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1 **Manipulating badges of status only fools strangers**

2

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14

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28 Author contributions

29 ASC, DS, and BEL designed research. ASC, TAB, LZ and BEL conducted trapping and aviary
30 experiments. ASC performed analyses. ASC and BEL wrote the initial manuscript and all
31 authors contributed to revisions.

32 **Abstract:**

33 Conflict is risky, but mechanisms that allow animals to assess dominance status without
34 aggression can reduce such costs. Two different mechanisms of competitor assessment are
35 expected to evolve in different contexts: badges of status are expected in larger, anonymous
36 groups whereas individual recognition is feasible in small, stable groups. However, both
37 mechanisms may be important when social interactions occur both within and across stable
38 social groups. We manipulated plumage in golden-crowned sparrows (*Zonotrichia atricapilla*)
39 and found that two known badges of status—gold and black head plumage patch sizes—
40 independently affect dominance among strangers but manipulations had no effect on dominance
41 among familiar flockmates. Moreover, familiar flockmates showed less aggression and increased
42 foraging relative to strangers. Our study provides clear experimental evidence that social
43 recognition affects badge function, and suggests that variation in social contexts maintains
44 coexistence and context-dependent use of these two dominance resolution mechanisms.

45 **Introduction**

46 Conflict over resources is ubiquitous among organisms. When the fitness stakes are high,
47 conflict can entail extreme aggression and even lethal fights, for example, when males battle for
48 access to females in polygynous mating systems. In contrast, when organisms compete over
49 resources with modest effects on fitness, such as a meal, animals often settle conflicts with
50 mechanisms that avoid the costs of overt aggression and injury (Maynard Smith & Price 1973;
51 Maynard Smith & Harper 2003). Two such mechanisms for competitor assessment have been
52 proposed: individual recognition and badges of status (Rohwer 1975; Barnard & Burk 1979;
53 Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Dale 2006; Tibbetts & Dale 2007;
54 Bradbury & Vehrencamp 2011). Individual recognition allows an organism to tailor its behavior
55 in aggressive interactions with familiar opponents based on past interactions (Barnard & Burk
56 1979; Tibbetts & Dale 2007) or through observations of interactions between other individuals of
57 known rank (i.e., transitive inference: Paz-Y-Miño C *et al.* 2004; Grosenick *et al.* 2007). In
58 contrast, badges of status are signals that correlate with an individuals' fighting ability that allow
59 any random pair of individuals to assess their chances of winning a given contest and therefore
60 avoid costly fights (Rohwer 1975, 1977, 1982). Both mechanisms are supported by ample
61 experimental evidence in the literature (Dale *et al.* 2001; Whiting *et al.* 2003; Senar 2006;
62 Tibbetts & Dale 2007), but there is relatively little data on whether and under what
63 circumstances these two mechanisms might co-occur (Sheehan & Bergman 2016b, but see Järvi
64 & Bakken 1984; Whitfield 1988; Sheehan & Tibbetts 2010; Sheehan *et al.* 2014).

65 Social structure—particularly group size and stability—should affect whether individual
66 recognition or badges of status are favored as assessment strategies (Figure 1) (Rohwer 1982;
67 Whitfield 1987; Shultz & Gersick 2016). Individual recognition is thought most likely to occur
68 in small, stable groups for two reasons: the number of individuals an animal can remember may
69 be constrained (Dukas 1999; Burns *et al.* 2011), and the benefits of memorizing individual
70 identities and adjusting dominance behavior accordingly are greater when the same individuals
71 repeatedly interact (Figure 1a) (Whitfield 1987; Ydenberg *et al.* 1988; Johnstone 1997; Tibbetts
72 & Dale 2007). Conversely, badges of status do not require memory of past encounters, and thus
73 could function in large groups where most interactions occur between newly interacting
74 individuals (Rohwer 1975, 1982; Whitfield 1987) (Figure 1c). Taken together, individual
75 recognition should be favored in societies that feature small stable groups, while badges of status

76 should be favored in systems with large groups where repeated contests are relatively rare, and
77 also where individual recognition may not be feasible (Figure 1a vs c) (Rohwer 1982; Whitfield
78 1987; Shultz & Gersick 2016). This contrast in conditions has sometimes led to the perception
79 that the two conflict resolution mechanisms are unlikely to coexist.

80 The debate over assessment strategies has often implied that the social organization of a
81 species can be neatly categorized into the two extremes—small and stable versus large and
82 fluid—that each favors different assessment strategies (Shields 1977; Rohwer 1982). However,
83 the social structure of many animal populations cannot be characterized along a simple gradient
84 of group size or group stability. Fission-fusion dynamics are pervasive in animals, even among
85 species that were not previously considered to be socially complex (Aureli *et al.* 2008; Mourier
86 *et al.* 2012; Silk *et al.* 2014), and social network analysis can help uncover these complex
87 patterns of social stability (Wey *et al.* 2008; Pinter-Wollman *et al.* 2014; Silk *et al.* 2014). For
88 example, stable long-term associations can exist in clusters, or ‘social communities’ within social
89 networks, but individuals in different social communities may nevertheless be connected weakly
90 through transient interactions. In such multilevel societies, stability of social associations can be
91 heterogeneous, where individuals often have encounters with both familiar *and* unfamiliar
92 competitors—i.e., contexts in which different dominance assessment mechanisms may be
93 favored (e.g. Figure 1b) (Whitfield 1987; Shultz & Gersick 2016). Even within stable social
94 communities, new recruits will be initially unfamiliar and may use badges of status to establish
95 dominance relationships prior to making use of individual recognition once established in the
96 group. In such cases, the function of badges of status would be context-dependent: they may play
97 an important role in mediating interactions between unfamiliar individuals but may be less
98 important between familiar individuals that can assess each other through individual recognition.

99 In this study, we investigated whether the use of badges of status depends on the
100 familiarity of contestants in a winter population of the migratory golden-crowned sparrow
101 (*Zonotrichia atricapilla*). In previous work, we provided evidence for multiple badges of status:
102 contests with both natural variation (Chaine *et al.* 2011) and experimental manipulation (Chaine
103 *et al.* 2013) showed that individuals with larger gold or larger black plumage patches win
104 contests among strangers (i.e. individuals from different populations). However, social network
105 analysis based on flock co-membership in a free-living population revealed these sparrows live
106 in small, stable winter social groups that are connected together by relatively weaker associations

107 across groups (Shizuka *et al.* 2014). Moreover, these groups are stable across years and many
108 individuals form affiliations that last many years; these affiliations reform anew each year after
109 migration to and from the breeding grounds. The fact that a significant amount of variation in
110 flocking patterns is explained by the effect of the previous year's affiliation, even after
111 controlling for the amount of overlap in home ranges (Shizuka *et al.* 2014), indicates that these
112 birds likely show individual recognition in some aspects of their social behavior. We already
113 know that sparrows use badges in some dominance contexts; the golden-crowned sparrow social
114 network may provide conditions under which both badges of status and individual recognition
115 are beneficial in resolving social dominance.

116 Empirical tests of individual recognition and badges of status adopt somewhat different
117 methods; showing that both occur in the same population requires careful experiments that
118 control for familiarity, the context that should determine which mechanism the birds use. Badges
119 of status are often documented through correlations between the size of a putative signal and
120 dominance rank [e.g. lizards (Thompson & Moore 1991), insects (Tibbetts & Dale 2004), birds
121 (Senar 2006; Tibbetts & Safran 2009), and mammals (Setchell & Wickings 2005)]. Confirmation
122 that a specific trait is used as a badge requires manipulation of the presumed badge, which
123 should trigger a change in the outcome of specific contests (Rohwer & Rohwer 1978; Pryke &
124 Andersson 2003; Chaine *et al.* 2013). Experimental contests to test for badges of status typically
125 involve unfamiliar contestants to remove the potential effect of prior information on the contest
126 outcome. In contrast, individual recognition is documented in one of three ways: by comparing
127 interactions between familiar and unfamiliar individuals (Hazlett 1969; Caldwell 1985; Watt
128 1986), by measuring changes over time in the behaviors and interactions of a pair of individuals
129 that become increasingly familiar with each other (Karavanich & Atema 1998; Tibbetts 2002;
130 Vedder *et al.* 2010) or, more rarely, through manipulation of a putative identity signal (Whitfield
131 1988; Tibbetts 2002). Here, we investigated the potential co-occurrence of badges of status and
132 social recognition by conducting experimental badge size manipulations in two types of
133 contests—dyads of birds that are familiar with each other and dyads of unfamiliar birds. This
134 design allowed us to determine if the badges that we have already shown to be effective among
135 unfamiliar birds (Chaine *et al.* 2011, 2013) are also used among familiar birds or, alternatively, if
136 these badges are ignored as would be expected if individuals use some form of social recognition
137 (individual or group). We provide definitive evidence that sparrows use both badges of status

138 and social recognition and demonstrate that variation in social context plays a key role in the
139 coexistence of these two dominance-resolving mechanisms. Because our experimental approach
140 was not designed specifically to discriminate between individual and group recognition, we
141 could not directly test for individual recognition, the form of recognition most discussed in the
142 extensive literature on badges of status (e.g. Rohwer 1975; Whitfield 1982). However, several
143 considerations suggest that the social recognition we observed involved individual recognition,
144 as we discuss below.

145

146 **Materials and Methods**

147 We used staged competition in aviaries to assess whether previous familiarity affected the
148 role of plumage traits on social dominance. We caught golden-crowned sparrows at four
149 different sites in January and February using Potter traps baited with millet seed. From 2007-
150 2009, we trapped birds at two locations near Pogonip City Park (36°59'25.6"N 122°02'12.9"W
151 and 36°59'04.2"N 122°02'49.0"W) and the University of California Santa Cruz (UCSC) campus
152 (36°58'40.1"N 122°03'04.8"W). In 2012-2014 we added a site at the Santa Cruz Waldorf School
153 (37°00'22.4"N 122°04'26.7"W). Birds were transported to the UCSC Arboretum soon after
154 capture. We measured all birds (mass, wing chord, tarsus, beak length), banded them with color
155 bands and a USFWS metal band for identifying individuals within experiments, and
156 photographed their crowns as in past studies (Chaine *et al.* 2011, 2013). All birds were then
157 placed in one of two outdoor aviaries for habituation before use in experimental trials the
158 following morning—these two aviaries were visually and acoustically isolated from each other,
159 had shelter, and both food and water *ad libitum*. The two birds used in each trial were put in
160 separate over-night aviaries to ensure a lack of contact immediately prior to the trial. Before
161 running the trials we measured size of gold and black crown patches (mm²) from photos with
162 Adobe Photoshop CS and these patch sizes were then used to assign birds to a trial such that the
163 two birds had similar pre-manipulation patch size, as in previous work (Chaine *et al.* 2011,
164 2013). Sex was not used as a criterion for assigning birds to a trial because previous work
165 showed that gender does not predict social dominance in this species (Chaine *et al.* 2011).

166 We conducted two different types of social dominance trials. “Unfamiliar trials” (N = 62)
167 used birds caught on the same day from two different populations >800m apart (often much
168 greater distances). This distance is much larger than the average home range of individual

169 sparrows (Shizuka *et al.* 2014) so the birds in the trial were very unlikely to have interacted with
170 each other prior to the trial. The “Familiar trials” involved birds that were trapped at the same
171 site and within a short time period (<30min); based on our detailed understanding of flocking
172 and feeding behavior from our color-banded population (Shizuka *et al.* 2014, unpubl. data), these
173 were birds that would be very likely to have been in the same flock when captured (2012-2014
174 only; N = 60). Unfamiliar trials analyzed here include some trials also used in a previous
175 publication (N = 32) (Chaine *et al.* 2013) as well as new Unfamiliar trials (N = 30) conducted at
176 the same time as Familiar trials to control for possible year effects and collect new data on
177 distance between birds not gathered in the earlier experiments (see below).

178 Social dominance trials were conducted in the morning between 8-11 AM in a third contest
179 aviary (same dimension as overnight aviaries) and each trial lasted 30 minutes. Food was
180 removed from the overnight aviaries at sundown the evening before the trials so birds in
181 dominance trials were motivated to access the single feeding tray at the center of the contest
182 aviary. Prior to the trial, one of the birds, chosen at random, had one of their color patches (either
183 black or gold) increased in size while the other received a sham manipulation using clear thinner
184 (gold) or brown permanent marker (black). Gold patch size was increased using acrylic paint
185 while black crown size was increased using a permanent ink pen; both colors were spectrally
186 similar to natural color patches (Chaine *et al.* 2013). As in our previous experiment (Chaine *et al.*
187 2013), the birds in each dyad did not differ in patch size before manipulation and the
188 manipulation significantly increased badge size (Supplemental Information). Because pre-
189 manipulation patch size of the two birds was similar, we would expect manipulated birds to be
190 dominant in half of the trials if patch size manipulation had no influence on dominance (Chaine
191 *et al.* 2011, 2013). As in our previous experiment, gold (N = 62) and black (N = 60)
192 manipulations showed similar outcomes, so we present combined results in the main text (results
193 split by treatment in Figure S1).

194 We scored social behavior in two ways. First, an observer watched trials from ~30m away
195 with binoculars and scored social interactions as aggression (peck, supplant), avoidance
196 (subordinate avoided challenging a dominant), or tolerance (no aggression while in close
197 proximity), and we also tallied feeding behaviors (Chaine *et al.* 2011, 2013) for the first and
198 second 15min time periods separately. We used the sum of the social interactions to determine
199 which bird was dominant or, in some cases, to conclude that dominance was not clear (Chaine *et*

200 *al.* 2011, 2013). We concluded that dominance was clear when one bird consistently won
201 encounters through supplants or avoidance behavior (Chaine *et al.* 2011, 2013). In contrast,
202 dominance was not clear when birds had the opportunity to interact (i.e. they moved around), but
203 either no dominance behaviors occurred or both birds won an equal number of encounters (very
204 rare). In a second approach, we scored tolerance behavior as a measure of flocking and social
205 affinity from videos taken from above the contest aviary. Generally, tolerance is a measure of
206 whether birds socialize at close proximity without any aggression, and we quantified this as the
207 number and duration of instances where the birds were within two body lengths of each other for
208 more than 3 seconds and did not show aggressive behaviors (i.e. no dominance interactions;
209 2012-2014 only). The person who conducted the trials was not blind to treatment but dominance
210 was evaluated as the sum of behaviors post data collection. In contrast, videos used to quantify
211 tolerance and social clustering were scored blind to treatment which should eliminate observer
212 bias. The results of the two approaches are concordant.

213 To evaluate the impact of our plumage manipulation on social dominance, and particularly
214 to be able to compare across the two sets of experiments, we examined two different outcomes:
215 the proportion of trials that showed a clear dominance winner and then the proportion of this
216 subset of trials where the manipulated (i.e. enlarged) bird was dominant. For the latter, the null
217 expectation is that each bird has a 50% chance of winning so we evaluated the impact of the
218 manipulation on dominance as the deviation from an expected 50:50 ratio using a binomial test.
219 This null expectation applies because pre-manipulation badge sizes were matched for each dyad
220 and because badge size predicted dominance in past studies (Chaine *et al.* 2011, 2013). In
221 contrast, there is no clear null expectation of what proportion of trials should show clear
222 dominance, so we simply provide the raw data for evaluation. We used Z-tests to compare the
223 differences between Familiar and Unfamiliar treatments in the probability of observing clear
224 dominance, as well as the probability of the bird with the experimentally enlarged patch winning
225 the contest (Fleiss *et al.* 2003). We used ANOVA to compare rates of each behavior (aggression,
226 avoidance, tolerance and feeding) between Familiar and Unfamiliar trials. Data were analyzed in
227 R 3.1.3 (R Development Core Team 2009) and are available on DRYAD (upon acceptance).

228 All protocols were approved by the UCSC IACUC (Animal Welfare Permit Number
229 A3859-01 to B. Lyon). Capture and banding was done under permits to B. Lyon: a California

230 Department of Fish and Wildlife Scientific Collecting permit, a Federal Fish and Wildlife Permit
231 and a Federal Banding Permit.

232

233 **Results**

234 Familiarity affected the likelihood of a trial showing clear dominance patterns. Trials with
235 unfamiliar birds (i.e., birds caught at different sites) nearly always had a clear dominant
236 individual (53 of 62 trials). In contrast, only about half of the familiar dyads (birds caught at the
237 same site at the same time) had clear dominance (27 of 60 trials). The proportion of trials where
238 dominance was clear was significantly greater in Unfamiliar trials than in Familiar trials
239 (comparison of two probabilities: $Z = 4.71$, $P < 0.0002$, Figure 2a).

240 The plumage manipulations influenced the outcome of dominance in trials involving
241 unfamiliar birds but not familiar birds. In the subset of trials where dominance was clear, the
242 manipulated bird was dominant over the sham individual in a significantly larger proportion of
243 trials between unfamiliar birds relative to trials between familiar birds (comparison of two
244 probabilities: $Z = 4.20$, $P < 0.0002$, Figure 2b). Indeed, the manipulated bird was dominant in
245 nearly all cases during Unfamiliar trials (49 of 53 trials, binomial test based on null expectation
246 of 0.5 probability that an individual will be dominant based on pre-manipulation crown size: $P <$
247 0.001). The sample here includes trials conducted in our previous study using the same methods
248 (Chaine *et al.* 2013), and thus simply increases the robustness of the previously reported patterns.
249 In contrast, the manipulated bird was not more likely to be dominant than the sham individual
250 among familiar dyads, which is what we would expect only if birds ignored the patch
251 manipulation (14 of 27 trials, binomial test with null expectation of 0.5 probability that
252 individual will be dominant based on pre-manipulation crown size: $P = 1$). These results are the
253 same regardless of which plumage patch was manipulated (i.e., black or gold: Figure S1).

254 Birds in Familiar trials had fewer costly social behaviors and spent more time feeding
255 relative to unfamiliar dyads. Familiar trials had fewer aggressive interactions (ANOVA: $F_{1,120} =$
256 3.46 , $P = 0.065$; Figure S2a), fewer avoidance interactions (ANOVA: $F_{1,120} = 24.63$, $P < 0.0001$;
257 Figure 3a), and a higher rate of tolerance (a lack of aggression when close; ANOVA: $F_{1,120} =$
258 96.50 , $P < 0.0001$; Figure S2b). Familiar birds also spent significantly more time in close
259 proximity relative to unfamiliar dyads (ANOVA: $F_{1,57} = 4.77$, $P = 0.033$; Figure 3b). Finally,
260 while birds in both types of trials accessed food at similar rates (ANOVA: $F_{1,120} = 1.31$, $P = 0.25$;

261 Figure S2c), birds in Familiar trials spent a significantly longer time at the feeder on each visit
262 compared to birds in Unfamiliar trials (ANOVA: $F_{1,101} = 13.07$, $P = 0.0004$; Figure 3c).

263

264 **Discussion**

265 Our experiments revealed that plumage manipulations affect dominance status in staged
266 contests among strangers (confirming the results of Chaine *et al.* 2013), but not among birds
267 previously familiar with each other. These contrasting results provide evidence that the familiar
268 birds recognized each other, either individually or at the group level, and that this recognition
269 allowed them ignore experimental changes to plumage badges. This also implies that the crown
270 plumage patches we manipulated were not the traits the birds use for social recognition. Finally,
271 our experiments suggest how familiar birds can benefit from social recognition during such
272 encounters—reduced aggression, tighter flocking, and increased access to resources.

273 The differences we observed between the familiar and unfamiliar trials imply some form of
274 recognition among familiar birds. We did not quantify the amount of prior social interaction
275 leading to this social recognition, nor did our experiments directly test for individual recognition
276 so there is a question of what type of recognition was involved—individual recognition or group
277 level recognition (e.g. familiar vs unfamiliar)? Regardless of the level of social recognition, our
278 results indicate that birds caught in the same place within a short time—i.e., those that are
279 typically very socially familiar due to close associations over long periods of time (Shizuka *et al.*
280 2014)—disregard manipulation of badges of status. However, distinguishing between these two
281 forms of recognition can be difficult and direct evidence for individual recognition requires
282 demonstrating that individuals vary their behavior in response to an individual specific cue like
283 an individually distinct vocalization or visual features, and not some group level attribute
284 (Tibbetts *et al.* 2008). For example, group recognition is common in social insects where
285 individuals respond differently to familiar (same colony) and unfamiliar (different colony)
286 individuals on the basis of colony specific olfactory cues (cuticular hydrocarbons, Hölldobler &
287 Wilson 1990). Thus, simply showing that these insects respond differently to familiar and
288 unfamiliar individuals may only show a group level response and not individual recognition. In
289 birds, there is some evidence for group-specific calls in various contexts, including seasonally
290 stable flocks (e.g., Nowicki 1983; Hausberger *et al.* 1995). However, we never observed
291 vocalizations in any of our trials so acoustic features cannot explain our results. Furthermore, our

292 past work suggests that recognition between familiar sparrows generally goes beyond group
293 membership and reflects true individual recognition. When winter social communities form anew
294 each fall after fall migration, variation in the strength of pair-wise affiliations is explained in
295 large part by the degree of affiliations between those individuals in the previous year, even after
296 controlling for shared space use by individuals, which strongly suggests individual recognition
297 (Shizuka *et al.* 2014). Based on these considerations, we believe that individual recognition is the
298 most likely explanation for the differences between familiar and unfamiliar trials. Identifying the
299 trait or traits used in individual recognition remains an interesting, if challenging, question for
300 future work.

301 Our study demonstrates how both badges of status and social recognition can mediate
302 social competition within the same population. Prior work shows that badges of status and
303 recognition (in particular, individual recognition) each provide a way to avoid costly conflict
304 over resources, yet each has different benefits and constraints. For example, badges of status may
305 allow rapid assessment of competitive ability and can function reliably even when groups are
306 large and fluid and individual recognition is not feasible (Rohwer 1982). However, badges can,
307 in theory, be susceptible to cheating (Rohwer & Ewald 1981). In contrast, individual recognition
308 could allow for more reliable assessment of competitive ability, but it is only beneficial when
309 there are repeated interactions between competitors (Ydenberg *et al.* 1988; Johnstone 1997;
310 Tibbetts 2004; Tibbetts & Dale 2007), and it may require investment in neural mechanisms to
311 allow for memory of the outcomes of past interactions associated with each contestant (Dukas
312 1999; Tibbetts & Dale 2007; Sheehan & Tibbetts 2011). There also may be a limit to the size of
313 the social group where individual recognition is cognitively feasible (Dunbar 1992).
314 Traditionally, researchers have sought evidence for either badges of status or individual
315 recognition for a given species, and evidence for one type of assessment strategy was held as
316 evidence against the other (e.g., Shields 1977). Our study provides valuable empirical data to
317 show that conditions favorable for both types of assessment strategies coexist in one social
318 system, and that golden-crowned sparrows selectively use badges of status or social recognition
319 depending on the social context. These findings should spur further progress in development of
320 theory related to the evolution of competitor assessment strategies, which has been highlighted in
321 a recent review by Sheehan and Bergman (2016b) and responding commentary (Barrett & Henzi
322 2016; Ridley *et al.* 2016; Sheehan & Bergman 2016a; Shultz & Gersick 2016).

323 We suggest that the context-dependent use of both badges of status and individual
324 recognition in the same species may be more common than currently suspected. In a handful of
325 species, both mechanisms of assessment have been tested but only one was found—e.g., the
326 various *Polistes* wasps studied in the impressive body of work by Tibbetts and colleagues
327 (Tibbetts 2004; Tibbetts & Dale 2004; Sheehan & Tibbetts 2010). However, the results are more
328 mixed in avian systems, with a few cases that hint at the co-occurrence of badges and
329 recognition. For example, blue tits (*Parus caeruleus*) use badges of status (Rémy *et al.* 2010),
330 but also show changes in the importance of badges for dominance across repeated interactions
331 suggestive of individual recognition (Vedder *et al.* 2010), although winner/loser effects cannot
332 be ruled out for this pattern (Hsu *et al.* 2006; Rutte *et al.* 2006). Likewise, white-crowned
333 sparrows (*Zonotrichia leucophrys*), a congener of the sparrows we studied, use badges of status
334 (Fugle *et al.* 1984), yet our reanalysis of experiments by Watt (1986) show that interactions
335 between familiar birds show fewer aggressive interactions than between unfamiliar birds
336 (reanalysis of data in Table 3 in (Watt 1986): comparison of the proportion of aggressive
337 interactions between familiar and unfamiliar birds: $Z = -2.67$, $P = 0.008$). This difference
338 between familiar and unfamiliar birds in levels of aggression suggests that individual recognition
339 may exist in white-crowned sparrows. Parsons and Baptista (1980) also showed that white-
340 crowned sparrows with manipulated crowns maintain status within their flock, further suggestive
341 of individual recognition. For these two sparrow species, careful experiments are now required to
342 confirm that individual recognition occurs.

343 An open question is whether there are predictable conditions under which a species or
344 population might use just one form of assessment or both assessment strategies. Complex social
345 structure may favor the use of both assessment strategies. Four decades ago, Whitfield (1987)
346 hypothesized that social organization might be sufficiently variable in many species to favor both
347 assessment mechanisms, and lamented the lack of understanding of social organization as an
348 impediment for understanding the evolution of badges and individual recognition. More recently,
349 Shultz and Gersick (2016) suggested that the dual use of quality signaling and social recognition
350 would be favored in multilevel animal societies in which close-knit social clusters exist within a
351 larger population because individuals would interact with both familiar and unfamiliar
352 individuals (e.g. Figure 1b). Our study system provides evidence to support this idea. Golden-
353 crowned sparrows in our population live in a complex social network characterized by cohesive

354 social clusters embedded within a larger population that interacts more loosely (Shizuka *et al.*
355 2014). This social structure is not driven by kinship (Arnberg *et al.* 2015), but rather preferences
356 for familiar flock-mates, even across years (Shizuka *et al.* 2014). Our experiments now show that
357 familiarity not only affects flock associations, but also the way competitors use badges of status
358 to mediate competition. In the natural social network context where interactions may occur with
359 a mix of familiar and unfamiliar competitors, within-cluster (familiar) interactions may be
360 mediated by recognition whereas interactions among clusters (unfamiliar) may use badges of
361 status, precisely as Whitfield (1987) predicted. The basic features of this social system—fission-
362 fusion dynamics characterized by a mix of stable long-term associations and diffuse short-term
363 associations—are likely widespread in avian systems (Silk *et al.* 2014). Even for systems in
364 which long-term stable social relations dominate, we suggest that there are likely periods of time
365 during which interactions among unfamiliar individuals occur and badge use would be favored,
366 such as during migration, the integration of new recruits into stable social groups, or periods of
367 social instability following the breakdown of some groups. A better understanding of the natural
368 patterns of social interactions throughout the annual cycle for birds generally may reveal
369 common patterns that favor the use of one or both mechanisms of competitor assessment.

370 Our study demonstrates how controlling the social context of contests is paramount to
371 accurately understand the dynamics of status signaling. This poses a challenge for researchers
372 because it also requires a detailed understanding of the social structure of the population—i.e.,
373 the extent to which social interactions are naturally confined to familiar *versus* unfamiliar
374 competitors. For example, earlier observational studies of badges of status suggested that the
375 failure of putative badges to accurately predict dominance cast doubt on whether they served as
376 badges (e.g. Whitfield 1987). However, it is also possible those studies contained a large
377 proportion of within group interactions where individual recognition rather than badges of status
378 mediated dominance. Moreover, testing the function of putative badges through observations in
379 the wild, rather than with experiments, may often produce weaker correlations between badge
380 and dominance when interactions involve a mix of strangers and familiar birds. Our results
381 suggest the relationship between putative badges and dominance in the wild will depend
382 critically on the frequency of interactions that are within groups of familiar individuals versus
383 between strangers, and highlight the importance of distinguishing between these two different
384 contexts.

385 Our experimental results also have implications for the maintenance of honest signaling.
386 A key question for badges of status has long been, why not cheat? Why don't poor fighters
387 produce badges that signal high fighting ability? In theory, the stability of badges of status as a
388 signaling system relies on some mechanism to prevent cheating, such as condition dependence
389 (Johnstone & Norris 1993; Tibbetts & Curtis 2007) or social punishment of cheaters (Webster *et*
390 *al.* in press; Rohwer 1982; Tibbetts & Dale 2004). However, our plumage manipulation with
391 familiar individuals apparently did not result in the rapid social punishment seen in similar
392 experiments in other systems (Tibbetts & Izzo 2010; Ligon & McGraw 2016). This begs the
393 question whether social recognition could change the dynamics of social enforcement of honesty
394 in badges of status. We suggest that, given individual recognition, it may be possible for delayed
395 social punishment to play out at timescales beyond the duration of a given dominance
396 experiment. In theory, the value of a dishonest badge should be diminished in systems where
397 both badges and individual recognition are used, because interactions within a social group no
398 longer rely only on badges of status. Specifically, badges of status might be used to settle
399 dominance when a bird initially joins a group, but recognition subsequently modulates
400 interactions. If detection makes it less likely that cheaters can join a group, or if they
401 subsequently develop weaker or more negative affiliations (i.e. individuals reduce interactions
402 with cheaters or affiliations involve more hostility), then social costs linked to individual
403 recognition could guard against cheating. For animals that live in stable long-lived groups, the
404 presence of such 'punishment' could have dire long-term consequences such as reduced
405 cooperation or even exclusion from a group. If there are important benefits to stable group
406 membership the risks of dishonest status signaling in the presence of individual recognition may
407 make it unlikely.

408 Finally, our experiments also demonstrate potential benefits of interacting with familiar
409 individuals, such as reduced aggression and increased food intake which are key components of
410 winter survival. Birds in Familiar trials spent much less time in conflict and more time in non-
411 aggressive (tolerant) interactions relative to those in Unfamiliar trials. Familiar birds also spent
412 much longer times at the feeder than unfamiliar birds, which in general would increase their food
413 intake. Finally, familiar birds spent much more time close to each other than unfamiliar birds and
414 such clustering could provide benefits such as reduced predation risk (Hamilton 1971; Lima *et*
415 *al.* 1999). These benefits, which result from recognition rather than badges of status, may be key

416 components that favor the stable community structure we see in golden-crowned sparrows
417 (Shizuka *et al.* 2014). Thus, our experimental results may provide a key link between competitor
418 assessment strategies and the social network structure of foraging flocks. The cues used for
419 recognition—which we have not yet identified—may play an outsized role in the winter social
420 system of golden-crowned sparrows by mediating flock membership as well as modulating the
421 function of badges of status in contests over food.

422

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431

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593

594

595 **Figure Legends**

596 Figure 1: Schematic representation of social networks predicted to favor different dominance
597 resolving mechanisms. A) Social (individual or group) recognition is expected to be favored in
598 smaller, stable groups where each individual only interacts with a few others on a regular basis
599 but only rarely encounters new or unfamiliar individuals. B) Intermediate networks that include
600 both frequent, repeated interactions within a stable group and some interactions with extra-group
601 individuals could favor the coexistence of both badges and social recognition. C) Badges of
602 status alone should be expected in fluid groups where individuals are likely to encounter a large
603 number of other individuals so that the costs of remembering this large number outweighs the
604 relative low benefit from rare repeat encounters. In each figure, circles represent individuals (e.g.
605 nodes), lines represent the frequency of interaction between two individuals (e.g. edges), and
606 colors represent social communities that are defined by high within-community interaction and
607 low among-community interaction.

608

609 Figure 2: Comparisons between Familiar (open) and Unfamiliar (grey) trials in the proportion of
610 trials where A) a dominance was clear and B) where the manipulated bird was dominant among
611 trials where dominance was clear. Confidence intervals were calculated using Wilson's
612 procedure described by (Newcombe 1998).

613

614 Figure 3: Comparison between Unfamiliar and Familiar trials in behaviors that reflect costs and
615 benefits of grouping behavior when dominance resolution occurs by recognition. A) The number
616 of dominance interactions where a subordinate avoided challenging a dominant (avoidance). B)
617 The total time the two birds spent very near each other without showing aggression (within two
618 body lengths). C) The average duration of feeding bouts. Figures show standard box and whisker
619 plots.