei vielen Kolibriarten gibt es ein entgegengesetztes Muster von Geschlechtsdimorphismus in der Schnabellänge und anderen morphometrischen Maßen der Körpergröße. Diese Unterschiede scheinen eng mit Unterschieden in der Nahrungsökologie und dementsprechend mit unterschiedlichen Strategien der Ressourcennutzung zusammenzuhängen. Das Ziel dieser Studie war es, abzuschätzen, ob natürliche Selektion über Flügellänge und Schnabelgröße auf Kolibri Männchen und -weibchen mit unterschiedlichen Ressourcennutzungsstrategien (d.h. territoriale Männchen und nicht-territoriale Weibchen) wirkt. Falls Ressourcenkonkurrenz als Selektionsfaktor Geschlechtsdimorphismus fördert, sollten Männchen negativer gerichteter Selektion über die Flügellänge, nicht jedoch die Schnabelgröße ausgesetzt sein, während Weibchen

positiver gerichteter Selektion über Flügellänge und Schnabelgröße unterworfen sein sollten. Morphometrische Daten für Männchen lassen darauf schließen, dass keine Selektion über Flügellänge und Schnabelgröße erfolgt. Im Gegensatz dazu wurde bei Weibchen positive gerichtete Selektion über beide Maße festgestellt. Obwohl wir nicht ausschließen können, dass hier sexuelle Selektion auf geschlechtsdimorphe Merkmale wirkt, deutet diese Studie darauf hin, dass natürliche Selektion Geschlechtsdimorphismus in Merkmalen fördern könnte, die eng mit der Nahrungsökologie und den Ressourcennutzungsstrategien von Kolibris zusammenhängen.

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CAPÍTULO V

ENERGETIC CONSEQUENCES OF SEXUAL DIMORPHISM IN COGNITIVE ABILITIES

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MANUSCRITO EN FORMATO PARA SER ENVIADO A ANIMAL BEHAVIOUR

SUMMARY

Episodic memory involves the ability to recall individual past events, involving what, where and when an event has been experienced. Sexual differences in episodic-like memory in non-human animals have not been described up to the present. In the Green-backed firecrown hummingbird, which has territorial males and opportunistic females, we evaluated the ability to recall the location, quality, and renewal rate of nectar of the most rewarding flowers among several less rewarding flowers with identical visual cues. The significantly higher cognitive performance observed in males appears to be closely related both to different resource exploitation strategies and to different selective pressures acting upon males and females. The different cognitive performance observed among individuals and sexes produced dramatic differences in the energy gained. Our results strongly suggest that complex cognitive traits can be modified by selective forces from the environment inhabited by individuals, and therefore are potentially tied to their survival probabilities.

INTRODUCTION

The ability to recall individual past events, involving what, when and where an individual event has been experienced, has been called episodic memory (Tulving 1972, Tulving 2002). This kind of memory must be flexible to the acquisition of new information in novel situations (Clayton et al. 2003, Clayton et al. 2005).

Additionally, the integrated representation of its elements implies that when one element is recalled (i.e., answering the when question), automatically the others are recalled as well (what and where). The ecology of different species strongly suggests that episodic memory should be frequently present (Clayton and Dickinson 1998, Emery and Clayton 2001). Nectivorous animals such as hummingbirds experience flowers containing nectar with different characteristics that are not evaluable through visual cues (Irwin 2000). Nectar varies in spatial location, concentration and renewal rate, therefore a hummingbird that remembers where, what and when the nectar will be available will obtain the highest quantity of nectar. Numerous experiments have demonstrated the ability of hummingbirds to recall the highest sucrose concentration among energetically poorer food sources (Blem et al. 2000, González-Gómez and Vásquez 2006) and their ability to visit consistently the locations that offer a reward and avoid non rewarding sites in the absence of visual cues (Cole et al. 1982, Healy and Hurly 1998). Additionally, hummingbirds can adjust their flower visits to a determined nectar renewal schedule (Gill 1988, Henderson et al. 2006). Therefore they are able to remember what, where and when the nectar is available. Recently, we showed that free-living hummingbirds can remember in a single event the three components of episodic-like memory (see Chapter number 3), using the obtained information in novel

situations. However, that study was carried out exclusively with territorial males. Many hummingbird species (Trochilidae) have morphological and behavioral sexual dimorphism (Bleiweiss 1999, González-Gómez and Estades 2009). These differences seem to be closely related to differences in foraging ecology and resource exploitation strategies (Temeles et al. 2000, Temeles and Kress 2003). 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 resources (Kodrick-Brown and Brown 1978, Temeles et al. 2005). Despite widespread evidence of morphological and behavioral sexual dimorphism, no experimental studies have empirically evaluated sexual differences in cognitive abilities to track the availability of high quality nectar. *Sephanoides sephaniodes* (green-backed firecrown), a species which inhabits central and southern Chile, exhibits morphological and behavioral sexual dimorphism. Males have significantly higher body mass and smaller bill size than females, and they actively defend feeding territories while females do not. González-Gómez & Vásquez (2006) conducted an experiment with 28 artificial nectar feeders, which were defended actively by male birds but not by females. The same pattern seems to occur in natural conditions (Authors, pers. obs.). In addition, foraging behavior of females consists of fast intrusions into male territories until the territory owner chases them aggressively (Authors, pers. obs). In the present study we evaluated the ability of males and females of the green-backed firecrown hummingbird to track and recall both the best reward location (i.e., the flower with the highest nectar concentration) among several less

rewarding flowers (with less concentrated nectar) and the temporal availability of the best quality nectar. If episodic memory is a sexual dimorphic trait, we expected that males would retain the location of the best quality flower and they should visit this position in the period when the best nectar is available. On the other hand, we expected females to exhibit poorer cognitive performance.

METHODS

The study was carried out during the Austral winter (2008) in the Andean foothills in central Chile (33°23'S, 70°31'W, 1100 m a.s.l.). Subjects were six male (6.83 ± 0.2 g, mean \pm se) and six female (5.42 ± 0.17 g) of *Sephaniodes sephaniodes*. The experiment was carried out in a 6.0x6.0x5.0 m aviary. After a training period of 24h we presented hummingbirds with different nectar qualities. We offered a feeder with 100ml of 15% weight/weight sucrose (low quality) and an identical feeder with 30% w/w sucrose (high quality) for 1h. In order to show hummingbirds the nectar schedules associated with nectar availability and quality, we replaced the feeders with two artificial flowers capable of holding 60 μ L. The high quality nectar flower was refilled every 10 min after the flower was drained. The low quality flower was refilled every 5 min. We maintained the temporal training for one hour or until the subject adjusted its visits to the nectar renewal rate.

For each trial, in the episodic memory protocol three feeders were assigned to three randomly chosen points among the nine points of the grid. At the beginning of each trial, each flower contained 60 μ L of sucrose liquid. One flower was refilled with high quality nectar every 10 min and the other two were refilled with low quality nectar every 5 min. We performed 6 trials with each subject during a given

morning. A trial had two phases; in the first phase (search phase), the hummingbird probed the flowers until it discovered the most rewarding one. In the second phase (returning phase), the hummingbird faced the same array of flowers. We recorded the position and the time in which flowers were revisited. After finishing the revisit to the grid, the trial was ended, and the following trial was initiated after 10 minutes.

RESULTS

The accuracy of spatial memory was assessed by recording the nectar quality (high or low) of the first flower visited in the second phase of the experiment. Males could remember significantly better the position of the best quality flower (Nested ANOVA, $F_{1,10}=11.37$, $p<0.001$). There were no significant differences among individuals (Nested ANOVA, $F_{10,56}=0.59$, $p=0.81$). The ability to track the interval when the best nectar was available (i.e., temporal memory performance) was significantly greater in males than in females (Nested ANOVA, $F_{1,10}=11.16$, $p<0.001$, Fig 1, Fig 2).

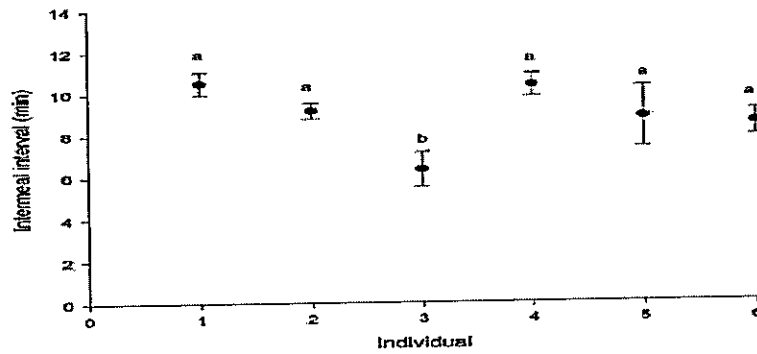


Figure 1. Adjustment of males green-backed firecrown hummingbirds to nectar availability schedules of the best nectar source (mean \pm SE, n= 6 trials for each subject). (*) Significantly differences among individuals are indicate with different letters, Tuckey Post Hoc Test, $p < 0.05$).

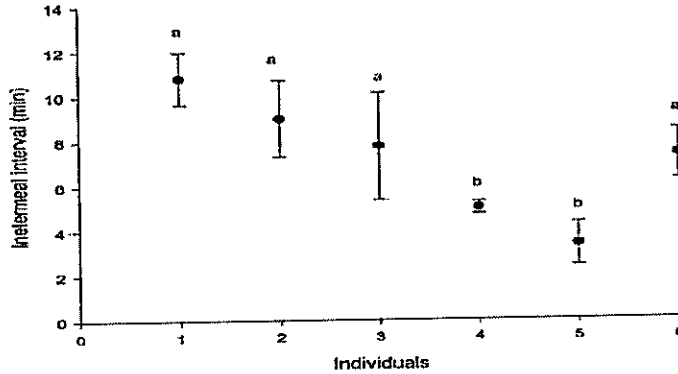


Figure 2. Adjustment of females green-backed firecrown hummingbirds to nectar availability schedules of the best nectar source (mean \pm SE, n= 6 trials for each subject). (*) Significantly differences among individuals are indicate with different letters, Tuckey Post Hoc Test, $p < 0.05$).

However, there were significant differences in individual performances (Nested ANOVA, $F_{10,56}=4.66$, $p<<0.001$, Fig 1, Fig 2).

To assess the ability to remember simultaneously the three elements of episodic memory, namely, time (when), spatial location (where), and the content of the feeders (what), we performed a Spearman correlation between the identity of the first feeder (15% or 30%) visited in the second phase of the experiment, independently of the presence of the reward, and the inter-meal time of the visit. Males had a significantly better cognitive performance than females (Slope test $t_8=14.41$, $p<<0.001$). Males who could successfully remember the nectar quality and location could accurately recall the timing of nectar availability (Spearman correlation, $t_4= 4.1$, Spearman $R=0.90$, $p<0.01$). In contrast, females could not recall simultaneously these elements (Spearman correlation, $t_4= 0.06$, Spearman $R=0.12$, $p=0.91$, Fig. 3).

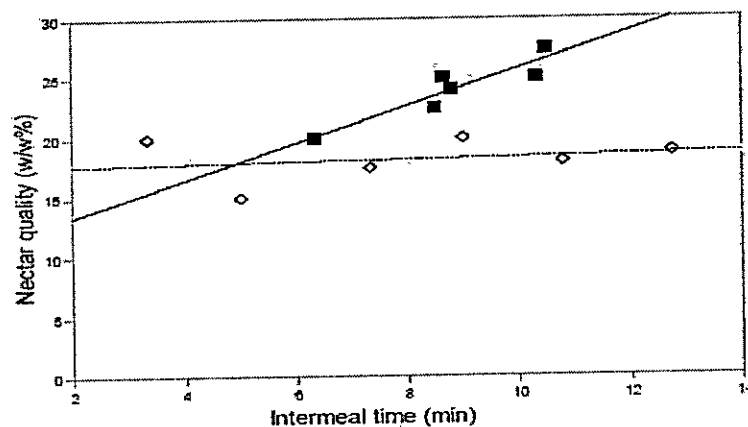


Figure 3. Association between spatial and temporal memory of *S. sephaniodes*. Black dots, males; white dots, females.

The energetic consequences of the ability to keep track of the best nectar sources

was assessed by transforming the mean of nectar obtained to energy units (joules, hereinafter, j), corrected for body mass. The energy intake of females was 0.40 times lower than in males, consistent with females being unable to keep track of the location, quality, and nectar availability intervals in the best flowers (Nested ANOVA, Table 1).

Source of variation	SS	df	MS	F
Sex	6992	1	6992	10.884***
Sex (Individuals)	14588	10	1459	2.271 *
Error	35974	56	642	

Table 1. Effect of cognitive ability in energy reward in males and females of *S. sephaniodes*. Nested ANOVA. *** $p < 0.001$, * $p < 0.05$.

As an example of this marked dimorphism, the male who had the best performance (individual number 1) obtained 10 times more energy than the female with the poorest performance (individual number 5, Fig. 4), while the male with the worst performance obtained 2.6 times more energy than this female.

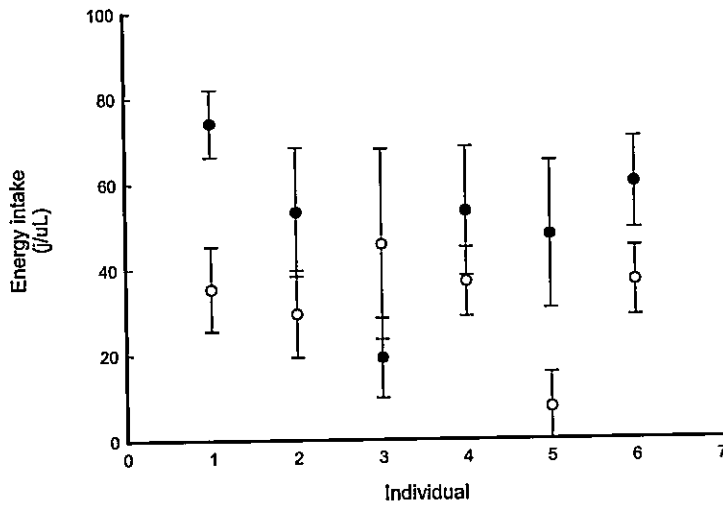


Figure 4. Energy reward obtained by individuals of green-backed hummingbirds as a result of the combination of the performance of spatial and temporal memory (mean \pm SE, $n=6$ trials for each subject), corrected by body mass for males (6.6 ± 0.19 g, mean \pm se, $N=6$) in black dots and for females (5.42 ± 0.16 g $N=6$) in white dots.

DISCUSSION

Sexual dimorphism in cognitive abilities has been recorded in several species of birds (Clayton et al. 1997, Healy et al. 2009) and mammals (Gaulin and Fitzgerald 1986, Galea et al. 1996). However, those studies have been focused on spatial cognition and not on complex cognitive abilities such as episodic-like memory. Cognitive traits such as morphological and physiological traits may be shaped by selective forces of the environment (Balda et al. 1996, Dunlap et al. 2006). The significantly higher spatial and temporal memory performances of males, and their ability to remember simultaneously the three elements that define episodic memory, that is, time (when), spatial location (where), and the content of the feeder

(what), seem to be closely related to different resource exploitation strategies, with different selective pressures acting on males and females. This suggests that in males of the Green-backed firecrown hummingbird, spatial and temporal abilities have co-evolved linked with their territorial condition. This condition would have acted as a selective pressure improving memory abilities supported by regular feeding events, based on remembering the exact location, quality, and time availability of potential resources. Additionally, we suggest that the increase in gained energy simultaneously stimulated the territorial defense. For females, in contrast, a phenotypic selection analysis showed that they possess adaptations such as a longer bill and wings that make them able to forage as intruders within male territories (González-Gómez and Estades 2009). Longer bills represent an advantageous trait, implying that females have the potential to feed from longer flowers than males, and that they can do so more quickly (Temeles et al. 2002, Temeles and Roberts 1993). Furthermore, longer wings can allow females to save energy during the trips between different male territories (Feisinger and Chaplin 1975, Hainsworth and Wolf 1972). The opportunistic strategy observed in females appears to be consistent with their poor cognitive performance, although we cannot reject the possibility that females could remember resources at a higher spatial scale rather than recalling individual flower characteristics.

In the extremely challenging scenario faced by Green-backed firecrowns composed of cold field winter temperatures (i.e., below -5°C), high metabolism (López-Calleja and Bozinovic 1995), and low capacity to store energy (Hiebert 1993), differential fitness would be enhanced by superior cognitive abilities in males, and foraging-selected morphological traits in females. For males, the ability

to keep track of the best nectar sources in order to increase the energy gain rate may improve survival probability, especially in periods of high thermoregulatory costs (Hainsworth 1978). In fact, we found individual variability in the ability to recall the nectar characteristics, which was translated in dramatic differences in energy intake. Even though females have lower energy requirements due to their lighter body mass, their poor performance strongly suggests that they are using a foraging strategy that does not involve the tracking of flowers at small scales. In this sense, individual differences in episodic-like memory performance probably are a sign of the ability to use an alternative resource exploitation strategy. Although males showed a significantly better performance than females, their cognitive abilities showed important individual differences and they were significantly poorer than the performance recorded for the same experiment in the field with territorial males (see Chapter 3). Free-living hummingbirds gained 1.33 times more energy than laboratory individuals (Nested anova $F_{1,14}=9.13$, $p<0.01$). One possible explanation is that in the present study we captured subordinate males to use in the laboratory. In fact, ten feeders were located immediately next to the mist net, and during the experiments we observed individuals sharing the feeders (4.33 ± 1.1 birds/15 min⁻¹ mean \pm se), and we did not record any territorial individual defending the area in 120 min of observation. This hypothesis is consistent with the idea that cognitive traits can be modified by selective forces from the environment inhabited by individuals (Balda et al. 1996) but also influenced by their social context (Dally et al. 2005, Dally et al. 2006). In this scenario, future research is needed to explore how plastic are complex cognitive abilities faced in contrasting social contexts.

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DISCUSIÓN

La ecología del forrajeo de animales nectarívoros como picaflores (Trochilidae) se encuentra estrechamente ligada a las dinámicas del néctar en las flores y por ello es esperable que habilidades cognitivas les permitan explotar el néctar eficientemente (Cole et al. 1982; Wolf and Hainsworth 1990). En este contexto una pregunta central es cuál es el margen en que aspectos conductuales como preferencias dietarias o el conocimiento acerca del ambiente, puede expresarse dado un escenario de limitantes fisiológicas. En la ecología del forrajeo de picaflores estas limitaciones están dadas por el tiempo de procesamiento intestinal de alimento y la tasa de vaciamiento del buche, entre otros (Karasov et al. 1986; Hainsworth 1989, Fernández et al. 2002). Si bien la fisiología digestiva de los picaflores impone un marco en el que se desarrolla la conducta, nuestros resultados sugieren fuertemente que los picaflores pueden modular, al menos parcialmente la frecuencia de forrajeo para maximizar la energía obtenida.

La obtención de la mayor cantidad de energía derivada del néctar esta relacionada a la habilidad de recordar, como primer elemento, la ubicación de los recursos de mejor calidad. Los experimentos realizados con *Sephanoides sephaniodes* en campo muestran que ellos son capaces de recordar la ubicación del mejor néctar en ausencia de pistas visuales. Estos resultados son consistentes con estudios similares en *Selasphorus rufus* los que son capaces de visitar sitios con recompensa y evitar los que no la

entregan (Cole et al. 1982) y recordar las flores que han visitado pero no vaciado por completo, en ausencia de pistas visuales (Hurly & Healy 1996). Estos resultados son también consistentes con otros estudios que muestran que los sujetos prestan más atención a la ubicación espacial de los recursos que a sus pistas visuales (Healy & Hearnly 1998, Healy & Hurly 2003).

Además del componente espacial la dieta nectarívora de los picaflores impone la necesidad de recordar características de las flores como el tiempo en que se encuentra disponible el mayor néctar acumulado y la calidad de éste (Henderson et al 2006). La representación integrada de estos tres componentes i) dónde se encuentra el néctar, ii) a qué calidades de néctar es posible acceder y iii) cuándo se obtendrá la mayor cantidad de néctar acumulado ha sido denominada memoria episódica (Tulving 2002; Schwartz and Evans 2001; Clayton et al. 2003;). Nuestros experimentos, simulando condiciones naturales, son la primera evidencia a cerca de que nectarívoros de vida libre que son capaces de recordar los tres componentes de la memoria episódica de forma integrada y aplicar este conocimiento en nuevas situaciones, otro de los requisitos de esta categoría de memoria (Tulving 1972).

Como Henderson et al. (2006) sugirieron, la memoria episódica debiera ser parte de la vida diaria de nectarívoros territoriales. Aquellos individuos que logren recordar de mejor manera e incorporar este conocimiento a su experiencia, aseguran no solo la obtención de la mayor cantidad de energía posible dado un parche de flores si no también la oportunidad de explorar nuevas fuentes de recursos y volver a las de mejor

calidad (Healy & Hurly 2003). Se encontró una importante variabilidad a nivel individual en las habilidades espaciales y temporales lo que se tradujo en la energía obtenida por cada sujeto. El picaflor chico experimenta temperaturas invernales bajo los -5°C en su rango de distribución, lo que representa un escenario extremadamente demandante en términos termorregulatorios (López-Calleja & Bozinovic 1995). Sumado a lo anterior, las altas tasas metabólicas y baja masa corporal de estos animales reducen sus posibilidades de almacenar energía (Hiebert 1993; Suárez and Gass 2002). A partir de lo anterior es posible sugerir que diferencias en el éxito de forrajeo, derivado de diferencias en habilidades cognitivas afectan la posibilidad de sobrevivencia y por lo tanto, la adecuación biológica de los individuos.

En este contexto la selección natural debiera favorecer fenotipos que incrementen las habilidades de los individuos para explotar los recursos eficientemente, dado una estrategia de forrajeo. En el picaflor chico, machos y hembras resultaron tener diferentes estrategias de forrajeo. Las hembras tienen una estrategia de forrajeo no territorial sino principalmente oportunista que involucra rápidas intrusiones en los territorios de los machos. De hecho, presentan picos y alas más largos que los machos y están sujetas a selección direccional positiva en estos rasgos lo que les confiere la posibilidad de acceder a más recursos, más rápido y ahorrar energía en vuelos entre los territorios de machos (Feinsinger and Chaplin 1975; Temeles and Roberts 1993; Temeles 1996; Temeles et al. 2002). Más aún, dado que esta es una especie migratoria, alas más largas proveerían de un

ahorro energético durante la migración (Hainsworth and Wolf 1972). Así podrían haber dos presiones selectivas actuando en la misma dirección (i.e., competencia y migración). En contraste, ni alas ni picos de los machos fueron sujetos de selección. El tiempo de manipulación del alimento como presión selectiva, podría haberse relajado dado que machos territoriales tienen acceso ilimitado a las flores dentro de su territorio. Por el contrario, se esperaba encontrar una fuerte selección hacia alas más cortas (i.e., mayores cargas alares) las que producen mayor poder de aceleración y por lo tanto mejor defensa del territorio (Feinsinger and Chaplin 1975). La ausencia de selección sobre las alas podría deberse a dos alternativas. La carga alar es un pobre predictor de las habilidades competitivas (Altshuler et al. 2004; Altshuler 2006) o las alas son sujeto de dos presiones selectivas al mismo tiempo, direccional positiva para ahorrar energía durante la migración y otra direccional negativa para defensa territorial.

En términos de habilidades cognitivas el dimorfismo sexual en ha sido registrado en diversas especies de aves y mamíferos (Gaulin & Fitzgerald 1986; Galea et al. 1996; Jones et al. 2003). Sin embargo, estos estudios se han enfocado principalmente en memoria espacial más que en habilidades complejas como memoria episódica. Los rasgos cognitivos tanto como los morfológicos y fisiológicos pueden ser moldeados por presiones selectivas (Balda et al. 1996; Dunlap et al. 2006). Nuestros resultados muestran que los machos recordaron significativamente mejor los tres elementos de la memoria episódica, es decir, la ubicación, calidad y tiempo al que estaba disponible el mejor néctar. La significativa diferencia entre machos y

hembras en cuanto la habilidad de recordar parece cercanamente relacionada a diferencias en la estrategia de explotación de recursos y presiones selectivas diferenciales actuando sobre ellos. En machos de picaflor chico, las habilidades temporales y espaciales habrían co-evolucionado con la condición territorial. La capacidad de recordar ubicaciones y tiempos de los recursos en un territorio se habría visto reforzada por la energía ganada debido a la defensa territorial. Por otra parte, la baja habilidad cognitiva de las hembras es coincidente con adaptaciones al forrajeo como oportunistas (Hainsworth & Wolf 1972; Feisinger & Chaplin 1975). Las diferencias en habilidades cognitivas entre machos y hembras se tradujeron en diferencias altamente significativas en energía ganada, aun cuando ello se corrigió por masa corporal, lo que sugiere que las hembras habrían desarrollado rasgos cognitivos distintos a los machos los que, por ejemplo, les permitieran recordar a escalas espaciales más amplias, más que recordar características de flores individuales.

El desarrollo de habilidades cognitivas complejas hasta ahora solo había sido descrito para pocos organismos (Crystal 2009) y aún sin contemplar los efectos de estos rasgos en la adecuación biológica de los individuos. A través de los experimentos desarrollados, se propone un contexto evolutivo para explicar la aparición de la memoria episódica y el desempeño cognitivo diferencial tanto intra como intersexualmente.

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