

1 **Superciliums in white-eared hummingbirds as badges of status**
2 **signaling dominance**

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4 ^aJuan Manuel González-García, ^{b,*}Carlos Lara, ^cJavier Quesada, ^dCarlos A. Chávez-Zichinelli,
5 ^eMartín A. Serrano-Meneses

6

7 ^aDoctorado en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, Carretera Tlaxcala-
8 Puebla Km 1.5, 90070 Tlaxcala, Mexico.

9

10 ^bCentro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, Km 10.5
11 Autopista Tlaxcala-San Martín Texmelucan, San Felipe Ixtacuixtla, Tlaxcala 90120, Mexico.

12

13 ^cNatural History Museum of Barcelona, Chordates Laboratory, Passeig Picasso s/n, 08003
14 Barcelona, Spain.

15

16 ^dEl Colegio de Puebla, Calle Tehuacán Sur 91, La Paz, 72160 Puebla, Puebla, Mexico.

17

18 ^eUniversidad de las Américas Puebla Sta. Catarina Mártir. Cholula, Puebla. C. P. 72810, Mexico.

19

20 *Author for correspondence; email: carlos.lara.rodriguez@gmail.com

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22 Running head: Badges of status signaling dominance in hummingbirds

1 **Abstract** The role of badges as indicators of contest ability has been previously described. In
2 hummingbirds, the exhibition of a badge is expected to save energy expenditure in agonistic
3 interactions and to favour energy intake. Here we investigate whether variable supercilium size
4 in the white-eared hummingbird has a role in dominance status signaling. Firstly, 45
5 hummingbird males were captured and their superciliums were photographed to investigate
6 variation in size and any possible allometric relationships. Secondly, 42 male birds were used to
7 analyze whether the supercilium has a role in dominance status signaling in a dyadic contest. We
8 found that supercilium size varied continuously but that, despite variability between individuals,
9 there was no relationship between supercilium size and body size. However, our dyad
10 experiment indicated that birds with larger badges were able to make more visits to the feeders
11 than individuals with smaller badges. We suggest a status signaling function of the supercilium.

12

13 **Keywords** dominance, *Hylocharis leucotis*, recognizing dominance, signal reliability, status
14 badge

15 **Introduction**

16 The most common means of resource-holding in animals is territoriality, that is, the basic
17 behavior of a resident individual aimed at defending and excluding others from a specific area
18 (Brown and Orians 1970). Prior to a territorial dispute, contesting individuals are often able to
19 evaluate each other through the use of signals that are reflections of their inherent ability in a
20 contest (Smith and Harper 1995; Rat et al. 2015). The signals used for either a context of intra-
21 sexual competition for sexual resources (e. g. mates) or social competition for food resources
22 involve similar traits, such as conspicuous displays, weaponry, aggressive behaviors, and costly
23 signals (Tobias et al. 2012). These types of signals have been found in many avian species and
24 include auditory cues and visual signals associated with plumage – e.g. the size of ornaments and
25 both pigmented or structural plumage coloration – that prevent birds from engaging in costly
26 contests with predictable outcomes (Rohwer 1975; Smith and Harper 2003; Senar 2006; Pryke
27 2013).

28 The conspicuous coloration patches in the plumage of many birds that are made up of
29 different pigments, termed by convention ‘badges’, often reflect different individual health and
30 condition (e. g. carotenoids) but mostly reflect social status (e. g. melanin-based colours)
31 (Rohwer 1975; Senar 2006; Santos et al. 2011; Young et al. 2015). The role of badges as
32 indicators of contest ability has been analysed, above all, in bird species from temperate areas of
33 the world via the evaluation of territorial performance of individuals exhibiting a gradient in the
34 size and/or intensity in their badges (i.e. Møller 1987; Senar et al. 1993; Rémy et al. 2010;
35 Quesada et al. 2013; Mercadante and Hill 2014). These studies have shown that larger and
36 brighter badges (less dark) indicate better competitive abilities.

37 Generally, the maintenance and development of these visual signals are energetically
38 costly, which makes them reliable signals (Zahavi 1975; Husak et al. 2015). Ornament
39 production and maintenance have associated drawbacks: they may increase the risk of predation
40 (Endler 1978; Stuart-Fox et al. 2003; Pascual and Senar 2014), reduce immune-competence
41 (Ressel and Schall 1989; Dunlap and Schall 1995; Salvador et al. 1996; Calisi et al. 2008) and
42 have social costs in the event of aggressive contests that are both physiologically expensive and
43 time-consuming (Tibbetts and Dale 2004). Therefore, the ability to exhibit this type of signal
44 may be an honest indicator of an individual's health and its physical capabilities in a contest
45 (Hamilton and Zuk 1982; Folstad and Karter 1992), particularly if these traits are more
46 exaggerated in larger-than-average individuals (hyperallometric). This is because, according to
47 indicator traits (Gould 1974; Petrie 1988, 1992), only males in overall good conditions will be
48 able to invest relatively more on these traits with respect to body size (Álvarez, et al. 2013).
49 Disentangling these various factors is a challenge for the current signaling theory underlaying
50 that the evolution and maintenance of these badges are still poorly understood.

51 White plumage ornaments, however, have often been assumed to be inexpensive because
52 their production requires neither pigment nor specialized feather structure (McGlothlin et al.
53 2007). Proposed mechanisms for maintaining the honesty of unpigmented signals have usually
54 focused on various costs of maintaining the trait, such as greater risk of feather abrasion and
55 breakage, colonization of keratinolytic bacterias, reduced attractiveness or its role of inducing
56 male–male aggression (Fitzpatrick 1998; Kose and Møller 1999; Török et al. 2003; McGlothlin
57 et al. 2005; Justyn et al. 2017). But some studies have shown trade-offs between life history traits
58 such as brood size (Gustafsson et al. 1995) and diet quality (McGlothlin et al. 2007) in the

59 expression of white plumage patterns, which suggest a role as honest signals of individual
60 quality.

61 Hummingbirds (Trochilidae) are endemic to the Americas and are the second most
62 diverse family of birds in this continent (approximately 350 taxa). These small birds inhabit all
63 types of environments (Schuchmann 1999) and are known for their agility in flight, high
64 metabolism, iridescent plumage, and both anatomical and physiological adaptations to a
65 specialized diet of nectar (Stiles 1981). Hummingbirds have physiologically demanding flying
66 abilities, which is fueled by the energy obtained from the flowers they visit, while also having
67 evolved due to their feeding strategies (Wagner 1946; Wolf et al. 1976; Stiles 1995; Altshuler et
68 al. 2004). As a result, competition (through territorial behavior) for feeding territories between
69 certain hummingbird species is frequent and plays an important role in determining the structure
70 of their communities (as opposed to the trapliner behavior displayed by non-territorial
71 hummingbirds in which an individual visits food sources on a regular repeatable sequence
72 involving an specific route) (Feinsinger and Colwell 1978; Montgomerie and Gass 1981; Hixon
73 et al. 1983; Dearborn 1998; Camfield 2006)

74 Dominance (both intra and interspecific interactions) in hummingbirds has been found to
75 be associated with the individual physical state, sexual dimorphism, body size, wing disc chord
76 loading, species identity (e. g. some species dominate others at floral patches or feeders) and
77 territorial quality (Kodric-Brown and Brown 1978; Carpenter et al. 1993; Ornelas et al. 2002;
78 Stiles et al. 2005; Németh and Moore 2012). These characteristics have been postulated and
79 tested in hummingbird species at particular moments of their biological cycles such as migration
80 and reproduction (i.e. Gass 1979; Ewald 1985). It has also been suggested that variation in
81 behavioral profile or “personalities” may affect the establishment of dominance relationships and

82 risk sensitivity, where previous research has found hummingbirds to show a steroid-correlated
83 boldness scale (Goloff and Burch 2012; Chávez-Zichinelli et al., 2014). However, despite male
84 hummingbirds employ their iridescent plumage (visual signals) in a variety of contexts,
85 including nuptial displays, aggressive sexual displays, and aggressive displays associated with
86 nectar-centered feeding territoriality (Stiles 1982), the possible role of structural coloration
87 (iridescent or not) and badges during territorial intra and interspecific disputes has only rarely
88 been examined (but see Ewald and Rohwer 1980). This is somewhat surprising, above all if we
89 note that not iridescent signals such as the postocular lines – often white in colour (hereafter
90 referred as superciliums) – are common in hummingbirds. For example, 56 out of the 70
91 hummingbird species that occur in Mexico and North and Central America (Howell and Webb
92 1995) have some type of white spot or patch on their heads (males, females, and juveniles).

93 The white-eared hummingbird (*Hylocharis leucotis*) earns its common name from its
94 supercilium (this patch is not iridescent, so it can be observed at all angles, not specific ones). As
95 opposed to the trapliner behavior displayed by females, the males of this species establish
96 feeding territories that they aggressively defend against conspecifics and other heterospecific
97 small-sized hummingbird species (Lara 2006). When passively (e.g. territorial calls) or actively
98 (e.g. chases and physical contacts) defending a territory, the supercilium is always visible, so that
99 this signal is obvious to any intruders during a territorial contest (hence we focus here only in
100 males). In this study, dominance is defined as success in intraspecific contests, a synonym for
101 resource holding potential, i. e. individuals with the higher resource holding potential (RHP) win
102 disputes (Parker 1974). Thus, resource holding potential reliably reflects male quality. Hence we
103 hypothesized that the supercilium could play a role in signaling to intruders an individual's
104 resource-holding potential, where individuals with larger-sized superciliums will tend to

105 monopolize the available resources, i.e. pay more frequent visits to a food source, to the
106 detriment of individuals with smaller-sized superciliums. However, many supposed ornaments
107 that could be related to dominance may actually signal other qualities such as age or size (see
108 Senar 2006 for a discussion), aspects that require consideration in signaling studies. The goals of
109 our study were thus (1) to assess supercilium size variation in males captured in natural
110 conditions and analyze its possible relationship with body size (allometry). This first approach
111 allowed us to rule out possible allometric effects on supercilium size. Subsequently, (2) we used
112 a manipulative approach to experimentally evaluate the role of supercilium size as a badge of
113 status signaling dominance.

114

115 **Methods**

116 **Study site and species**

117 From February 2013 to March 2015, white-eared hummingbirds (*Hylocharis leucotis*) were
118 studied in La Malinche National Park (LMNP), Tlaxcala, Mexico (19°14'N, 98°58'W, 3000 m
119 a.s.l.). Ethical approval was received from the relevant local authorities (SEMARNAT, license
120 number FAUT-0296). The vegetation in the study area consists mainly of a mosaic of pine forest
121 and second-growth vegetation (Villers et al. 2006). These small hummingbirds (ca 3.1–3.4 g) are
122 residents in LMNP and both sexes feed throughout the year on a wide range of hummingbird-
123 pollinated plants (Lara 2006). Males are highly territorial and are frequently observed defending
124 clumps of flowers on firecracker bushes *Bouvardia ternifolia* (Rubiaceae), beardtongues
125 *Penstemon roseus* (Lamiaceae), and pineapple sages *Salvia elegans* (Lamiaceae). Both sexes
126 have a distinctive white line above and behind the eye (supercilium), and their pigmented

127 underparts are whitish, heavily speckled with green, but males have a bluish violet iridescent
128 forecrown and chin, and a glittering green throat (absents in females).

129

130 **Natural variation in supercilium size**

131 To evaluate variation in supercilium size in males, 45 hummingbirds were captured with mist
132 nets in different areas of the LMNP, but most in areas where patches of flowering firecracker
133 bushes, beardtongues, and pineapple sages abounded. We took the following measurements from
134 each captured individual: (1) total length (mm), (2) bill length (mm), (3) tail length (mm), (4)
135 wing chord (mm), and (5) weight (g; sensu Pyle 1997). Body measurements were taken using a
136 digital caliper (Mitutoyo SC-6, ± 0.2 mm error) and a digital scale (US-SONIC-500, 0.1 g
137 resolution).

138 After measurements, the superciliums (on the right and left sides of head) of each
139 individual were laterally photographed twice with a digital camera (Sony Alpha SH0006) from a
140 constant position and distance. The number of pixels per square millimeter (area) and 1 mm
141 (linear) were calculated using a ruler to get the scale for each photograph using Adobe
142 Photoshop CS6. This methodology is commonly used in studies of plumage colour (Muck and
143 Goymann 2011). The photographed birds were marked by clipping the fifth rectrice (to avoid
144 pseudoreplication), and were then released back to sites from which they were captured. Time
145 from capture to release for each bird was approximately 20 minutes.

146 We assessed the repeatability of supercilium area by comparing the size estimated from
147 photographs 1 and 2 of only the left-side supercilium of each captured individual. These two
148 samples turned out to be highly repeatable for the same individual (adjusted repeatability: 0.92;
149 confidence interval, CI: 0.87—0.93, $P < 0.0001$; following Nakagawa and Schielzeth 2010).

150 In order to assess whether variation in supercilium size in males is allometrically
151 determined, we performed major axis regressions between supercilium size and body
152 measurements (MA regression; Sokal and Rohlf 2012). MA regressions were performed using
153 the ‘smatr’ package in R (Warton et al. 2012), which calculates allometric slopes between two
154 continuous variables, as well as their 95% confidence intervals (CIs; upper CI – lower CI). A
155 slope was considered to be significantly different from 1 if the confidence intervals excluded $\beta =$
156 1, and the associated P value was ≤ 0.05 (Álvarez et al. 2013).

157

158 **Experiment: supercilium as a badge of status signaling dominance**

159 After discarding potential allometric relationships between supercilium size and body
160 measurements (see Results), we evaluated whether this badge has a role in signaling dominance
161 status. Dominant individuals usually prevail over others and take a disproportionate share of
162 available resources (Barnard 1984). Thus, here we considered an individual to be dominant if it
163 made a greater number of visits to a feeder during an experimental trial (Tiebout 1996). A total
164 of 42 adult hummingbird males were captured in the field using mist-nets (different individuals
165 to those used for measuring badges). After capture, the males were measured following the
166 protocol described above (including supercilium size). The birds were housed individually for 24
167 h in collapsible field cages (dimensions: 1.5× 2.0×1.5 m), which contained a perch and a feeder
168 with 120 ml of 20% (by mass) sucrose solution. During this period, feeding by the birds was
169 taken as evidence that they were acclimatized to the enclosure. Individuals that did not feed
170 during the first hour of confinement were released and not used for experimental procedures.
171 Prior to the trials, individuals were not fed for 20 min so that by the time of the experiment they
172 were presumably hungry.

173 An experimental trial consisted of placing two captured individuals for 60 minutes in a
174 collapsible field cage with the characteristics described above, the only difference being the
175 existence of two perches. During this period, a videocamera (Panasonic Camcorder model SDR-
176 H4OP) recorded for both hummingbirds the latency of feeder visits, the number and duration of
177 visits, and the number of agonistic displays (physical contact between the two birds). The great
178 individual variation in the shape and size of the supercilium allowed us to distinguish the
179 individuals used in each dyad and to be able to collect their data. We predicted that the greater
180 the differences between contestants' supercilium sizes, the more differences there would be in
181 the magnitude of the evaluated variables. Based on variation across individuals, half of the male
182 dyads ($n = 11$) had a specific supercilium-size difference ranging from 0–0.04 cm² (similar
183 contenders), and the remaining half from 0.05–0.17 cm² (different contenders). Thus, the
184 contests were classified into two types in terms of the differences in supercilium size between the
185 contenders (Contest type). For analyses we use patch size differences (that vary continuously)
186 among contenders. All subjects ($N = 42$) were used only once in the experiment and were
187 subsequently released as per the protocol described above.

188 To assess the contribution of differences in supercilium size between contenders to the
189 intensity of feeder use during the experimental trials, two statistical approaches were used. In the
190 first approach, four separate regressions test each of the behavioural measures (dependent
191 variables: differences in latency of visits, number of visits, duration of visits, and number of
192 disputes between contenders) against difference in badge size (independent variable) and
193 considering the contest type (contestants with similar or different badge size).

194 In the second approach, we used the R package 'lme4' (Bates et al. 2014) to build five
195 candidate generalized linear mixed-effects models (GLMM), to be compared using an

196 information theoretic approach (Burnham and Anderson 2002). All continuous variables were
197 \log_{10} -transformed prior to analyses. Each candidate model included supercilium size differences
198 among contenders as independent variable (predictor) and foraging and agonistic variables, and
199 contest type as dependent variables (response variables). Contest identity was included in the
200 models as a random effect due to variation shown in supercilium size in each dyad. For each
201 model an Akaike weight (Akaike 1981) was calculated, which indicates its level of support
202 (since Akaike weights sum to 1, models with Akaike weights approaching 1 receive the most
203 support relative to other models). By summing Akaike weights of all models containing a
204 particular variable, a measure of the relative “evidence of importance” for that predictor
205 variable is produced (Burnham and Anderson 2002). However, this value of predictor
206 importance does not indicate the magnitude or direction of the relationship between predictor
207 and response variables. To provide such an understanding, we subsequently used model
208 averaging to calculate the average parameter estimates based on all GLMM models in which the
209 parameter appeared, weighted by their Akaike weights. The BMS package was used to calculate
210 the posterior inclusion probability (PIP) and standardised posterior mean coefficient (PMC) for all
211 dependent variables. The prior probability for the model was set using the default, which uses the
212 median of the number of available parameters and draws from a normal distribution (of the
213 number of possible parameters).

214 All statistical analyses were performed using the software R (R Development Core Team
215 2014).

216

217 **Results**

218 **Allometry of supercilium size**

219 Supercilium size in male white-eared hummingbirds ranged between 15 to 35 mm², with a mean
 220 of 21 mm² (standard error of 0.13 mm²; $N = 45$). Table 1 summarizes the calculated MA
 221 regression slopes between supercilium size and the six male body-size measurements. The
 222 results from the MA analyses showed that supercilium size is not allometrically related to body
 223 size.

224

225 **Supercilium size and dominance status signaling**

226 No significant relationships were found between the differences in latency of visits (similar
 227 contest types: $Y = 3.42x - 6.6$, $R^2 = 0.16$, $N = 11$, $P = 0.06$; different contest types $Y = 2.20x + 6.12$,
 228 $R^2 = 0.17$, $N = 10$, $P = 0.10$), duration of visits ($Y = 1.13x - 01.54$, $R^2 = 0.06$, $N = 11$, $P = 0.54$; $Y =$
 229 $0.97x + 3.21$, $R^2 = 0.02$, $N = 10$, $P = 0.51$), and number of disputes between contenders ($Y = 0.10x$
 230 $+ 5.24$, $R^2 = 0.14$, $N = 11$, $P = 0.09$; $Y = 0.73x + 0.48$, $R^2 = 0.001$, $N = 10$, $P = 0.89$), against
 231 difference in badge size. However, we found a significant relationship between the difference in
 232 number of visits to a feeder versus difference in badge size (Figure 1).

233

234 Table 2 summarizes the results of GLMMs investigating the effects of supercilium size
 235 on the foraging and agonistic variables, by considering contest type. Variance in supercilium size
 236 among contenders had the stronger effect on the number of visits, with a posterior inclusion
 237 probability value of 0.683 (Table 2). Thus, individuals with larger superciliums were able to
 238 make more visits to the feeders (Figure 1) irrespective of contest type (i.e. of whether contenders
 239 had similar or different supercilium sizes). All other dependent variables (latency of visits,
 240 number of visits, duration of visits, number of disputes between contenders, contest type) did not
 241 significantly contribute to the models tested.

242

243 **Discussion**

244 Typically, the evolution of sexual traits and, in particular, their hyperallometric patterns, has
245 been explained by sexual selection given the supposed advantages that they confer in mate
246 selection or access to reproductive mates (Gould 1974; Petrie 1992; Kodrick-Brown et al. 2006).
247 However, the theory of social competence (Lyon and Montgomerie 2012) states that competition
248 for limited resources – rather than for mates – may also promote the use of such elaborate traits.
249 Our study demonstrated the lack of hyperallometry in supercilium size in white-eared
250 hummingbird males. These results, along with the demonstration that differences in badge size
251 between contestants affects the level of intraspecific dominance at a food source (feeder),
252 suggest that superciliums may be used as a status signal in a context of social competence.

253 The promiscuous reproductive system of hummingbirds (Stiles and Wolf 1979) seems to
254 favor the use of multiple signals to females (Candolin 2003; Chaine et al. 2013). For example,
255 these signals can serve as multiple messages that either indicate general mate quality or enable
256 females that differ in mate preferences to choose the most suitable male (i.e. the iridescent
257 plumage on cheeks and throat). Likewise, the function of these features as status signals of social
258 communication, particularly in a intraspecific territorial context, has been previously
259 demonstrated for both sexes in a number of different species (Wolf 1969; Ingles 1976; Stiles
260 1982; Bleiweiss 1985). However, to our knowledge this is the first documented study of the use
261 of non-iridescent plumage for status signaling in hummingbirds. More than 50 species of
262 hummingbirds in Mexico and North and Central America exhibit superciliums (Howell and
263 Webb 1995) and appear in both males and females in approximately 25% of these species. The
264 practice of territorial defense in both sexes in several hummingbird species has been used as an

265 evolutionary explanation for the iridescent coloration in monomorphic species (Wolf and Stiles
266 1970); thus it is possible that this selective pressure may also be acting on non-iridescent
267 structural colorations such as the supercilium.

268 The white-eared hummingbird males evaluated in our study showed an important
269 variation in supercilium size (from 15 to 35 mm²), which was independent of body size. The
270 adaptive significance of intraspecific variation in plumage characters has received much
271 attention, and a large number of hypotheses have been advanced to explain the variation (e. g.
272 Butcher and Rohwer 1989; Lank 2002; Fowlie and Kruger 2003). Here, we suggest that
273 superciliums serve as badges and can be signals of intraspecific dominance when males are
274 foraging. But, our data could not determine whether supercilium size changes with age (this
275 would require a longitudinal study). However, given the lack of hyperallometry, it is possible
276 that supercilium (badge) size may be related to individual quality characters for dominance status
277 signaling such as body size (important in interspecific contests for nectar sources, e.g. Justino et
278 al. 2012), body condition and many other physiological factors. This relationship has been
279 established in other birds such as the american yellow warbler *Setophaga petechia* (Studd and
280 Robertson 1985), the house sparrow *Passer domesticus* (Møller 1987) and the eurasian siskin
281 *Carduelis spinus* (Senar et al. 1993). Here, we show that birds with larger badges were usually
282 more dominant over the food resource than individuals with smaller badges (individuals with
283 larger superciliums were more likely to visit the feeders), suggesting that white plumage patch
284 exhibited in male white-eared hummingbirds may act as a badge of intraspecific dominance
285 status. The small size and high metabolic rate of hummingbirds prevent them from surviving for
286 long if energy expenditure exceeds income (Kodric-Brown and Brown 1978). Because physical
287 conflict over limited resources (as occur in hummingbirds) can be costly in terms of both time

288 and health (Chaine et al. 2013), the exhibition of a badge (i.e. supercilium) can save energy
289 expenditure associated with competitive interactions and favor energy intake (individuals with
290 larger badges are expected to have a better resource holding potential), such savings can be
291 highly beneficial in a species with a such high metabolism.

292 Not all signals are honest (e. g. lures, sensory exploits, sensory traps) but when they are,
293 this honesty is maintained by the cost of the signal (Zahavi 1975). Nutrients required to maintain
294 the plumage pigments colours are different. For example, carotenoids are scarce in the
295 environment and exclusively obtained from diet (Goodwin 1984), but melanins are synthesised
296 from amino acids that are basic dietary components and usually not a limiting resource (Griffith
297 et al. 2006). In this regard, the presence of white color patches on melanized body structures
298 could be of particular importance because their size and brightness seem to be affected by
299 rearing conditions, parasite infections and diet quality (Kose and Møller 1999; Gustafsson et al.
300 1995; McGlothlin et al. 2007). Hummingbirds do not have different breeding and nonbreeding
301 plumages and molt only once per year. Because this process is stressful, birds usually molt
302 during periods when there are neither breeding nor migrating (Williamson 2001). Likewise,
303 parasite infection is common in hummingbirds not only in plumage but rather with
304 gastrointestinal and blood presence, and so far little known effects (Matta et al. 2014). Therefore,
305 it is expected that if despite the extra cost involved in molting and parasites, the size of a badge
306 (i. e. supercilium) is maintained over time, then the honesty of the signal is reaffirmed, but
307 studies are needed to prove it.

308 The most common type of agonistic interaction in territorial species occurs when an
309 animal displaces an opponent and forces it to move away (i.e. Paton and Caryl 1986). However,
310 due to the inherent costs of disputes, contestants can use their opponent's traits or features to

311 avoid fights and aggressive interaction (Smith and Harper 2003). A number of studies have
312 demonstrated that this occurs in several bird species, mainly because sex and age are usually
313 associated with different plumage colorations (the dominant birds typically have darker or
314 blacker patches), and birds learn to associate coloration with the degree of dominance of a given
315 individual (Krebs and Davies 1987; Whitfield 1987). Plumage thus becomes, indirectly, a status
316 signal (i.e. Senar et al. 1993; Smith and Harper 2003; Quesada et al. 2013). Our study revealed
317 that individuals with larger superciliums showed an increased resource-holding ability (number
318 of visits to the feeder) compared to intraspecific contestants with small badges. These results
319 suggest that individuals are able to assess the difference in status of an opponent on the basis of
320 their relative supercilium sizes; thus, plumage will determine the outcome of any encounter
321 (Whitfield 1987).

322 It has been suggested that status signals should be selected above all in species with
323 unstable group composition or in species where contests are usually between individuals with no
324 previous social contact, as in these cases the cost of status assessment would be lessened
325 whenever two individuals confront each other (Rohwer 1982; Senar et al. 1990, Vedder et al.
326 2010). For example, high quality sites are often visited by many conspecific and heterospific
327 hummingbird species so that familiarity between individuals may be low and hence the
328 exhibition of reliable badges beneficial. In this respect, the males of most northern temperate
329 hummingbird species (and several tropical species) defend their territories by sitting on exposed
330 perches in the open, thereby providing visual signals to scare away potential intruders (Skutch
331 1940; Pitelka 1942).

332 Given that our data show that supercilium size was not related to body size, it is possible
333 that other factors may explain why individuals with larger badges forage more in captivity. For

334 example, Chávez-Zichinelli et al. (2014) showed that testosterone (T) levels seem to influence
335 foraging preferences in male white-eared hummingbirds and that individuals with higher levels
336 of T make quicker and more frequent visits to flowers with variable rewards – and behave
337 consistently as risk-prone foragers – than males with low T levels. These findings suggest that
338 behavioral profiles or personalities of the birds used in the dyadic contest could influence our
339 results. In this context, we predicted that individuals with larger badges should show higher
340 levels of steroids and have higher levels of boldness and intraspecific dominance. Such a study
341 could help us to understand the possible relationship between steroid hormones, badge size, and
342 the signaling of dominance status in hummingbirds, a topic heretofore unexplored.

343 In short, we showed that white-eared hummingbird males with larger superciliums had
344 enhanced access to the food resource than males with smaller superciliums: more visits to a
345 feeder than their adversaries suggests a role for superciliums in dominance status signaling.
346 Further future studies might seek to apply experimental manipulation, either artificially
347 modifying the size or presence of this trait in individuals within a dyadic contest, to verify the
348 status signaling function of supercilium.

349

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356

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358

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363

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365

366 **Ethical approval** All experiments comply with the current Mexican laws

367

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626 Figure 1. Relationship between the difference in the number of visits to a feeder and the difference in
627 the supercilium size between contenders. Dyads had bird contenders with similar (black dots) or
628 different (open dots) badge size. The relationship was significant for both similar ($Y = 0.59x - 0.13$,
629 $R^2 = 0.34$, $N = 11$, $P < 0.01$) and different contest types ($Y = 0.86x + 3.02$, $R^2 = 0.71$, $N = 10$, $P < 0.01$), and
630 the comparison of both slopes showed that they are statistically different ($t = 4.281$, $d.f. = 18$, $P < 0.001$).
631 Photograph of a White-eared hummingbird male showing his supercilium is by Carlos Lara.

632 Table 1. Slopes, 95% confidence intervals (CIs), R^2 , and P values obtained from MA regressions
 633 fitted between supercilium size (dependent variable) and six body-size measurements of White-
 634 eared hummingbird males. All values were \log_{10} transformed prior to analyses.

Body measurement	Slope	Lower CI, Upper CI	R^2	P value
Body mass	34.788	5.227 - 7.660	0.003	0.711
Bill length	-29.000	39.764 - 10.597	0.033	0.248
Body length	51.395	17.858 - 58.723	0.029	0.287
Tail length	48.128	8.743 - 13.802	0.005	0.651
Tarsus length	-13.484	18.969 - 4.914	0.038	0.240
Wing chord	39.381	14.286 - 52.327	0.032	0.255

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1 Table 2. Results from Bayesian model averaging analyses for parameters affected by the
 2 supercilium size difference among contenders. Shown are posterior inclusion probabilities (PIP)
 3 and estimates of standardised mean coefficients (PMCs) for each dependent variable. The higher
 4 PIPs signify the importance of a dependent variable to be included in the true model. All models
 5 included Contest identity as random effects.

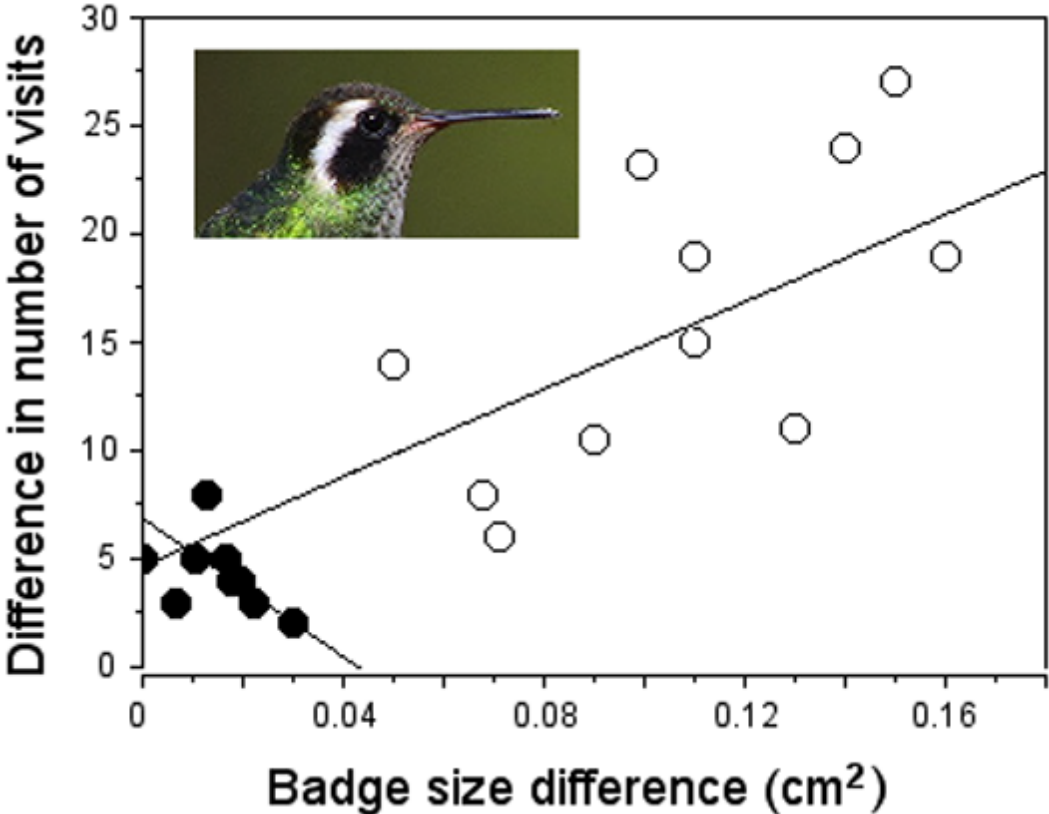
6

Dependent variables	PIP	PMC
Number of visits	0.683	0.024
Duration of visits	0.480	-0.013
Latency of visits	0.160	0.025
Contest type	0.158	0.017
Number of disputes	0.140	0.089

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