Behavioral
Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2015), 26(1), 21–29. doi:10.1093/beheco/aru182

Editor's choice

Original Article

Bills as daggers? A test for sexually dimorphic weapons in a lekking hummingbird

Alejandro Rico-Guevara[a] and Marcelo Araya-Salas[b]
[a]Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N Eagleville Rd. U-3043, Storrs, CT 06269, USA; [b]Department of Biology, New Mexico State University, Foster Hall, MSC 3AF, Las Cruces, NM 88003, USA

Received 13 May 2014; revised 1 September 2014; accepted 11 September 2014; Advance Access publication 18 October 2014.

One way in which secondary sexual traits can influence differential reproductive success is by playing a key role in the outcome of direct physical contests for mates. Here we describe an undocumented trait in a species of hummingbird with a lek mating system, the Long-billed hermit (LBH, *Phaethornis longirostris*). The trait under consideration is a dagger-like structure at the bill tip, which we hypothesize is a secondary sexual trait that functions as a sexually dimorphic weapon. We tested our hypothesis by examining 5 leks during 4 consecutive years, and by employing morphological analyses, performance experiments, and behavioral observations. We found that 1) adult male bill tips were longer and pointier than their counterparts in females and juvenile males, 2) juvenile males acquired dagger-like tips during their transition to adulthood, 3) variation in bill tip morphology reflected puncture capability, and 4) males with larger and pointier bill tips were more successful in achieving lek territory tenure. Our study provides the first evidence of sexually dimorphic weapons in bird bills and stands as one of the few examples of male weaponry in birds. Our results suggest a role of sexual selection on the evolution of overall bill morphology, an alternative hypothesis to the prevailing "ecological causation" explanation for bill sexual dimorphism in hummingbirds.

Key words: **animal weaponry, bill morphology, ecological causation, intrasexual competition, male combat, secondary sexual traits, sexual dimorphism, trochilidae.**

INTRODUCTION

Secondary sexual traits are usually selected for through mate choice, for example, ornaments (Endler 1990), or intrasexual competition, for example, weapons (Emlen 2008). Here we describe a previously unnoticed bill trait in a lekking species, the long-billed hermit (*P. longirostris*, Figure 1, Supplementary Movie A1), and test if this trait is a secondary sexual one and if it could be considered a sexually dimorphic weapon. In order to consider a given feature as a secondary sexual trait, it has to: 1) be present or enlarged (relative to body size) in members of one of the sexes, usually in males (Andersson 1994), and 2) appear or become enlarged during puberty (Radford and du Plessis 2004). In order to establish the conditions under which to consider a trait a sexually dimorphic weapon, we first need to point out that in general terms, sexually dimorphic weaponry in animals has evolved through sexual selection in the form of intraspecific fighting (e.g., male-male combat; Emlen 2008). Under this framework, sexual differences that have evolved to provide an advantage during a battle, and ultimately act to influence fitness (through enhanced mating opportunities), could be considered part of that organism's sexually dimorphic weaponry. Sometimes a trait that has not evolved specifically for fighting can show strong sexual dimorphism, for example, elongated and stronger arms in male Kangaroos (Warburton et al. 2013), or larger male canine teeth in some primates (Leigh et al. 2008; Plavcan 2012). In this case, it is the difference in muscle mass and/or bone structure rather than the presence of the trait itself (arms or teeth) that makes these examples of sexually dimorphic weapons. To formalize this notion, we consider sexually dimorphic weapons to be structures that are 1) used to inflict damage during intrasexual agonistic encounters (Andersson 1994), and 2) traits that increase dominance and subsequently the bearer's mating success (Darwin 1871; Székely et al. 2000).

Here, we describe a needle-shaped bill tip in long-billed hermits (*P. longirostris*), a type of structure never before reported in birds. Sexual dimorphism in bill tip morphology of few species of hummingbirds has been known for a long time (*Ramphodon*, *Androdon* and *Glaucis*: Salvin 1892), but in those cases the males have hooked bill tips. For *Phaethornis*, or any other hummingbird, the dagger-shaped bill tip has not been reported (cf. Delattre 1843;

Address correspondence to A. Rico-Guevara. E-mail: a.rico@uconn.edu.
A. Rico-Guevara and M. Araya-Salas contributed equally to this paper.

Figure 1
Long-billed hermit (*P. longirostris*). Photo by M. Aliaga.

Salvin 1892; Hinkelmann 1996; Hinkelmann and Schuchmann 1997; Hinkelmann and van den Elzen 2002; Piacentini 2011). We assessed the variation in bill morphology and functional performance (puncture capability) of the bill tip among adult males, adult females, and juveniles. Since *P. longirostris* is a lek-breeding hummingbird, we examined the relationship between male bill tip morphology, puncture capability, and their ability to defend a territory in the lek. Among territorial males, there is still controversy over whether females prefer males in central territories to males in peripheral ones (Apollonio et al. 1992) or show no such preference (Clutton-Brock et al. 1989). Nonetheless, it is clear that in species in which a lekking system has evolved, males holding lek territories will have a reproductive advantage over males incapable of holding territories (Balmford et al. 1992; Andersson 1994) in the absence of alternative reproductive strategies, that is, sneaker males (Sinervo and Zamudio 2001). In fact, in lek-breeding species, 10–20% of the males often obtain 70–80% of the mating events (Wiley 1991). In lekking hummingbirds, territory tenure gives priority or exclusive access to females (e.g., Stiles and Wolf 1979).

To test our hypothesis that the structure described here is a secondary sexual trait and a sexually dimorphic weapon, we evaluated 4 specific predictions: 1) the trait is more developed or only present in male hummingbirds; 2) it becomes enlarged and better developed (pointier bill tips) when juvenile males reach adulthood; 3) males with enlarged and pointier bill tips have a potential fighting advantage, in the form of enhanced puncture capability; and 4) males with enlarged and pointier bill tips are more successful in defending lek territories.

METHODS

Behavioral observations

Fieldwork was carried out at 5 long-billed hermit leks at La Selva Biological Station, Costa Rica during the breeding seasons (~December–August) from 2009 to 2012 (for details of the lek sites see Araya-Salas and Wright 2013). To perform focal sampling, we individually marked males capturing birds in the lek and surrounding areas (including feeding territories), determining the sex via discriminant function analysis, and attaching color-coded back-tags. We captured birds using standard 6 and 12 m mist nets (19 mm mesh size), and ringed all captured hummingbirds with numbered bands. Long-billed hermits do not exhibit obvious plumage sexual dimorphism, but individuals can be sexed by a discriminant function analysis on standard measurements (Stiles and Wolf 1979). We used a cross-validation discriminant function analysis by creating several functions using published morphological data for 204 individuals of this species (Stiles and Wolf 1979), and selecting the function that provided the best classification of sexes (>90% for each sex); which included wing chord length (flattened), bill length (exposed culmen), and body mass. Stiles and Wolf (1979) only provided sample size, mean and standard deviation for each of the measurements mentioned above. Thus, for each sex we created 100 normally distributed cases using the mean, variation and sample size reported by Stiles and Wolf (1979) to generate the dataset for the discriminant function analysis. When applied to an independent dataset from specimens at the Museum of Zoology of Universidad de Costa Rica 100% of females ($N = 5$) and 77% of males ($N = 13$) were correctly classified. In the field, we measured bill and right tarsus lengths, flattened wing chord length, and body mass using a digital caliper (±0.005 mm), a stopped wing ruler (±0.1 mm), and a digital scale (±0.01 g). Individuals classified as males in the field by the discriminant function analysis (using a field laptop) were marked with plastic stripes that had unique 3-color combinations attached to the back of the bird with nontoxic eyelash glue, LashGrip-Ardell® (Stiles and Wolf 1973; Baltosser 1978; González and Ornelas 2009; Kapoor 2012).

We observed marked individuals at leks using binoculars (and video cameras when possible) from 5:00 to 11:00 h and from 14:00 to 17:00 h, encompassing the previously reported peaks of activity for this species (Stiles and Wolf 1979). We used focal observations and territory mapping to ensure that all males in a lek were sampled in a given period and the status of the males was correctly assessed (territorial vs. floater). We identified adult males as "territorial" when they defended a set of perches at the lek and sang from them during the observation period (>5 days per male in all cases). Conversely, we identified individuals as non-territorial lekking males or "floaters" when they were observed at least 2 times within the lek during a single season, but were unable to defend perches from other males. These floaters were seen intermittently on perches defended by other males but were always displaced from them (>5 days per male), that is, they did not hold territories. We confidently classified these males as floaters since we did not observe them holding a territory in any lek. Perches of singing males were mapped using a 20 × 20 m grid system as reference. Then, a map of lek territories based on an initial observation period was used to identify areas for further intensive netting and observations until we marked and mapped all territorial males on each lek. A perch was considered to belong to a given male's territory when it was repeatedly and successfully defended during the observation period (>5 days per male). We measured the distance (using a rangefinder) and angle of the perches to the closest landmark. Perch locations were plotted using ArcGIS 9.3 creating a minimum convex polygon (Zach and Falls 1979; Smith and Shugart 1987) describing the shape, size and location of each territory.

Morphological analyses

We made a photographic catalogue of the lateral view of bills (e.g., Supplementary Figure A1a) and bill tips including all the hummingbirds captured. Bill tip pictures were taken by coupling a digital camera (Nikon D5100) to a field dissecting microscope (30× magnification) with a built-in scale and millimeter paper background (Supplementary Figure A1b). Using these field macrophotographs, we measured bill tip length as the extension of the maxillary rhamphotheca (keratinous covering of the maxilla) tip beyond the mandibular rhamphotheca tip in lateral view. This is a conservative estimate, given that both maxillary and mandibular tips seem to be elongated and pointier in adult males. However, we limited our analyses to the maxillary tip because as it extends past the mandibular tip, it would be the first point of contact if the bill were used as a weapon. We assessed the reliability of bill tip elongation measurements by comparing the length obtained from lateral and ventral photos from the same individual using linear regressions. We also determined the relationship between the discriminant function scores used to sex individuals and bill tip elongation using linear regressions. A high correlation between bill tip length and discriminant scores would have rendered the comparison of bill tip elongation between the sexes redundant.

We outlined the contour of the most distal 2 mm of the bill tip from lateral photos using the program tpsDig version 2.16 (Rohlf 2010). We subsampled the outline of the bill tip obtaining 50 semi-landmarks (Bookstein 1997; details in Mitteroecker and Gunz 2009), which were used to evaluate pointiness. To do this, we calculated the area of different sections of the bill tip using the package PBS mapping in R (R Development Core Team 2013). Pointier objects, from a bi-dimensional perspective, have a smaller area in the tip when compared to a section of similar length in the base of the object. Hence, we defined our pointiness index as the ratio of the area enclosed by the distal 20 semi-landmarks to the area of the basal 20 semi-landmarks, from our 2-millimeter long tip outline. We subtracted these values from 1 in order to match higher pointiness to higher index values. Lastly, we evaluated differences in bill tip length and pointiness between sexes and age classes. In the field, hummingbirds were aged based on bill characteristics: juveniles have clear distinguishable corrugations covering a large extent of the maxillary rhamphotheca (upper bill), whereas adult males show corrugations in less than 10% of the upper bill, near its base (Ortiz-Crespo 1972).

To examine differences in overall bill shape, we calculated a bill curvature index as the arc:chord ratio of exposed culmen (maxillary curvature; Stiles 1995). Arc length was measured following the dorsal profile of the bill from the feathered base to the tip, and chord was measured as a straight-line distance from the feathered base to the tip. These measures were taken on the lateral photographs of complete bills using ImageJ (Schneider et al. 2012). We used the maxillary curvature index because it provided the most conservative estimate, based on Berns and Adams' (2010) comparison among several methods. More subtle differences can be uncovered with the mandibular curvature index (Paton and Collins 1989), the reciprocal of the radius (Temeles et al. 2009), and landmark-based geometric morphometrics (Berns and Adams 2010). By using the most conservative index (maxillary curvature), we ensure that any signal we obtain is more apt to convey biological relevance.

We assessed whether bill measurements differ among sexes and age classes using 2-way analysis of variance (ANOVA). Tukey HSD or univariate tests were used *a posteriori* for assessing the relationship to single factors. Multivariate analysis of variance (MANOVA) was used to assess the effect of sex and age in bill shape variables. MANOVA was also used to compare changes in overall bill shape in 2 consecutive years, with "year" as a fixed effect. Paired *t*-tests were used as post-hoc tests for individual variables. For birds that were recaptured and measured in different years, only the first measurements were included in order to increase the sample size for juveniles. Differences between floaters and territorial males were assessed using ANOVAs to emphasize comparisons between these groups within the same leks/years. We used a logistic regression to evaluate the relationship between bill tip length and territory tenure.

Functional assessment

We experimentally estimated bill puncture capability by measuring the force needed for the bill to puncture a Polyvinyl chloride film (12.5 μm) placed taut on top of a tubular plastic vial (31.8 mm diameter). We held each hummingbird up to its bill base, in a similar way as they are held to measure exposed culmen, in order to ensure that the bill tip contacted the film at the approximate centre and at a 90-degree angle (maximizing compression and minimizing fracture-risk forces, cf. Bock 1966). We positioned the vial with the film on a digital scale (AWS-100 ± 0.01 g) and moved the bill downwards until the bill tip punctured the film (Supplementary Figure A1c). When the bill tip contacted the film, the mass readings started to increase and reached a maximum right before the film was punctured. We converted maximum mass measurements, recorded with a digital camera (Fujifilm FinePix HS 10, 120 f/s), to milliNewtons of force. This technique allowed us to evaluate the capacity of the whole bill to transfer force from the body to the bill tip, as is expected in nature. Bills with sharper tips are expected to puncture the film (or the skin of an opponent) at lower force values. We performed trials on both living birds and museum specimens. The results did not differ between museum and field experiments (Nested ANOVA: $F_{1,43} = 0.039$, $P = 0.844$), allowing us to pool the data for further analyses. The effects of sex and age were tested using females, juvenile males and adult males. Differences in force were analyzed with a nested ANOVA, with puncture trial nested within individual.

RESULTS

Behavioral observations

During our field observations, we recorded chases and agonistic encounters during disputes for perches and territory supremacy. We placed cameras in front of defended perches and documented aerial displays that sometimes escalated to mounting attempts and/or chases (e.g., Supplementary Movie A1). We recorded agonistic interactions involving physical contact demonstrating the use of bills as weapons by males. Specifically, we observed males stabbing their opponents with their bills (e.g., attack in the throat, Supplementary Movie A2). We also observed territorial males perching in front of each other and pecking their opponent repeatedly in the throat before a struggle (e.g., Supplementary Movie A3). Finally we observed copulations when females approached territorial males (e.g., Supplementary Movie A4).

Bill tip variation with sex, age, size, and territory tenure

We captured and measured a total of 159 individuals in 5 leks. Using a cross-validation discriminant function analysis on morphological measurements in situ, we determined that 144 were males and 15 were females. These unbalanced sample sizes for each sex are due to the fact that we concentrated our mist-netting efforts within lek boundaries, where males move frequently and females are rare visitors (Stiles and Wolf 1979). La Selva Biological Station is located at the tip of a narrow biological corridor and it is surrounded by farmland unsuitable for lekking arenas (McDade et al. 1994). We thoroughly scouted the study area and consider unlikely that there were leks that we did not detect, in agreement with previous studies (Stiles and Wolf 1979). Only 4.1% of the males captured were found in 2 different leks, and 31% of the males were floaters. These observations support the inference that there are males without territories attending regularly at the leks (i.e., true floaters); these are not just territorial males visiting from other leks (i.e., erroneously classified as floaters).

We report a hitherto unknown sexually dimorphic trait for hummingbirds: in adult males only, the tip of the upper bill becomes elongated, and conical (Figure 2a). Given that, bill tip elongations measured in lateral and ventral views across individuals were highly correlated (R = 0.92, degrees of freedom [df] = 65, P < 0.0001), in subsequent analyses we used only elongation measured in lateral views. Tip elongation differed significantly between sexes ($F_{1,156}$ = 10.39, P = 0.0015) and age classes ($F_{1,156}$ = 38.33, P < 0.0001, Figure 2b). Post-hoc analysis revealed that adult males have significantly longer bill tips (Tukey HSD test: P < 0.02 in all cases; Figure 2b). Adult males showed significantly pointier bill tips than juveniles ($F_{2,77}$ = 4.69, P = 0.012). When all adult males (without discriminating between territorial and floaters) were included and compared to females, pointiness did not differ between sexes ($F_{1,77}$ = 0.15, P = 0.69); however, when males were subdivided by territoriality, territorial males showed significantly pointier bill tips than both females and floaters ($F_{2,76}$ = 5.03, P = 0.009; Tukey HSD test: P < 0.001 in both cases; Figure 2c). Pointiness index was positively correlated to tip elongation in males ($F_{1,65}$ = 21.41, R^2 = 0.236, P < 0.0001; Supplementary Figure A2). Bill tip elongation also differed between lekking males (Figure 3a). Territorial individuals showed significantly longer bill tips than floaters ($F_{1,119}$ = 10.04, P = 0.002; Figure 3b), and bill tip length significantly predicts the probability of holding a lek territory (X^2 = 10.58; df = 1; P = 0.003); this test result remained significant after excluding juveniles and duplicated (present in more than 1 lek/year) individuals (X^2 = 6.67; df = 1; P = 0.023).

We tracked the bill tip development in 20 males during consecutive years and found that bill tip length significantly increased through time (Paired t-test: t = −2.53, df = 19, P = 0.020; Figure 4a). Such result is influenced by the fact that bill tip length increased in all juvenile males included in the analysis; juvenile males acquired longer bill tips when they reached adulthood (points inside squares, Figure 4a). When focusing on the males that we captured for more than 2 consecutive years however, we found that in some males the bill tip always increased in length, in some it always decreased, in some the bill tip first increased and then decreased, and in some it first decreased and then increased (Supplementary Figure A3). To test for the influence of body size over bill tip length, we used a $\log_{10}$-$\log_{10}$ transformation on the data and estimated allometric lines using the standardized major axis tests and routines package (SMATR: Warton et al. 2012). We did not find any significant fit between bill tip length against weight (Supplementary Figure A4), tarsus length, exposed culmen, and wing chord (P > 0.1 in all cases).

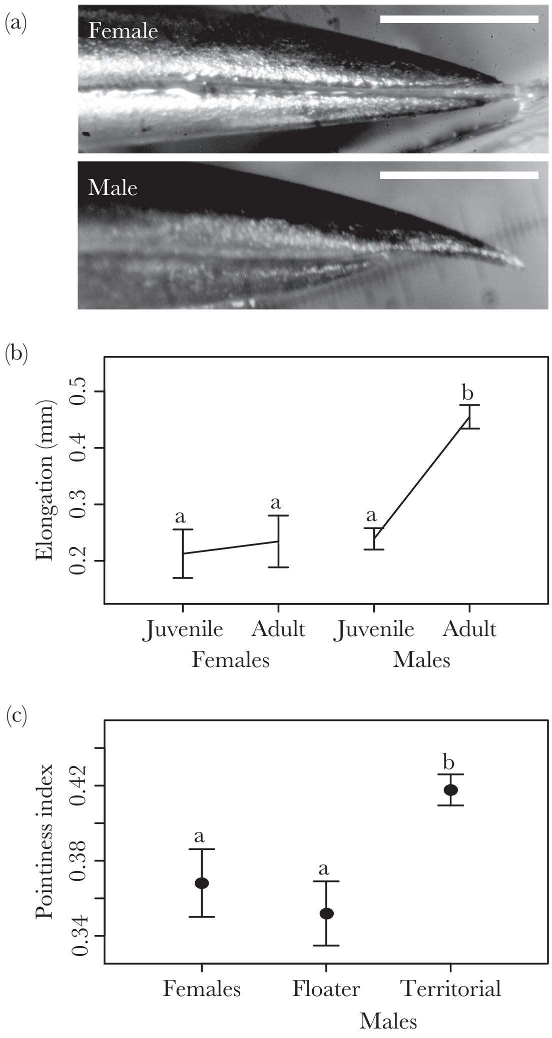

Figure 2
Sexual dimorphism in bill tip length (elongation) and pointiness, subdivided by age and territory class, respectively. (a) Field macro-photographs of the bill tips of a representative individual of each sex. Scale bars (white) = 0.5 mm. (b) Length of the maxillary elongation measured in lateral view (mean ± SE) for sexes and age classes in long-billed hermits. Letters represent significant differences after post-hoc tests. (c) Pointiness index (mean ± SE) for females and males (by territory tenure). Letters represent significant differences after post-hoc tests.

Bill morphology in relation to sex, age, size, and territory tenure

Sex and age classes also differed in overall bill morphology when compared on 3 parameters: height, length and curvature (sex: Pillai's Trace = 0.336, $F_{3,156}$ = 26.33, P < 0.0001; age: Pillai's Trace = 0.094, $F_{3,156}$ = 5.44, P = 0.0013). Females showed significantly shorter bill heights ($F_{1,158}$ = 8.17, P = 0.005) and more curved bills than males ($F_{1,158}$ = 22.53, P < 0.0001). Bill curvature was significantly correlated to bill length, although bill length explained only 3.4% of the variation in curvature ($F_{1,160}$ = 6.59, R^2: 0.034, P = 0.014). Adults showed longer bills ($F_{1,158}$ = 9.51, P = 0.002) and greater bill height ($F_{1,158}$ = 4.65,

$P = 0.032$) than juveniles, but did not differ in curvature ($F_{1,158} = 0.34$, $P = 0.55$). Bill shape changed through time in males measured in consecutive years (Pillai's Trace = 0.33, $F_{3,32} = 4.93$, $P = 0.007$); bill curvature decreased (Paired t-test: $t = 3.35$, df = 16, $P = 0.004$; Figure 4b), but not bill length (Paired t-test: $t = 0.71$, df = 16, $P = 0.48$) or height (Paired t-test: $t = 1.17$, df = 16, $P = 0.26$). Using the SMATR package for allometric trends, we did not find any significant fit between bill length against weight, tarsus length, exposed culmen, and wing chord (Supplementary Figure A5, $P > 0.05$ in all cases).

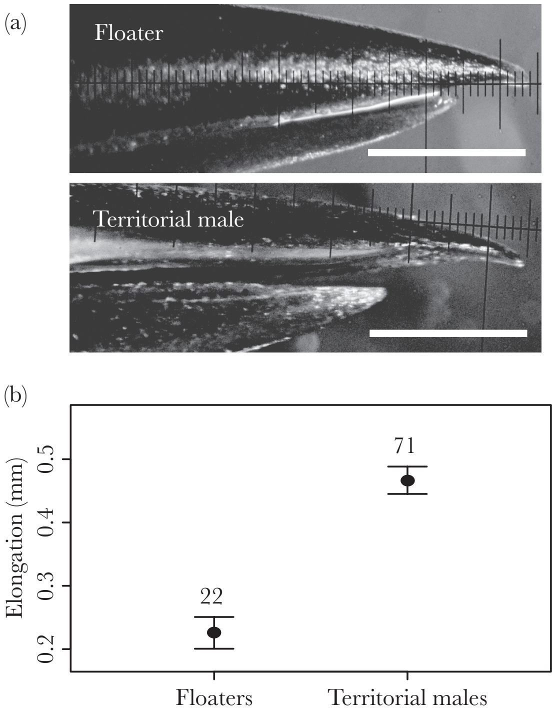

Figure 3
Bill tip length differences between floaters and territorial males. (a) Field macro-photographs of the bill tips of a representative floater and a territorial male. Scale bars (white) = 0.5 mm. (b) Length of maxillary elongation measured in lateral view (mean ± SE) for floaters and territorial males. Sample sizes are given above.

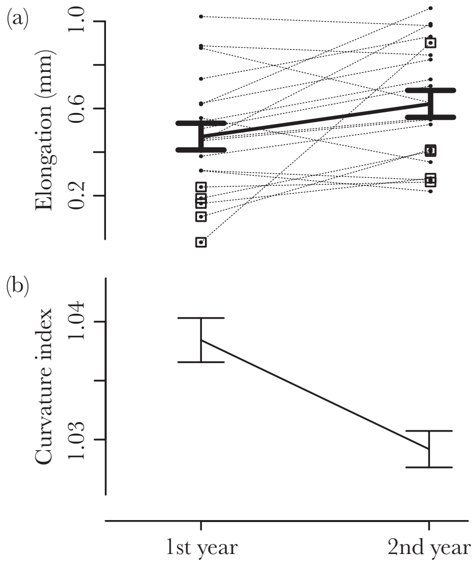

Figure 4
Ontogenetic change in overall bill morphology and bill tip length in male long-billed hermits. (a) Change in bill tip length (mean ± SE, $N = 20$) for males measured in 2 consecutive years. Points around means show individual bill tip lengths. Points inside squares denote lengths for individuals that were juveniles when the first measurement was taken. (b) Change in bill curvature (mean ± SE, $N = 20$) for males measured in 2 consecutive years.

Functional assessment

Bill puncture capability analyses revealed significant differences between adult males, juvenile males, and females ($F_{2,33} = 69.23$, $P < 0.0001$). Adult male bills required less force to perforate the film than those of juvenile males or females (Tukey pos-hoc test: $P < 0.001$ in both cases; Figure 5a). In addition, we noted that bill tips in adult males were stiffer to the touch than those of females and juveniles, which tended to bend slightly when gently touched. Bill curvature and bill tip pointiness (interaction) explained together (Multiple regression: $F_{2,29} = 4.23$, $R^2 = 0.17$, $P = 0.024$, Figure 5b), but not individually (curvature: $P = 0.083$; pointiness: $P = 0.073$), a significant proportion of the variation in puncture force. Bill curvature was positively correlated with force ($\beta = 2208$) while a negative relationship was found between pointiness and force ($\beta = -353$). Bootstrap subsampling tests supported the results in all unbalanced comparisons above.

DISCUSSION

The role of sexual selection in hummingbird bill morphology

We found supporting evidence for the hypothesis that the dagger-like bill tip in the long-billed hermit is a secondary sexual trait and

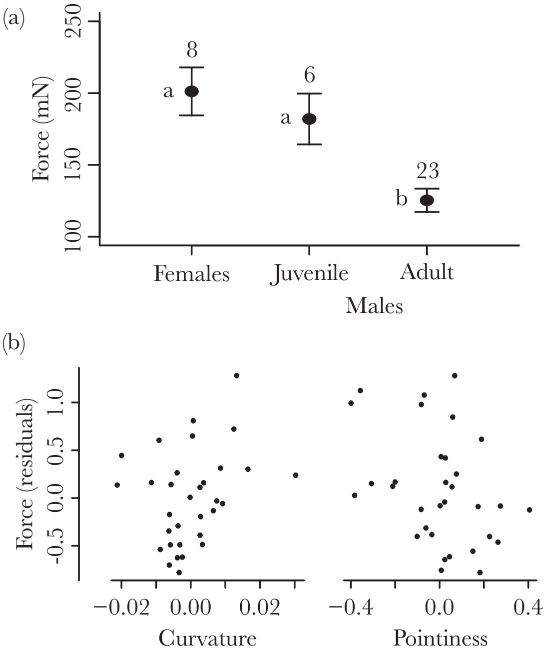

Figure 5
Results of puncture assessment experiments, and the roles of bill tip curvature and pointiness for explaining differences in performance. (a) Applied force (mean ± SE) required to perforate the experimental film by sex and age classes (among males). Sample sizes are given above. Letters represent significant differences after post-hoc tests. (b) Partial regression plots showing the effect of bill curvature (*left*) and pointiness index (*right*) on the force required to puncture the experimental film. Plots represent the effect of each variable after correcting by the other (interaction is significant, see Results: Functional assessment).

a sexually dimorphic weapon. All our predictions were met: 1) longer and pointier bill tips were only present in males and were most developed in adults; 2) fully developed bill tips were acquired during the transition to male adulthood; 3) variation in bill tip morphology reflected puncture capability (i.e., pointier bill tips pierced with less force than the non-pointed bill tips); and 4) males with larger and pointier bill tips were more successful in defending lek territories. Our hypothesis is further supported by our behavioral observations during 4 years: we recorded the displays described by Stiles and Wolf (1979) that usually escalated to chases (e.g., Supplementary Movie A1) or led to copulations (e.g., Supplementary Movie A4). We also observed males using their bills while fighting; confirming the use of the bill tip as a functional weapon, specifically for stabbing rivals (e.g., Supplementary Movie A2). Overall, our results support the hypothesis that this secondary sexual trait is the first documented sexually dimorphic weapon in hummingbirds. Interestingly, hooked bill tips and serrated tomia have been shown to be sexually dimorphic in the tooth-billed hummingbird (*Androdon*: Gould 1863) and the saw-billed hermit (*Ramphodon*: Elliot 1879). The function of these dimorphic bill tips has puzzled scientists for over a century, and it might be explained under our theory of sexually dimorphic weapons.

In some males, bill tip length decreased from 1 year to the next, and even during 3 consecutive years. Hence, although the acquisition of a dagger-like bill tip is delayed until adulthood, older males do not necessarily possess longer bill tips. Similar results have been found in male Mandrills; canines become longer with age up to a point, but then decrease again in the oldest males (Leigh et al. 2008). Teeth in diphyodont vertebrates (most mammals) are not replaced during adulthood (review in Wang et al. 2014) then once they stop growing they would decrease in size due to wear. However, in birds the rhamphotheca continues to grow even in adult individuals (e.g., Lüdicke 1933; Hieronymus and Witmer 2010), therefore the interplay between growth and wear may ultimately determine the final size of the bill tip. Among the individuals in which we tracked bill tip length across years, we did not find any consistent pattern (Supplementary Figure A3) besides the fact that the juvenile males that did not have elongated maxillary tips (bill tip length ~0.0 mm) when captured for the first time, acquired elongated bill tips in subsequent years, once they became adults (Figures 4a and Supplementary Figure A3). We surmise that in such a dynamic system, the differences between territorial and floaters are not mere age-related byproducts. We did not notice any damage to the bill tips of the males included in the analyses of bill tip length differences between years, thus discarding the possibility of broken tips confounding our results. We excluded from these analyses one male in which we clearly observed a broken maxillary tip the second time it was captured (the following year). This male had lost his territory by the time of the second capture, but regained territory tenure by the time of the third capture (about a year after the second capture) when its bill tip had grown back close to its original size and shape thus reinforcing the connection between bill tip length and form, and territory tenure (cf. Figures 2c and 3b).

In a similar manner, if the differences in bill tip morphology were due simply to overall body size (larger males having longer bill tips), one would expect an isometric scaling in maxillary and mandibular tips. Such isometry would yield proportional lengthening of both mandibular and maxillary rhamphothecae, roughly preserving the distance between upper and lower bill tips (i.e., no maxillary elongation). Isometric scaling by definition would preserve the shape of the structures involved, in this case, bill tips. What we found, however, was a drastic change in shape between juvenile and adult males, and significant shape differences between floaters and territorial males. When testing for allometric scaling on the bill traits (e.g., Supplementary Figures A4 and A5), we did not find significant trends using bivariate line-fitting methods (Warton et al. 2012; but see Martin et al. 2005). The absence of significant isometry or allometry in our data could be explained by the lack of a robust estimate of body size in hummingbirds; weight is highly variable due to their small size, tarsus length is susceptible to proportionally large measurement error using calipers, wing chord could be subject to variation in the final stages of moulting and due to selection under varying aerodynamic requirements (related to displays and chases), and exposed culmen is a circular proxy because it includes the bill tip. Since bill tips do not necessarily grow longer with age (Supplementary Figure A3) or body size (e.g., Figure A4), and since there is a strong correlation between bill tip length/shape and territory tenure (Figures 2c and 3), our findings support the importance of the maxillary tip morphology (elongation and sharpness) *per se* as a determinant of successful territoriality.

We found that adult males have pointier, longer and straighter bills, and that curvature and pointiness partially explain the lower force adult males need for puncturing (Figure 5b). Therefore, an adult male bill will inflict more damage during an attack with its bill, compared to a female or a juvenile. Male LBHs have longer bills than females (present study; Stiles and Wolf 1979; Temeles et al. 2010), which could be advantageous to win bill-sparring contests, as has been shown for Ibises (Babbitt and Frederick 2007). We found that females have more curved bills than males, agreeing with Temeles et al. (2010) in this and other species of large hermits (using a different curvature index). Moreover, we found that juvenile males transitioned from curved to straighter bills (Figure 4b) and acquired longer bill tips (Figure 4a) once they reached adulthood. Straight elongated structures (e.g., slender beams) are mechanically more resistant to buckling, when loaded axially, than curved ones (Kuo and Yang 1991; Dahlberg 2004). Bending is disadvantageous for a stabbing weapon since it results in less force applied at the tip, and hence less damage to an opponent. In hummingbirds, straighter bills transmit more force without bending, and pointier bills transform that force into perforation capacity (cf. Figure 5). We also found that males have bills that are thicker (greater bill heights) at the base, potentially providing increased support to resist bending forces at the bill base when stabbing. The arguments above provide an alternative explanation to intersexual resource partitioning or ecological causation for sexual dimorphism in hummingbird bills (see below).

Sexual selection, in the form of female choice, has been proposed as an explanation for sexual dimorphism in hummingbird bills (Stiles 1995). Female choice has been shown as a driver of sexual dimorphism in some species of birds (e.g., Olsen et al. 2013). We observed some territorial males pecking the throat of recently arrived birds (e.g., Supplementary Movie A3). We hypothesize that this could function as a courtship display and/or a warning signal and weapon assessment. However, in the interactions that led to copulations (e.g., Supplementary Movie A4) we did not observed pecking. Although female choice does not seem to be a plausible mechanism for the evolution of dagger like bill tips given the courtship behavior in this species (Stiles and Wolf 1979, Supplementary Movie A4), sexually dimorphic weapons in other animals function both as armaments and ornaments (e.g., deer: Goss 1983; fiddler crabs: Allen and Levinton 2007; but see Callander et al. 2013).

Alternative hypotheses

Sharp bill tips could be useful in nectar thievery (cf. Ornelas 1994), which has been reported predominantly in short-billed hummingbirds (reviews in Ornelas 1994; Irwin et al. 2010). All the species of *Phaethornis* that have been reported robbing nectar, in fact, are small (<4 g) and have short bills (<25 mm): *P. longuemareus (LBH)* (McDade and Kinsman 1980), *P. striigularis* (Schuchmann 1999), *P. ruber* (Lopes et al. 2002, among others). Additionally, species of small *Phaethornis* exhibit reduced (or absent) sexual dimorphism in bill curvature when compared to large *Phaethornis* (Temeles et al. 2010). In multiple studies *P. longirostris* (LBH) has always been reported to visit flowers legitimately (account in Schuchmann 1999). Floral larceny usually emerges when a nectarivore cannot access the nectar in the usual way (Irwin et al. 2010). LBHs, with bills of ~41 mm, have no trouble legitimately accessing flowers. Nonetheless, if there were evolutionary pressure to adapt to a nectar robbing strategy, it would most likely affect the sex with shorter bills, in this case, females. Conversely, we found the needle-like bill tips to be present in adult males only. We thus consider nectar theft an unlikely explanation for this sexually dimorphic trait in hummingbirds.

Sexually dimorphic traits in hummingbird bills have been traditionally explained through the intersexual resource partitioning (IRP) hypothesis (Darwin 1871; Temeles and Roberts 1993; Bleiweiss 1999; Temeles et al. 2000, 2010). In some species of hermits, it has been shown that males and females feed on different plant species (e.g., Temeles et al. 2010), but it is unclear if the hummingbirds have adapted to the plants or *vice versa*. If sharp bill tips were advantageous for feeding on flowers (e.g., to prop open closed corollas), there is no *a priori* reason to speculate that such a trait would favor males but not females. In the cases in which intersexual resource partitioning has been shown, both sexes forage on very similar flowers (different species of the same plant genus; e.g., *Heliconia*: Temeles et al. 2010), and feed in the same way (i.e., no differential robbing between sexes). Furthermore, differences in floral resource use between sexes of *P. longirostris* have not been reported (cf. Temeles et al. 2010). Given that the dagger-like bill tips that we describe in this paper do not seem to convey any gender-biased foraging advantage, nor to be related to differential feeding strategies between the sexes, we infer that this sexually dimorphic trait in hummingbird bills does not fit the IRP explanation regarding floral visitation.

A related hypothesis is that IRP explains sexual dimorphism in bill traits with respect to arthropod capture. Female hummingbirds need to acquire the necessary protein for egg production and nurturing of hatchlings during the breeding season (Wolf and Stiles 1970; Remsen et al. 1986; Chavez-Ramirez and Dowd 1992). Consequently, females spend more time hunting for arthropods, targeting prey at higher trophic levels (higher nitrogen content; e.g., spiders: Rico-Guevara 2008; Hardesty 2009). Among hummingbirds, hermits have been shown to rely more heavily on substrate prey (Stiles 1995). Since longer bills could be advantageous for gleaning prey such as spiders (longer reach, Stiles 1995), increased bill length would be expected in females, who hunt and successfully capture prey more frequently than males (Stiles 1995; Rico-Guevara 2008; Hardesty 2009). Nevertheless, in large *Phaethornis* bills have been found to be longer in males than in females (Stiles 1995; Colwell 2000; Rodríguez-Flores and Stiles 2005; Temeles et al. 2010). For those reasons, predictions of bill sexual dimorphism as a result of arthropod foraging contradict the observed pattern.

As a final alternative hypothesis, modifications of the bill tip could be useful for grooming. Maxillary overhangs in birds have been hypothesized (Clayton and Walther 2001) and proven (Clayton et al. 2005) to enhance preening, which is the first line of defense against ectoparasites. Although preening behavior *per se* has not been found to be sexually selected (Griggio and Hoi 2006), it appears to maintain feather colors that may signal male condition to females (Griggio et al. 2010). It would be plausible then that sexually dimorphic bill tip overhangs evolved to enhance male preening abilities. We discard this alternative hypothesis by pointing out the morphological and mechanical differences between the "maxillary overhang" used for preening (Clayton and Walther 2001; Clayton et al. 2005) and the "maxillary elongation" described in this paper. The preening bill overhang consists of a curved, flattened extension of the maxillary rhamphotheca over the mandibular tip (see Figure 3a in Clayton and Walther 2001). This contrasts with the maxillary elongation we describe here, which is a straight, conical extension of the maxillary tip beyond the mandibular tip. A flattened, curved overhang generates a shearing force (sufficient to damage ectoparasites) when the mandible moves forward and scrapes the inside of the overhang (Clayton et al. 2005). The larger the internal area of the maxillary overhang, before a critical break point, the better the ectoparasite removal (Figures 1 and 4 in Clayton et al. 2005). Conversely, the maxillary elongation we found in LBHs becomes conical at the tip, offering less shearing surface area. Additionally, since the elongation in LBH bill tips is straight rather than curved, it would exert a comparatively weaker vertical force (Figure 3b in Clayton and Walther 2001) detrimental for preening purposes.

Having considered alternative hypotheses for the existence of a needle tipped bill of male LBHs, we argue that it is likely that more than one selective force could operate synergistically in the evolution of a sexually dimorphic trait (Hedrick and Temeles 1989). For instance, for the species in which a correlation between bill sexual dimorphism and nectar foraging has been shown (e.g., Temeles et al. 2010), both IRP and sexual selection could play a role in the existence and maintenance of such dimorphism. We argue, however, that IRP would be restricted to particular species-poor communities, in which interspecific competition is decreased (Hedrick and Temeles 1989). We expect that sexual selection in the form of male-male combat is most important in species with high levels of aggressive physical interactions (e.g., lekking hummingbirds).

Sexually dimorphic weaponry

Most of the animal weaponry studied to date is found in arthropods or non-avian vertebrates (Emlen 2008) and the documented examples of bird sexually dimorphic weapons are restricted to leg spurs in Phasianids and wing spurs in 5 families of aquatic birds (Rand 1954; Davison 1985). Leg spurs have been suggested to evolve due to competition for females or for resources attractive to females (Andersson 1994). There have been previous suggestions of male birds using their bills in physical combat against conspecifics (Babbitt and Frederick 2007; Chaine and Lyon 2008; Navarro et al. 2009; Greenberg and Olsen 2010; Greenberg et al. 2013), but there have been no previous descriptions of sexually dimorphic weapons in bird bills. In Emlen's 2008 comprehensive review of animal weapons, there is not a single reference to birds' weaponry highlighting the importance of studying armaments in such a diverse group. This study stands as one of the few unambiguous examples of sexually dimorphic weapons in birds.

Hummingbirds' extremely pugnacious nature has been acknowledged since they first marveled pioneering naturalists (cf. Wallace 1878), but only now have we started to appreciate its ecological and evolutionary implications, for example, fighting and the presence of weapons. Our discovery of a new sexually dimorphic weapon encourages future comparative studies and reinterpretations of sexual dimorphism of bill traits in hummingbirds. Additionally, this sexually dimorphic weapon in hummingbirds is a direct modification of the feeding apparatus; possessing a weapon is advantageous in the mating process but may be disadvantageous for feeding (e.g., salmon: Darwin 1859; Witten and Hall 2002). Hummingbirds feed on nectar by extruding the liquid from the tongue using their bill tips (Ewald and Williams 1982; Rico-Guevara and Rubega 2011), the bill tip modifications described in this paper would impose a functional trade-off between fighting ability and feeding performance. Comparative studies to understand and quantify the costs (or lack thereof e.g., beetles: McCullough and Emlen 2013) of sexually dimorphic weapons in nature, and studies on sexual differences in feeding efficiency in species with sexually dimorphic weapons (e.g., fiddler crabs: Weissburg 1993; Mokhlesi et al. 2011) are warranted.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

FUNDING

This work was supported by the Organization for Tropical Studies; Department of Ecology and Evolutionary Biology at University of Connecticut National Science Foundation (IOS- DDIG 1311443); College of Arts and Science and Biology Department at New Mexico State University; National Geographic Society (CRE 9169-12); and Animal Behavior Society. All of the activities were reviewed and authorized by the Institutional Animal Care and Use Committee at the New Mexico State University, IACUC 2011-020, and were performed under the research permits 152-2009-SINAC and 063-2011-SINAC.

We thank G. Stiles, W. Eberhard and G. Barrantes for stimulating discussion of ideas on early stages of this manuscript, K. Wells, J. Velotta, D. Sustaita, P. Allen, P. González-Gómez, C. Clark, and anonymous reviewers for comments on the manuscript, and M. Rubega, K. Schwenk, T. Wright, B. Ryerson, and the participants in the Vertebrate Biology Seminar at UConn for debates on various hypotheses. Special thanks to J. Rack and K. Hurme for grammar and style advice. Finally we thank S. Ehlman, X. Sanloz, O. Kolodny, D. Boyce, W. Tsai, D. Sanchez, D. Ocampo and M. Percy for fieldwork assistance, and the Museum of Zoology of Universidad de Costa Rica for logistic support.

Handling editor: Paco Garcia-Gonzalez

REFERENCES

Allen BJ, Levinton JS. 2007. Costs of bearing a sexually selected ornamental weapon in a fiddler crab. Funct Ecol. 21:154–161.

Andersson M. 1994. Sexual Selection. Princeton (NJ): Princeton University Press.

Apollonio M, Festa-Bianchet M, Mari F, Mattioli S, Sarno B. 1992. To lek or not to lek: mating strategies of male fallow deer. Behav Ecol. 3:25–31.

Araya-Salas M, Wright T. 2013. Open-ended song learning in a hummingbird. Biol Lett. 9:20130625.

Babbitt GA, Frederick PC. 2007. Selection for sexual bill dimorphism in ibises: an evaluation of hypotheses. Waterbirds. 30:199–206.

Balmford A, Albon S, Blakeman S. 1992. Correlates of male mating success and female choice in a lek-breeding antelope. Behav Ecol. 3:112–123.

Baltosser WH. 1978. New and modified methods for color-marking hummingbirds. Bird Banding. 49:47–49.

Berns CM, Adams DC. 2010. Bill shape and sexual shape dimorphism between two species of temperate hummingbirds: Black-Chinned hummingbird (Archilochus alexandri) and Ruby-Throated hummingbird (A. colubris). Auk. 127:626–635.

Bleiweiss R. 1999. Joint effects of feeding and breeding behaviour on trophic dimorphism in hummingbirds. Proc R Soc Lond B Biol Sci. 266:2491–2497.

Bock WJ. 1966. An approach to the functional analysis of bill shape. Auk. 83:10–51.

Bookstein FL. 1997. Morphometric tools for landmark data: geometry and biology. Cambridge (UK): Cambridge University Press.

Callander S, Kahn AT, Maricic T, Jennions MD, Backwell PR. 2013. Weapons or mating signals? Claw shape and mate choice in a fiddler crab. Behav Ecol Sociobiol. 67:1163–1167.

Chaine AS, Lyon BE. 2008. Intrasexual selection on multiple plumage ornaments in the lark bunting. Anim Behav. 76:657–667.

Chavez-Ramirez F, Dowd M. 1992. Arthropod feeding by two Dominican hummingbird species. Wilson Bull. 104:743–747.

Clayton DH, Walther BA. 2001. Influence of host ecology and morphology on the diversity of Neotropical bird lice. Oikos. 94:455–467.

Clayton DH, Moyer BR, Bush SE, Jones TG, Gardiner DW, Rhodes BB, Goller F. 2005. Adaptive significance of avian beak morphology for ectoparasite control. Proc R Soc Lond B Biol Sci. 272:811–817.

Clutton-Brock TH, Hiraiwa-Hasegawa M, Robertson A. 1989. Mate choice on fallow deer leks. Nature. 340:463–465.

Colwell RK. 2000. Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. Am Nat. 156:495–510.

Dahlberg T. 2004. Procedure to calculate deflections of curved beams. Int J Eng Educ. 20:503–513.

Darwin C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London: J. Murray.

Darwin C. 1871. The descent of man and selection in relation to sex. London: J. Murray.

Davison GWH. 1985. Avian spurs. J Zool. 206:353–366.

Delattre PA. 1843. Oiseaux-Mouches nouveaux au peu connus, découverts au Gualimala. In L'Echo Du Monde Savant. 45:1068–1070.

Elliot DG. 1879. A classification and synopsis of the Trochilidae. Washington: Smithsonian Institution.

Emlen DJ. 2008. The evolution of animal weapons. Annu Rev Ecol Evol Syst. 39:387–413.

Endler JA. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biol J Linn Soc. 41:315–352.

Ewald PW, Williams WA. 1982. Function of the bill and tongue in nectar uptake by hummingbirds. Auk. 99:573–576.

González C, Ornelas JF. 2009. Song variation and persistence of song neighborhoods in a lekking hummingbird. Condor 111:633–640.

Goss RJ. 1983. Deer antlers: regeneration, function, and evolution. London: Academic Press.

Gould J. 1863. On a new genus of Humming-Birds. Ann Mag Nat Hist. 3:246–247.

Greenberg R, Olsen B. 2010. Bill size and dimorphism in tidal-marsh sparrows: island-like processes in a continental habitat. Ecology. 91:2428–2436.

Greenberg R, Etterson M, Danner RM. 2013. Seasonal dimorphism in the horny bills of sparrows. Ecol Evol. 3:389–398.

Griggio M, Hoi H. 2006. Is preening behaviour sexually selected? An experimental approach. Ethology. 112:1145–1151.

Griggio M, Hoi H, Pilastro A. 2010. Plumage maintenance affects ultraviolet colour and female preference in the budgerigar. Behav Processes. 84:739–744.

Hardesty J. 2009. Using nitrogen-15 to examine protein sources in hummingbird diets. Ornitol Colomb. 8:19–28.

Hedrick AV, Temeles EJ. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends Ecol Evol. 4:136–138.

Hieronymus TL, Witmer LM. 2010. Homology and evolution of avian compound rhamphothecae. Auk. 127:590–604.

Hinkelmann C. 1996. Systematics and geographic variation in long-tailed hermit hummingbirds, the Phaethornis superciliosus-malaris-longirostris species group (Trochilidae), with notes on their biogeography. Ornitol Neotrop. 7:119–148.

Hinkelmann C, Schuchmann KL. 1997. Phylogeny of the hermit hummingbirds (Trochilidae: Phaethornithinae). Stud Neotrop Fauna E. 32:142–163.

Hinkelmann C, van den Elzen R. 2002. Verwandtschaftsbeziehungen bei Schattenkolibris (Gattung *Phaethornis*, Aves, Trochilidae), ein Methodenvergleich. Bonn Zool Beitr. 51:35–49.

Irwin RE, Bronstein JL, Manson JS, Richardson L. 2010. Nectar robbing: ecological and evolutionary perspectives. Annu Rev Ecol Evol Syst. 41:271–292.

Kapoor JA. 2012. Improved methods for color-marking hummingbirds. J Field Ornithol. 83:186–191.

Kuo SR, Yang YB. 1991. New theory on buckling of curved beams. J Eng Mech. 117:1698–1717.

Leigh SR, Setchell JM, Charpentier M, Knapp LA, Wickings EJ. 2008. Canine tooth size and fitness in male mandrills (Mandrillus sphinx). J Hum Evol. 55:75–85.

Lopes AV, Vogel S, Machado IC. 2002. Secretory trichomes, a substitutive floral nectar source in Lundia A. DC. (Bignoniaceae), a genus lacking a functional disc. Ann Bot. 90:169–174.

Lüdicke M. 1933. Wachstum und Abnutzung des Vogelsehnabels. Zoo Jahrb. 57:465–533

Martin RD, Genoud M, Hemelrijk CK. 2005. Problems of allometric scaling analysis: examples from mammalian reproductive biology. J Exp Biol. 208:1731–1747.

McCullough EL, Emlen DJ. 2013. Evaluating the costs of a sexually selected weapon: big horns at a small price. Anim Behav. 86:977–985.

McDade LA, Kinsman S. 1980. The impact of floral parasitism in two neotropical hummingbird-pollinated plant species. Evolution. 34:944–958.

McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS. 1994. La Selva: ecology and natural history of a neotropical rain forest. Chicago: University of Chicago Press.

Mitteroecker P, Gunz P. 2009. Advances in geometric morphometrics. Evol Biol. 36:235–247.

Mokhlesi A, Kamrani E, Backwell P, Sajjadi M. 2011. Sexual differences in foraging behavior of fiddler crab, Uca sindensis (Decapoda: Ocypodidae). J Persian Gulf. 2:37–44.

Navarro J, Kaliontzopoulou A, González-Solís J. 2009. Sexual dimorphism in bill morphology and feeding ecology in Cory's shearwater (Calonectris diomedea). Zoology (Jena). 112:128–138.

Olsen BJ, Greenberg R, Walters JR, Fleischer RC. 2013. Sexual dimorphism in a feeding apparatus is driven by mate choice and not niche partitioning. Behav Ecol. 24:1327–1338.

Ornelas JF. 1994. Serrate tomia: an adaptation for nectar robbing in hummingbirds? Auk. 111:703–710.

Ortiz-Crespo FI. 1972. A new method to separate immature and adult hummingbirds. Auk. 89:851–857.

Paton DC, Collins BG. 1989. Bills and tongues of nectar—feeding birds: a review of morphology, function and performance, with intercontinental comparisons. Aust J Ecol. 14:473–506.

Piacentini VDQ. 2011. Taxonomia e distribuição geográfica dos representantes do gênero Phaethornis Swainson, 1827 (Aves: Trochilidae) [dissertation]. São Paulo (Brazil): Universidade de São Paulo.

Plavcan JM. 2012. Sexual size dimorphism, canine dimorphism, and male-male competition in primates. Hum Nat. 23:45–67.

R Development Core Team. 2013. R: a language and environment for statistical computing. Reference index version 2.16. Vienna (Austria): R Foundation for Statistical Computing. ISBN 3-900051-07-0. Available from http://www.R-project.org.

Radford AN, du Plessis MA. 2004. Extreme sexual dimorphism in Green Woodhoopoe (*Phoeniculus purpureus*) bill length: a case of sexual selection? Auk. 121:178–183.

Rand AL. 1954. On the spurs on birds' wings. Wilson Bull. 65:127–134.

Remsen JV, Stiles FG, Scott PE. 1986. Frequency of arthropods in stomachs of tropical hummingbirds. Auk. 103:436–441.

Rico-Guevara A. 2008. Morphology and arthropod foraging by high Andean hummingbirds. Ornitol Colomb. 7:43–58.

Rico-Guevara A, Rubega MA. 2011. The hummingbird tongue is a fluid trap, not a capillary tube. Proc Natl Acad Sci U S A. 108:9356–9360.

Rodríguez-Flores CI, Stiles FG. 2005. Ecomorphological analysis of a community of hermit hummingbirds (Trochilidae, Phaethorninae) and their flowers in Colombian Amazonia. Ornitol Colomb. 3:7–27.

Rohlf FJ. 2010. TpsDig, Version 2.16. New York: Department of Ecology and Evolution, State University of New York at Stony Brook.

Salvin O. 1892. Catalogue of the Picariae in the collection of the British Museum: Upupae and Trochili. London (UK): Longmans & Co. Press.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Methods. 9:671–675.

Schuchmann L. 1999. Family Trochilidae (hummingbirds). In: del Hoyo J, Elliott A, Sargatal J, editors. Handbook of the birds of the world. Vol. 5. Barcelona (Spain): Lynx Editions. p. 468–680.

Sinervo B, Zamudio KR. 2001. The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. J Hered. 92:198–205.

Smith TM, Shugart HH. 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology. 68:695–704.

Stiles FG. 1995. Behavioral, ecological and morphological correlates of foraging for arthropods by the hummingbirds of a tropical wet forest. Condor. 97:853–878.

Stiles FG, Wolf LL. 1973. Techniques for color-marking hummingbirds. Condor. 75:244–245.

Stiles FG, Wolf LL. 1979. Ecology and evolution of lek mating behavior in the long-tailed hermit hummingbird. Am Ornithol Union Monogr. 27:1–78.

Székely T, Reynolds JD, Figuerola J. 2000. Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. Evolution. 54:1404–1413.

Temeles EJ, Roberts WM. 1993. Effect of sexual dimorphism in bill length on foraging behavior: an experimental analysis of hummingbirds. Oecologia. 94:87–94.

Temeles EJ, Pan IL, Brennan JL, Horwitt JN. 2000. Evidence for ecological causation of sexual dimorphism in a hummingbird. Science. 289:441–443.

Temeles EJ, Koulouris CR, Sander SE, Kress WJ. 2009. Effect of flower shape and size on foraging performance and trade-offs in a tropical hummingbird. Ecology. 90:1147–1161.

Temeles EJ, Miller JS, Rifkin JL. 2010. Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (Phaethornithinae): a role for ecological causation. Phil Trans R Soc B. 365:1053–1063.

Wallace AR. 1878. Humming-birds: as illustrating the luxuriance of tropical nature. In: Wallace AR, editor. Tropical nature, and other essays. London: Macmillan. p. 124–157.

Wang F, Xiao J, Cong W, Li A, Song T, Wei F, Xu J, Zhang C, Fan Z, Wang S. 2014. Morphology and chronology of diphyodont dentition in miniature pigs, Sus Scrofa. Oral Dis. 20:367–379.

Warburton NM, Bateman PW, Fleming PA. 2013. Sexual selection on forelimb muscles of western grey kangaroos (Skippy was clearly a female). Biol J Linn Soc. 109:923–931.

Warton DI, Duursma RA, Falster DS, Taskinen S. 2012. smatr 3–an R package for estimation and inference about allometric lines. Methods Ecol Evol. 3:257–259.

Wiley RH. 1991. Lekking in birds and mammals: behavioral and evolutionary issues. Adv Stud Behav. 20:201–291.

Witten PE, Hall BK. 2002. Differentiation and growth of kype skeletal tissues in anadromous male Atlantic salmon (Salmo salar). Int J Dev Biol. 46:719–730.

Weissburg M. 1993. Sex and the single forager: gender-specific energy maximization strategies in fiddler crabs. Ecology. 74:279–291.

Wolf LL, Stiles FG. 1970. Evolution of pair cooperation in a tropical hummingbird. Evolution. 24:759–773.

Zach R, Falls JB. 1979. Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogeneous habitat. J Anim Ecol. 48:33–52.