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3 **The fitness consequences of honesty: under-signalers have a survival advantage in song**  
4 **sparrows**

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22

**23 Abstract**

24           How honest or reliable signaling can evolve and be maintained has been a major question  
25 in evolutionary biology. The question is especially puzzling for a particular class of signals used  
26 in aggressive interactions: threat signals. Here we report a study on song sparrows (*Melospiza*  
27 *melodia*) in which we assayed males with playbacks on their territories to quantify their  
28 aggressiveness (flights and close proximity) and aggressive signaling levels (rates of soft song, a  
29 close range signal reliably predicting attack) and asked whether these traits affect individuals'  
30 survival on territory. We found that the effect of aggressive signaling via soft song interacted  
31 with aggressive behaviors such that there was a negative correlational selection: among males  
32 with low aggression, those males that signaled at higher levels (over-signalers) had higher  
33 survival whereas among males with high aggression those that signaled at low levels (under-  
34 signalers) survived longer. In other words, males who deviate from reliable signaling have a  
35 survival advantage. These results, along with previous research that suggested most of the  
36 deviation from reliable signaling in this system is in the form of under-signaling (high aggression  
37 males signaling at low levels) pose a puzzle for future research on how this reliable signaling  
38 system is maintained.

39

## 40 Introduction

41 In signaling interactions between two unrelated individuals, the interests of signalers and  
42 receivers rarely coincide perfectly, which poses the question of how animal signals can evolve to  
43 be reliable (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). This question is  
44 particularly prominent in the case of threat signals used in aggressive situations, when the  
45 interests of signalers and receivers are opposed to each other. Some threat signals reveal traits  
46 like physical size or strength of the signaler in a way that cannot be cheated (e.g. parallel walk in  
47 red deer that emphasizes the body size; Clutton-Brock et al. 1979) but many threat signals are  
48 not intrinsically tied to an easily observable and costly trait. These signals, termed “conventional  
49 signals” because of the arbitrary relationship between the signal structure and signal message  
50 (Guilford and Dawkins 1995), are seemingly easy to cheat and therefore their reliability  
51 represents an empirical and theoretical puzzle (Maynard Smith and Harper 2003). Although  
52 conventional signals were initially thought to be unreliable and non-predictive in contests over  
53 all but trivial resources (Maynard Smith 1974; Dawkins and Krebs 1978; Caryl 1979; Maynard  
54 Smith 1979; Maynard Smith et al. 1988), recent research has shown many such signals to be at  
55 least partially reliable in predicting further escalation (Waas 1991; Searcy et al. 2006; Laidre  
56 2009; Akçay et al. 2013).

57 Although conventional signals can be statistically reliable in predicting an escalation, the  
58 reliability is often imperfect (Searcy et al. 2013). Furthermore, signaling strategies of at least  
59 some species appear to be individually consistent over time, i.e., with some individuals signaling  
60 consistently at high levels and others consistently at low levels, even though conventional signals  
61 are generally assumed to be flexible behaviors. For example we recently showed that male song  
62 sparrows (*Melospiza melodia*) show individually consistent signaling strategies in repeated

63 aggression assays even after accounting for their aggression levels (Akçay et al. 2014a), e.g.,  
64 some low-aggression individual consistently signal higher than expected, and some high-  
65 aggression individuals lower than expected. These results suggest that at least part of the  
66 variation present in imperfectly reliable signals is correlated with consistent individual  
67 differences (Botero et al. 2010).

68         The last decade has seen a proliferation of studies focused on consistent individual  
69 differences, sometimes termed animal personality (Gosling 2001; Sih et al. 2004; Bell et al.  
70 2009; Dingemanse and Wolf 2010). These consistent individual differences often affect fitness  
71 (Dingemanse et al. 2004; Dingemanse and Réale 2005; Smith and Blumstein 2008; Seyfarth et  
72 al. 2012). Aggressiveness in particular has been subject of a number of studies (Smith and  
73 Blumstein 2008; Bell et al. 2009). The costs and benefits of aggressive signaling however has  
74 only been studied in the short-term by looking at immediate receiver responses (e.g. Templeton  
75 et al. 2012; Anderson et al. 2013). To the best of our knowledge no prior study has examined the  
76 long-term fitness consequences of individual differences in variation in aggressive signaling  
77 together with aggressiveness in a wild animal.

78         In this paper we report aggression and aggressive signaling measures from a population  
79 of male song sparrows that were assayed multiple times over a period of several years. Our  
80 previous studies found that both aggressive behaviors and aggressive signaling were individually  
81 repeatable over this time period as well as positively correlated with each other (Akçay et al.  
82 2014a). Crucially, when aggressive behavior levels were controlled for, residual signaling was  
83 also repeatable, suggesting individually consistent signaling strategies (Akçay et al. 2014a). Here  
84 we ask whether these deviations from reliability have fitness consequences and whether the  
85 selective forces can explain the maintenance of the reliability of aggressive signaling.

## 86 **Methods**

87 *Study site and subjects:* We studied male song sparrows breeding in Discovery Park, Seattle,  
88 WA. The song sparrow population has been subject of a long term field study since 1986  
89 (Stoddard et al. 1988; Beecher et al. 1994). Each male was banded with a US Fish and Wildlife  
90 Service aluminum band and a unique combination of 3 color bands for individual identification  
91 in the field. Subjects were randomly selected 69 males that held territories in June 2009 which  
92 was a little over half the breeding males in our study area (n=123, Akçay et al. 2014b).

93 *Aggression and aggressive signaling assays:* We carried out repeated playbacks to simulate  
94 territorial intrusions and assay aggressive behaviors and aggressive signaling. The details of the  
95 protocol have been reported by Akçay and colleagues (2014a). Briefly, we placed a speaker  
96 (Pignose Inc.) at the territory center connected to an iPod (Apple Inc.) with a 20 m audio cable.  
97 We played each subject two of his own songs (self song) that had been recorded earlier using a  
98 Marantz PMD 660 digital recorder and a Sennheiser ME66/K6 directional microphone. Each  
99 song was played for 5 minutes at a rate of 1 song every 15 seconds for a total 10-minute trial.  
100 The amplitude song amplitude was approximately 80 dB SPL measured at 1 m (Radio Shack 33-  
101 2055 sound meter). In previous research, song sparrows have shown no behavioral differences in  
102 response to stranger song and self-song (Searcy et al. 1982; Stoddard et al. 1992).

103 The playbacks were carried out in September and October 2009 and January, February  
104 and May 2010, and we attempted to test each male once in each of these months for a total of  
105 five trials. The achieved sample sizes varied due to disappearance of subjects, either temporarily  
106 or permanently. Eleven subjects were tested once, 13 subjects were tested twice, 12 subjects 3

107 times, 19 subjects 4 times, and 14 subjects all 5 times (mean+SD trials per subject: 3.17+1.38,  
108 total number of trials: 219).

109         During each trial two investigators stood at about 20 m from the speaker and observed  
110 the subject. One of the observers also recorded the trial using the same recording gear as above.  
111 We noted verbally the following behavioral measures by narrating the behaviors as they  
112 occurred: flights, distance from the speaker at each flight, loud songs, soft songs, wing waves.  
113 Although the amplitude variation in song sparrow songs is continuous, an experienced observer  
114 can reliably classify loud songs and soft songs in the field (Anderson et al. 2008). The trial  
115 recordings were later viewed and annotated using Syrinx (John Burt, Seattle, WA;  
116 [www.syrinxpc.com](http://www.syrinxpc.com)).

117 *Behavioral measures:* We extracted the following behaviors as our measure of aggression from  
118 each trial: rate of flights (per minute), proportion of time spent within 5m of the speaker, and  
119 closest approach to the speaker during the trial. These three measures were highly correlated  
120 with each other and therefore entered into a principal component analysis (PCA). The first  
121 component of the PCA explained 67.9% of the variance and was taken as the aggression score.  
122 We reported earlier that the average aggression scores from these trials in 2009-2010 predicted  
123 whether the birds would attack a taxidermic mount in Spring 2011(Akçay et al. 2014a).  
124 Additionally, a similar PCA score in another study with a taxidermic mount was able to predict  
125 attackers and non-attackers with 92% accuracy, whereas individual variables that went into the  
126 PCA were able to predict attacks and non-attacks 77 to 81% of the time (Akçay et al. 2013).  
127 Therefore the PCA aggression scores capture most of the important variation in aggressive  
128 behavior.

129 We use the definition of a signal proposed by Otte (1974): “behavioral, physiological, or  
130 morphological characteristics fashioned or maintained by natural selection because they convey  
131 information to other organisms” (p. 738). This definition explicitly excludes behaviors that may  
132 yield information to receivers but are selected primarily for other purposes. The behaviors we are  
133 classifying as aggressive fall into this latter category. Although flying at and staying close to a  
134 receiver may convey information to him, under this definition they don’t qualify as aggressive  
135 signals, since flying towards the receiver and staying close have likely evolved for physically  
136 dealing with an intruder rather than because of their signal value. Previous work on song  
137 sparrows showed that soft songs (low amplitude songs given at close distance) and wing waves  
138 (rapid fluttering of the wings without taking off) are reliable signals on average that predict  
139 attack on a taxidermic mount (Searcy et al. 2006; Akçay et al. 2013; Searcy et al. 2014). These  
140 behaviors have no intrinsic function in a physical fight and their only function in the aggressive  
141 interactions is that they are selected to be a reliable indicator of (i.e. correlated with) an  
142 impending attack. Our definition of the signals are explicitly *a priori* but not arbitrary as it draws  
143 upon extensive observational and experimental work on the natural history of this species (Nice  
144 1943; Arcese et al. 2003 ; Akçay et al. 2013; Searcy et al. 2014). Such an a priori distinction  
145 between signals and non-signaling behaviors is required to study the evolution and maintenance  
146 of signal reliability. Nevertheless, we also demonstrate that the putative signaling behaviors and  
147 aggressive behaviors correspond to separate behavioral modules using a confirmatory factor  
148 analysis (CFA), as suggested by Araya-Ajoy and Dingemanse (2014). We ran two separate CFA  
149 models using the package “sem” in R (Fox et al. 2013), one with a single latent variable  
150 explaining variation in five behavioral measures (the three aggressive behaviors and two  
151 signaling behaviors), and another with two latent variables one explaining variation in the

152 aggressive behaviors and the other explaining variation in the signaling behaviors. The second  
153 model had a lower AIC value ( $\Delta$ AIC of the single latent variable model: 9.55) indicating  
154 significantly higher support for two behavioral modules as opposed to one behavioral module.

155 We extracted the number of soft songs and wing waves and converted these to rates per  
156 minute to account for unequal durations of observation due to different latencies of first  
157 response. Note that although we also counted loud songs, loud songs in song sparrows  
158 consistently have been shown not to predict attack nor to correlate with the signals that do  
159 predict attack, soft songs and wing waves (Searcy and Beecher 2009; Akçay et al. 2013; Searcy  
160 et al. 2014). Therefore loud songs were not included as an aggressive signal. The same goes for  
161 song type matching (replying to the playback with the same song type), which has been shown to  
162 predict attack early in a sequence of escalation in this population (Akçay et al. 2013) but not  
163 when playbacks are only done at the territory center (Akçay et al. 2011; Searcy et al. 2014). We  
164 focus on soft songs as the representative signaling behavior in the analyses below as it is the  
165 most reliable close-range signal in this and several other songbird species (Akçay et al. 2015),  
166 and is highly correlated with wing waves.

167 *Survival:* We censused the study area at least once every two weeks in between January 2010  
168 and February 2015 except in November and December of each year to determine whether  
169 subjects were still alive on territory. Survival on territory is a major component of male fitness  
170 (Smith 1988), as territory ownership is a prerequisite both to being paired with a female and to  
171 obtaining extra-pair copulations in song sparrows (Sardell et al. 2010; Hill et al. 2011). Each  
172 territory was searched extensively, using playback as necessary. In cases where a new male was  
173 detected, we continued to check the territory as well as the neighboring territories for the former  
174 owner. We considered a subject to have died if the subject was not seen on his territory or any of



175 the nearby territories (within two territories of the original one) and the area was being actively  
176 defended by a new male. This operational measure of survival is based on 25 years of continuous  
177 study of our study population, validated by studies in other populations (Smith 1988; Arcese  
178 1989; Hughes and Hyman 2013). These studies show that song sparrows, once they establish a  
179 territory, do not move more than 2 territories away, and once they lose their territory, do not  
180 establish another one at a later time, effectively ending their reproductive careers (floater males  
181 do not sire any offspring; Sardell et al. 2010; Hill et al. 2011). Two of the subjects held territories  
182 that were adjacent to an army base where we could not engage in extensive searching and so  
183 were excluded from the analyses, as we could not be sure whether they had disappeared or  
184 simply made a short move (short moves are not uncommon). In the analyses below we consider  
185 years survived past 2009 as our response variable. Of our 67 subjects, 7 did not survive past  
186 2009 (were gone in January 2010), 34 survived only to 2010, 10 survived to 2011, 4 survived to  
187 2012, 7 survived to 2013 and 5 survived to 2014. All of the original subjects had disappeared by  
188 January 2015.

189 *Data Analysis:* The repeatabilities for aggression scores ( $r=0.48$ , 95% CI: 0.35, 0.62;  $p<0.0001$ ,  
190  $n=219$  trials, 69 subjects), soft song rates ( $r=0.31$ , 95% CI: 0.18, 0.46,  $p<0.0001$ ,  $n=219$  trials,  
191 69 subjects) and wing wave rates ( $r=0.50$ , 95% CI: 0.36, 0.63,  $p<0.0001$ ,  $n=219$  trials, 69  
192 subjects) were all highly significant (Akçay et al. 2014a). Here we focus on average aggression  
193 scores and average soft song rates across all trials for a given subject.

194 Our main analysis was the phenotypic selection analysis proposed by Lande and Arnold  
195 (1983). The phenotypic selection analysis yields selection gradients that are readily comparable  
196 across different studies and different analyses and is therefore a valuable way of quantifying  
197 selection. We standardized the aggression scores and soft song and wing wave rates (taking their

198 z-scores), and took the relative fitness of individuals by dividing the number of years a bird  
199 survived by the average number of years survived for the entire sample. We then ran a linear  
200 regression model on the relative fitness scores with the predictor variables standardized  
201 aggression scores, standardized soft song rates, the quadratic terms of the two variables and the  
202 cross-products. These correspond to directional, non-linear (e.g. stabilizing or disruptive) and  
203 correlational selection. We report the selection gradients, which are equal to the regression  
204 coefficients in the Lande-Arnold regression, except for the quadratic terms for which the  
205 coefficients and their standard errors are doubled to get the selection gradients (Stinchcombe et  
206 al. 2008). We also drew a selection surface using the coefficients from the full model to visualize  
207 the nature of selection (Sinervo and Svensson 2002). All analyses were carried out in R (R Core  
208 Team 2012; the code is available as a supplementary material). In the supplementary materials  
209 we report additional analyses on the effect of age that show that age does not interact with either  
210 aggression scores or soft song in determining survival.

## 211 **Results**

212 In the phenotypic selection analysis with aggression scores and soft songs, two selection  
213 coefficients were significant: the quadratic term for soft songs with a positive coefficient  
214 (indicating disruptive selection, Figure S1) and the interaction term with a negative coefficient,  
215 indicating negative correlational selection (Table 1). The selection surface displayed in Figure 1  
216 indicates that selection favors males with high aggression scores and low rates of soft song  
217 (under-signalers) and males with low aggression scores and high rates of soft song (over-  
218 signalers). The negative correlational selection remained significant in the subset of subjects with  
219 age data (supplementary materials). Looking at the survival of subjects as a function of  
220 aggression scores and soft song rates (Figure 2) one sees that males that are closer to the back of

221 the 3-D plot (high aggression/low signaling) tend to have higher survival, i.e. under-signalers are  
222 favored. Note also although the selective forces would favor over-signalers, there are few such  
223 males (i.e. the closer corner of the plot is mostly empty).

## 224 **Discussion**

225 In this study we examined the effects of aggression and aggressive signaling on an  
226 important component of fitness, survival on territory. We found evidence of disruptive selection  
227 on soft songs on the one hand and a negative correlational selection on the other. The latter  
228 finding suggests that males that deviate from reliable signaling have a survival advantage and the  
229 correlation between the signal and the aggressive behaviors (i.e. reliability) will tend to decrease  
230 over time in the absence of a counteracting selection effect (assuming heritability of these  
231 behaviors).

### 232 *Correlational selection, behavioral syndromes and evolution of reliability*

233 Our main questions in this study were (1) what are the fitness consequences of variation  
234 in aggressive signaling and aggression and (2) does selection explain the evolution and  
235 maintenance of reliability? In recent years, the evolution of behavioral syndromes (correlations  
236 between suites of individually consistent behaviors, sometimes in different contexts (Sih et al.  
237 2004)) has attracted a great deal of research effort. The evolution of reliability in individually  
238 consistent signaling behaviors can be viewed as an analogous problem in which individually  
239 consistent levels of signaling and aggressive behaviors are correlated with each other, although  
240 in this case, the behaviors are given in the same context, namely aggression. Behavioral traits  
241 can become correlated with each other to yield behavioral syndromes either through pleiotropic  
242 effects of a genetic, hormonal or developmental pathway or through correlational selection that

243 creates linkage disequilibrium in the genes controlling the traits (Ketterson and Nolan 1999;  
244 Dingemanse and Réale 2005; Bell 2007).

245 In this context the most interesting finding from the perspective of honest signaling is the  
246 significant correlational selection between the two signaling behaviors on the one hand and  
247 aggressive behaviors on the other. Interestingly, the direction of this correlational selection is not  
248 what would be expected from the hypothesis that correlational selection underlies the evolution  
249 of reliability. Multiple previous studies had shown that soft songs reliably predict attack in this  
250 and several other species (Searcy et al. 2014; Akçay et al. 2015) but our results show significant  
251 *negative* correlational selection that would tend to disrupt the reliability of soft songs in the long  
252 term (assuming a non-zero heritability of signaling and aggression). These results therefore rule  
253 out correlational selection as the ultimate cause of the reliability between signaling and  
254 aggressive behavior.

255 The above conclusion is also consistent with a handful of previous studies which  
256 considered correlational selection as a possible cause in the emergence of behavioral syndromes  
257 but failed to support that hypothesis (Bell and Sih 2007; Adriaenssens and Johnsson 2013; Han  
258 and Brooks 2013). These previous studies and our study differ significantly however in that the  
259 former have detected no significant correlational selection either way whereas we detected a  
260 significant correlational selection, but the direction of the selection is opposite of what one  
261 would expect based on the reliability of the system. Indeed, the negative correlational selection,  
262 appears to select for non-reliable signaling and therefore leaves open the question of how signal  
263 reliability is maintained. There are a few possible answers. Previous behavioral studies have  
264 suggested a social cost of using soft songs in the form retaliation from the receivers which could  
265 stabilize and maintain honesty of soft song (Anderson et al. 2012; Templeton et al. 2012;

266 Anderson et al. 2013). It is not clear however, how this short-term cost translates to long-term  
267 fitness and the present results should sound a cautionary note on extrapolating from short-term  
268 costs to long term fitness. Another hypothesis is that variation in threat signals is dependent on a  
269 pleiotropic effect of a genetic locus or loci or a hormonal pathway (Sinervo and Svensson 2002;  
270 Bell 2007; McGlothlin and Ketterson 2008). It is also possible that the negative correlational  
271 selection on survival on territory may be offset by an opposing selective gradient on annual  
272 fledging success. Finally, the positive correlation between signals and aggressive behaviors may  
273 also come about through shared developmental pathways. These hypotheses have yet to be tested  
274 in the field.

275         It is worth noting that the effect of the negative correlational selection on reliability may  
276 not be as disruptive as the selection gradients suggest. First we do not yet know the heritability of  
277 signaling and aggression in this species although it is likely to be greater than zero (Turkheimer  
278 2000). Second, selection acts on existing variation. Previous research by our group and others  
279 have shown that most deviations from reliability are under-signalers, males that signal at low  
280 levels but attack a taxidermic mount while there are only very few instances of actual over-  
281 signalers, males that signal at high levels but don't attack (Akçay et al. 2013; Searcy et al. 2013).  
282 Specifically, in an experiment in which 31 of 48 subjects attacked the mount, rates of soft songs  
283 correctly predicted 88% of non-attacks (i.e. these non-attackers sang soft songs at low levels, and  
284 only 12% of non-attackers were over-signalers) while predicting only 55% of attacks (i.e. 45% of  
285 attackers also sang soft songs at low levels and thus were under-signalers). (Akçay et al. 2013).  
286 Figure 2 also shows a similar pattern in the current dataset (more under-signalers than over-  
287 signalers). Over-signaling ('bluffing') has been long recognized as a problem for the evolution  
288 and maintenance of reliability, e.g. (Maynard Smith 1979; Rowell et al. 2006). However the

289 effect of under-signalers on the maintenance of reliability has only been considered by a few  
290 models (reviewed in (Searcy et al. 2013)). It is possible that under-signalers could co-exist in an  
291 otherwise reliable signaling system: a male who attacks without signaling may not be a major  
292 problem for signal reliability so long as males who do signal do end up attacking. In other words,  
293 as long as signalers end up attacking at higher than chance levels, receivers will keep paying  
294 attention to the signals, even if some opponents do not signal and still attack.

295 Another question posed by our results is why the under-signalers and over-signalers seem  
296 to have a fitness benefit in terms of survival to start with. We provide two hypotheses, one for  
297 the apparent survival benefits of under-signaling and another for over-signaling. First, an over-  
298 signaling low aggression male might be more effective in holding on to his territory without  
299 paying the cost of physical fights if they are rare enough that receivers still pay attention to the  
300 signals. This is the standard argument that signaling systems can carry a limited amount of  
301 “cheaters” and be stable (Johnstone and Grafen 1993; Adams and Mesterton-Gibbons 1995;  
302 Rowell et al. 2006). The fact that over-signalers seem to be rare in our population would fit these  
303 models.

304 The fitness benefit to under-signalers may stem from the fact that signaling often exposes  
305 the signalers to risk of predation, a common cause of territory loss. Predation risk tends to be  
306 especially increased during aggressive encounters (Jakobsson et al. 1995). In our population,  
307 Cooper’s hawks (*Accipiter cooperii*) are a major predator of song sparrows, hunting from  
308 concealed perches through surprise attacks. Recently we showed that most (although not all)  
309 males cease singing (and wing waving) when the presence of a hawk is simulated through  
310 playbacks of hawk calls in the midst of a simulated intrusion by a male song sparrow (Akçay et  
311 al. in press). This result implies that aggressive signals, even soft song with its low amplitude,

312 may be intercepted by the hawks and increase predation risk. Such risk may be especially  
313 pronounced in males who respond with high aggression to intruders, as one of our trials in the  
314 present experiment illustrated when a subject was almost taken by a Cooper's hawk during a  
315 very close approach to the playback speaker in the middle of the trial (we aborted the trial and to  
316 our relief, the hawk "missed"). If signaling increases the risk of predation for aggressive males,  
317 then under-signalers may benefit from not signaling and avoiding the unwanted attention of  
318 eavesdropping predators while at the same time dealing with intruders effectively via high levels  
319 of aggression. This hypothesis, along with the hypothesis in the previous paragraph, may also  
320 explain the disruptive selection on soft song levels. Further research will be needed to test these  
321 hypotheses in the field.

322         In summary our study indicates that there may be opposing selective forces on reliable  
323 signaling just as theory to date has suggested (Maynard Smith and Harper 2003). Given the  
324 correlational nature of the current dataset, and the current lack of information on heritability, it is  
325 hard to gauge what the response to selection will be in this system but we can rule out current  
326 correlational selection as the cause of maintenance of reliability in this honest signaling system.  
327 The present study is a first step in understanding the role of individually consistent variation in  
328 aggression and aggressive signaling in the evolution and maintenance of reliable communication  
329 systems and suggests a multitude of hypotheses and new questions for future research as  
330 discussed above. Studies of long-term fitness consequences of variation in signaling phenotypes  
331 will be a fruitful avenue for further research.

332

333

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482 Table 1. Selection gradients from Lande-Arnold phenotypic selection analysis. Note that the  
483 coefficients and the standard errors for the quadratic terms are doubled.

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variable	Coefficient $\pm$ SE	<i>p</i>
Aggression scores	-0.04 $\pm$ 0.16	0.78
Soft song rates	0.13 $\pm$ 0.11	0.23
Aggression scores <sup>2</sup>	0.34 $\pm$ 0.18	0.15
<b>Soft song rates<sup>2</sup></b>	<b>-0.70 <math>\pm</math> 0.27</b>	<b>0.01</b>
<b>Aggression*soft song rates</b>	<b>-0.79 <math>\pm</math> 0.21</b>	<b>0.0003</b>

485

486 Figure 1. Selection surface as a function of soft songs and PCA aggression scores (both  
487 as z-scores). The arrows indicate z-scores getting larger. There are two fitness peaks, one for  
488 under-signalers (high aggression, low signaling) and another for over-signalers (low aggression,  
489 high signaling), with a valley in between them.

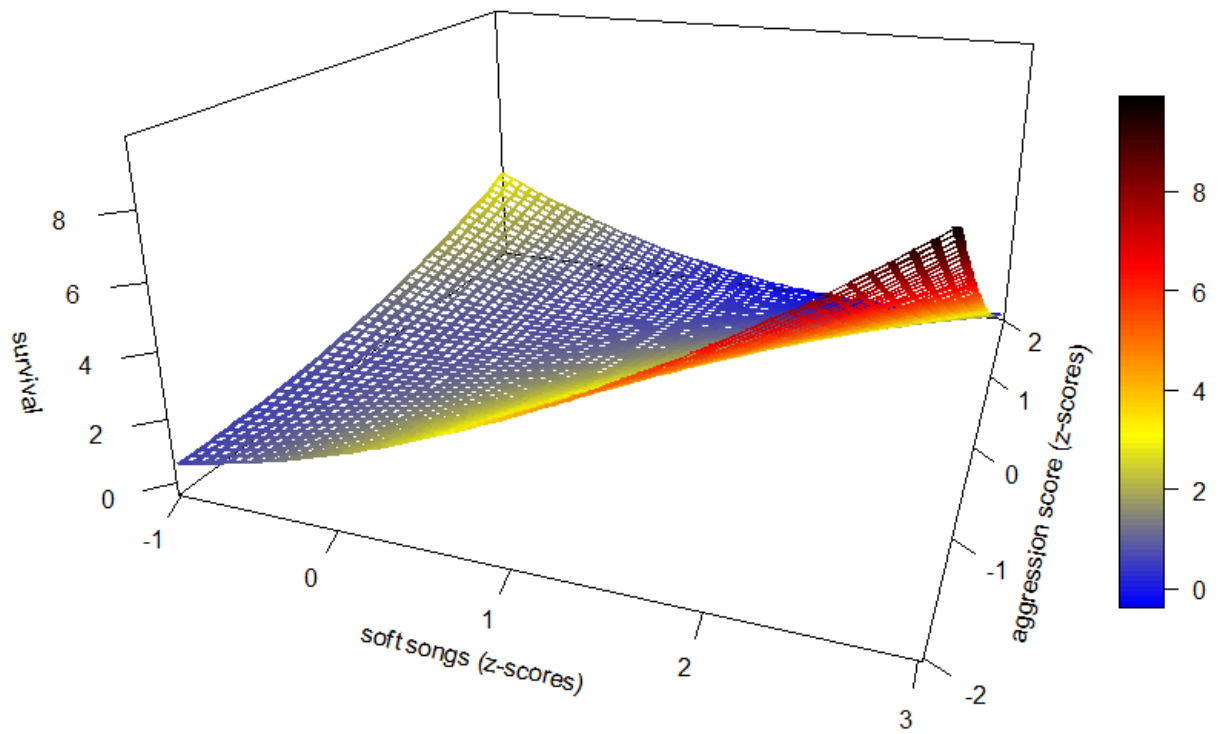
490 Figure 2. 3-D scatterplot of survival in years as a function of rates of soft songs and  
491 aggression scores. Note the lack of over-signalers but the relative abundance of under-signalers  
492 (towards the upper back corner of the plot).

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Figure 1



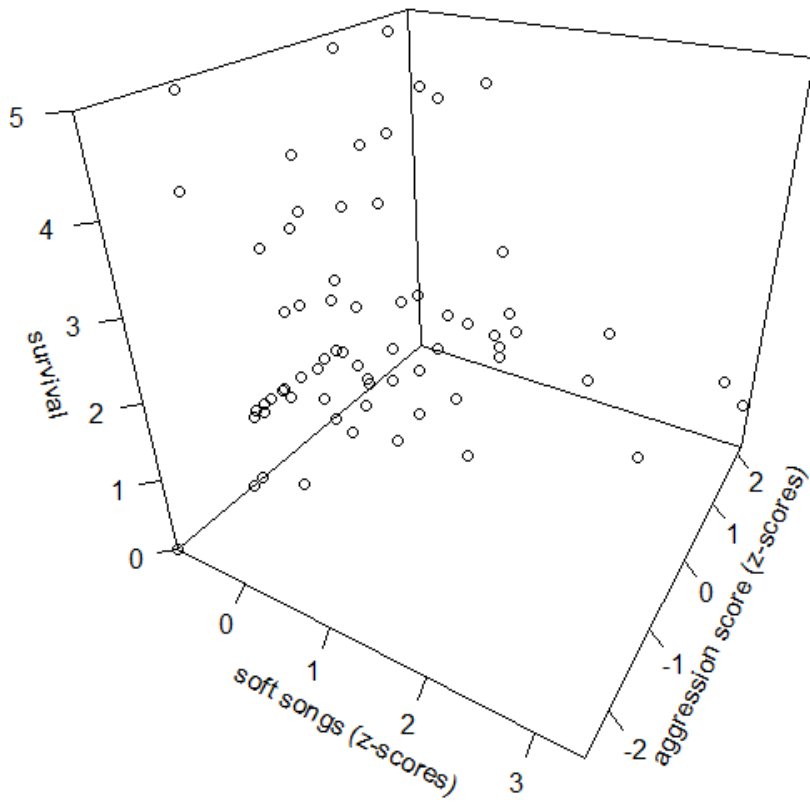
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Figure 2.



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