

The fitness consequences of honesty: Under-signalers have a survival advantage in song sparrows

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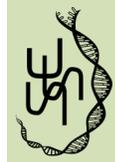
How honest or reliable signaling can evolve and be maintained has been a major question in evolutionary biology. The question is especially puzzling for a particular class of signals used in aggressive interactions: threat signals. Here, we report a study on song sparrows (*Melospiza melodia*) in which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

KEY WORDS: Aggression, competition, honest signaling, personality, soft songs, territoriality.

In signaling interactions between two unrelated individuals, the interests of signalers and receivers rarely coincide perfectly, which poses the question of how animal signals can evolve to be reliable (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). This question is particularly prominent in the case of threat signals used in aggressive situations, when the interests of signalers and receivers are opposed to each other. Some threat signals reveal traits such as physical size or strength of the signaler in a way that cannot be cheated (e.g., parallel walk in red deer that emphasizes the body size; Clutton-Brock et al. 1979) but many threat signals are not intrinsically tied to an easily observable and costly trait. These signals, termed “conventional signals” because of the arbitrary relationship between the signal structure and signal message (Guilford and Dawkins 1995), are seemingly easy to cheat and therefore their reliability represents an empirical and theoretical

puzzle (Maynard Smith and Harper 2003). Although conventional signals were initially thought to be unreliable and nonpredictive in contests over all but trivial resources (Maynard Smith 1974; Dawkins and Krebs 1978; Caryl 1979; Maynard Smith 1979; Maynard Smith et al. 1988), recent research has shown many such signals to be at least partially reliable in predicting further escalation (Waas 1991; Searcy et al. 2006; Laidre 2009; Akçay et al. 2013).

Although conventional signals can be statistically reliable in predicting an escalation, the reliability is often imperfect (Searcy et al. 2013). Furthermore, signaling strategies of at least some species appear to be individually consistent over time, that is, with some individuals signaling consistently at high levels and others consistently at low levels, even though conventional signals are generally assumed to be flexible behaviors. For example, we



recently showed that male song sparrows (*Melospiza melodia*) show individually consistent signaling strategies in repeated aggression assays even after accounting for their aggression levels (Akçay et al. 2014a), for example, some low-aggression individuals consistently signal higher than expected, and some high-aggression individuals lower than expected. These results suggest that at least part of the variation present in imperfectly reliable signals is correlated with consistent individual differences (Botero et al. 2010).

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

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

Methods

STUDY SITE AND SUBJECTS

We studied male song sparrows breeding in Discovery Park, Seattle, Washington. The song sparrow population has been subject of a long-term field study since 1986 (Stoddard et al. 1988; Beecher et al. 1994). Each male was banded with a U.S. Fish and Wildlife Service aluminum band and a unique combination of three color bands for individual identification in the field. Subjects were randomly selected 69 males that held territories in June 2009 which was a little over half the breeding males in our study area ($n = 123$, Akçay et al. 2014b).

AGGRESSION AND AGGRESSIVE SIGNALING ASSAYS

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

The playbacks were carried out in September and October 2009 and January, February, and May 2010, and we attempted to test each male once in each of these months for a total of five trials. The achieved sample sizes varied due to disappearance of subjects, either temporarily or permanently. Eleven subjects were tested once, 13 subjects were tested twice, 12 subjects three times, 19 subjects four times, and 14 subjects all five times (mean \pm SD trials per subject: 3.17 ± 1.38 , total number of trials: 219).

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

BEHAVIORAL MEASURES

We extracted the following behaviors as our measure of aggression from each trial: rate of flights (per minute), proportion of time spent within 5 m of the speaker, and closest approach to the speaker during the trial. These three measures were highly correlated with each other and therefore entered into a principal component analysis (PCA). The first component of the PCA explained 67.9% of the variance and was taken as the aggression score. We reported earlier that the average aggression scores from these trials in 2009–2010 predicted whether the birds would attack a taxidermic mount in Spring 2011 (Akçay et al. 2014a). Additionally, a similar PCA score in another study with a taxidermic mount was able to predict attackers and nonattackers with 92% accuracy, whereas individual variables that went into the PCA were able to

predict attacks and nonattacks 77–81% of the time (Akçay et al. 2013). Therefore, the PCA aggression scores capture most of the important variation in aggressive behavior.

We use the definition of a signal proposed by Otte (1974): “behavioral, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms” (p. 738). This definition explicitly excludes behaviors that may yield information to receivers but are selected primarily for other purposes. The behaviors we are classifying as aggressive fall into this latter category. Although flying at and staying close to a receiver may convey information to him, under this definition they do not qualify as aggressive signals, because flying toward the receiver and staying close have likely evolved for physically dealing with an intruder rather than because of their signal value. Previous work on song sparrows showed that soft songs (low amplitude songs given at close distance) and wing waves (rapid fluttering of the wings without taking off) are reliable signals on average that predict attack on a taxidermic mount (Searcy et al. 2006; Akçay et al. 2013; Searcy et al. 2014). These behaviors have no intrinsic function in a physical fight and their only function in the aggressive interactions is that they are selected to be a reliable indicator of (i.e., correlated with) an impending attack. Our definition of the signals is explicitly a priori but not arbitrary as it draws upon extensive observational and experimental work on the natural history of this species (Nice 1943; Arcese et al. 2002; Akçay et al. 2013; Searcy et al. 2014). Such an a priori distinction between signals and nonsignaling behaviors is required to study the evolution and maintenance of signal reliability. Nevertheless, we also demonstrate that the putative signaling behaviors and aggressive behaviors correspond to separate behavioral modules using a confirmatory factor analysis (CFA), as suggested by Araya-Ajoy and Dingemanse (2014). We ran two separate CFA models using the package “sem” in R (Fox et al. 2012), one with a single latent variable explaining variation in five behavioral measures (the three aggressive behaviors and two signaling behaviors), and another with two latent variables one explaining variation in the aggressive behaviors and the other explaining variation in the signaling behaviors. The second model had a lower AIC value (Δ AIC of the single latent variable model: 9.55) indicating significantly higher support for two behavioral modules as opposed to one behavioral module.

We extracted the number of soft songs and wing waves and converted these to rates per minute to account for unequal durations of observation due to different latencies of first response. Note that although we also counted loud songs, loud songs in song sparrows consistently have been shown not to predict attack nor to correlate with the signals that do predict attack, soft songs, and wing waves (Searcy and Beecher 2009; Akçay et al. 2013; Searcy et al. 2014). Therefore, loud songs were not included as an aggressive signal. The same goes for song type matching (re-

plying to the playback with the same song type), which has been shown to predict attack early in a sequence of escalation in this population (Akçay et al. 2013) but not when playbacks are only done at the territory center (Akçay et al. 2011; Searcy et al. 2014). We focus on soft songs as the representative signaling behavior in the analyses below as it is the most reliable close-range signal in this and several other songbird species (Akçay et al. 2015), and is highly correlated with wing waves.

SURVIVAL

We censused the study area at least once every two weeks in between January 2010 and February 2015 except in November and December of each year to determine whether subjects were still alive on territory. Survival on territory is a major component of male fitness (Smith 1988), as territory ownership is a prerequisite both to being paired with a female and to obtaining extra-pair copulations in song sparrows (Sardell et al. 2010; Hill et al. 2011). Each territory was searched extensively, using playback as necessary. In cases where a new male was detected, we continued to check the territory as well as the neighboring territories for the former owner. We considered a subject to have died if the subject was not seen on his territory or any of the nearby territories (within two territories of the original one) and the area was being actively defended by a new male. This operational measure of survival is based on 25 years of continuous study of our study population, validated by studies in other populations (Smith 1988; Arcese 1989; Hughes and Hyman 2011). These studies show that song sparrows, once they establish a territory, do not move more than two territories away, and once they lose their territory, do not establish another one at a later time, effectively ending their reproductive careers (floater males do not sire any offspring; Sardell et al. 2010; Hill et al. 2011). Two of the subjects held territories that were adjacent to an army base where we could not engage in extensive searching and so were excluded from the analyses, as we could not be sure whether they had disappeared or simply made a short move (short moves are not uncommon). In the analyses below we consider years survived past 2009 as our response variable. Of our 67 subjects, seven did not survive past 2009 (were gone in January 2010), 34 survived only to 2010, 10 survived to 2011, four survived to 2012, seven survived to 2013, and five survived to 2014. All of the original subjects had disappeared by January 2015.

DATA ANALYSIS

The repeatabilities for aggression scores ($r = 0.48$, 95% CI: 0.35, 0.62; $P < 0.0001$, $n = 219$ trials, 69 subjects), soft song rates ($r = 0.31$, 95% CI: 0.18, 0.46, $P < 0.0001$, $n = 219$ trials, 69 subjects), and wing wave rates ($r = 0.50$, 95% CI: 0.36, 0.63, $P < 0.0001$, $n = 219$ trials, 69 subjects) were all highly significant (Akçay

Table 1. Selection gradients from Lande–Arnold phenotypic selection analysis.

Variable	Coefficient \pm SE	<i>P</i>
Aggression scores	-0.04 ± 0.16	0.78
Soft song rates	0.13 ± 0.11	0.23
Aggression scores ²	0.34 ± 0.18	0.15
Soft song rates ²	0.70 ± 0.27	0.01
Aggression \times soft song rates	-0.79 ± 0.21	0.0003

Note that the coefficients and standard errors for the quadratic terms are doubled.

et al. 2014a). Here, we focus on average aggression scores and average soft song rates across all trials for a given subject.

Our main analysis was the phenotypic selection analysis proposed by Lande and Arnold (1983). The phenotypic selection analysis yields selection gradients that are readily comparable across different studies and different analyses and is therefore a valuable way of quantifying selection. We standardized the aggression scores and soft song and wing wave rates (taking their *z*-scores), and took the relative fitness of individuals by dividing the number of years a bird survived by the average number of years survived for the entire sample. We then ran a linear regression model on the relative fitness scores with the predictor variables standardized aggression scores, standardized soft song rates, the quadratic terms of the two variables, and the cross-products. These correspond to directional, nonlinear (e.g., stabilizing or disruptive), and correlational selection. We report the selection gradients, which are equal to the regression coefficients in the Lande–Arnold regression, except for the quadratic terms for which the coefficients and their standard errors are doubled to get the selection gradients (Stinchcombe et al. 2008). We also drew a selection surface using the coefficients from the full model to visualize the nature of selection (Sinervo and Svensson 2002). All analyses were carried out in R (R Core Team 2012; the code is available as a supplementary material). In the supplementary materials, we report additional analyses on the effect of age that show that age does not interact with either aggression scores or soft song in determining survival.

Results

In the phenotypic selection analysis with aggression scores and soft songs, two selection coefficients were significant: the quadratic term for soft songs with a positive coefficient (indicating disruptive selection, Fig. S1) and the interaction term with a negative coefficient, indicating negative correlational selection (Table 1). The selection surface displayed in Figure 1 indicates that selection favors males with high-aggression scores and low rates of soft song (under-signalers) and males with low-aggression

scores and high rates of soft song (over-signalers). The negative correlational selection remained significant in the subset of subjects with age data (see supplementary materials). Looking at the survival of subjects as a function of aggression scores and soft song rates (Fig. 2), one sees that males that are closer to the back of the three-dimensional plot (high aggression/low signaling) tend to have higher survival, that is, under-signalers are favored. Note also although the selective forces would favor over-signalers, there are few such males (i.e., the closer corner of the plot is mostly empty).

Discussion

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

CORRELATIONAL SELECTION, BEHAVIORAL SYNDROMES, AND EVOLUTION OF RELIABILITY

Our main questions in this study are as follows: (1) What are the fitness consequences of variation in aggressive signaling and aggression and (2) Does selection explain the evolution and maintenance of reliability? In recent years, the evolution of behavioral syndromes (correlations between suites of individually consistent behaviors, sometimes in different contexts; Sih et al. 2004) has attracted a great deal of research effort. The evolution of reliability in individually consistent signaling behaviors can be viewed as an analogous problem in which individually consistent levels of signaling and aggressive behaviors are correlated with each other, although in this case, the behaviors are given in the same context, namely aggression. Behavioral traits can become correlated with each other to yield behavioral syndromes either through pleiotropic effects of a genetic, hormonal, or developmental pathway or through correlational selection that creates linkage disequilibrium in the genes controlling the traits (Ketterson and Nolan 1999; Dingemanse and Réale 2005; Bell 2007).

In this context, the most interesting finding from the perspective of honest signaling is the significant correlational selection between the two signaling behaviors on the one hand and aggressive behaviors on the other. Interestingly, the direction of this correlational selection is not what would be expected from the hypothesis that correlational selection underlies the evolution of reliability. Multiple previous studies had shown that soft songs reliably predict attack in this and several other species (Searcy et al.

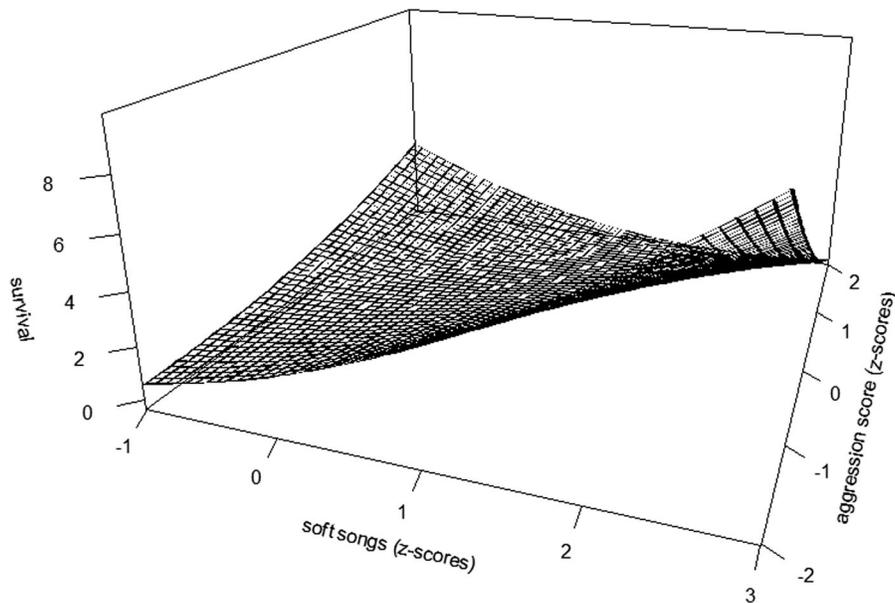


Figure 1. Selection surface as a function of soft songs and PCA aggression scores (both as z-scores). The arrows indicate z-scores getting larger. There are two fitness peaks, one for under-signalers (high aggression, low signaling) and another for over-signalers (low aggression, high signaling), with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

2014; Akçay et al. 2015) but our results show significant *negative* correlational selection that would tend to disrupt the reliability of soft songs in the long term (assuming a nonzero heritability of signaling and aggression). These results therefore rule out correlational selection as the ultimate cause of the reliability between signaling and aggressive behavior.

The above conclusion is also consistent with a handful of previous studies which considered correlational selection as a possible cause in the emergence of behavioral syndromes but failed to support that hypothesis (Bell and Sih 2007; Adriaenssens and Johnsson 2013; Han and Brooks 2013). These previous studies and our study differ significantly however in that the former have detected no significant correlational selection either way whereas we detected a significant correlational selection, but the direction of the selection is opposite of what one would expect based on the reliability of the system. Indeed, the negative correlational selection appears to select for nonreliable signaling and therefore leaves open the question of how signal reliability is maintained. There are a few possible answers. Previous behavioral studies have suggested a social cost of using soft songs in the form retaliation from the receivers which could stabilize and maintain honesty of soft song (Anderson et al. 2012; Templeton et al. 2012; Anderson et al. 2013). It is not clear however, how this short-term cost translates to long-term fitness and the present results should sound a cautionary note on extrapolating from short-term costs to long-term fitness. Another hypothesis is that variation in threat signals is dependent on a pleiotropic effect of a genetic locus or loci or a hormonal pathway (Sinervo and Svensson 2002; Bell 2007;

McGlothlin and Ketterson 2008). It is also possible that the negative correlational selection on survival on territory may be offset by an opposing selective gradient on annual fledging success. Finally, the positive correlation between signals and aggressive behaviors may also come about through shared developmental pathways. These hypotheses have yet to be tested in the field.

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

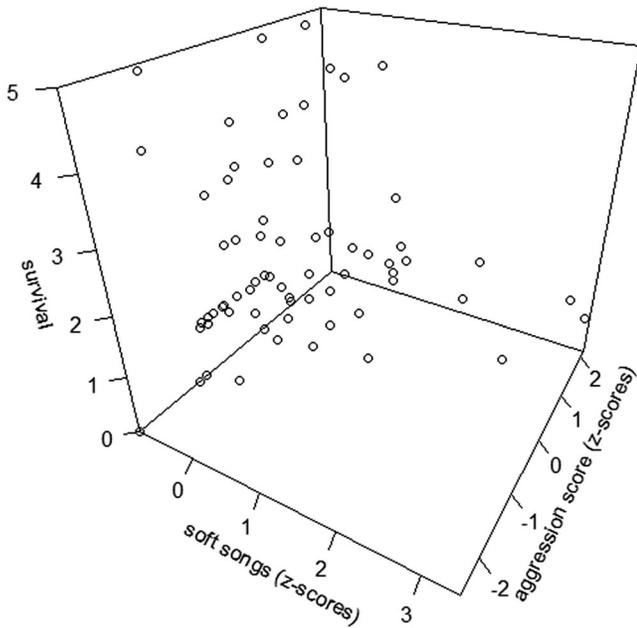


Figure 2. Three-dimensional scatterplot of survival in years as a function of rates of soft songs and aggression scores. Note the lack of over-signalers but the relative abundance of under-signalers (toward the upper back corner of the plot).

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

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

The fitness benefit to under-signalers may stem from the fact that signaling often exposes the signalers to risk of predation, a common cause of territory loss. Predation risk tends to be especially increased during aggressive encounters (Jakobsson et al. 1995). In our population, Cooper’s hawks (*Accipiter cooperii*)

are a major predator of song sparrows, hunting from concealed perches through surprise attacks. Recently, we showed that most (although not all) males cease singing (and wing waving) when the presence of a hawk is simulated through playbacks of hawk calls in the midst of a simulated intrusion by a male song sparrow (Akçay et al. 2015). This result implies that aggressive signals, even soft song with its low amplitude, may be intercepted by the hawks and increase predation risk. Such risk may be especially pronounced in males that respond with high aggression to intruders, as one of our trials in the present experiment illustrated when a subject was almost taken by a Cooper’s hawk during a very close approach to the playback speaker in the middle of the trial (we aborted the trial and to our relief, the hawk had “missed”). If signaling increases the risk of predation for aggressive males, then under-signalers may benefit from not signaling and avoiding the unwanted attention of eavesdropping predators while at the same time dealing with intruders effectively via high levels of aggression. This hypothesis, along with the hypothesis in the previous paragraph, may also explain the disruptive selection on soft song levels. Further research will be needed to test these hypotheses in the field.

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

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DATA ARCHIVING

All data are archived in the supplementary materials.

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Supporting Information

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Supporting Material

Figure S1. Predicted survival as a function of soft song (*z*-scores), averaged across aggression scores.

Table S1. Rates of soft songs (*z*soft) and time spent within 5 m (*z*time5).

Table S2. Rates of soft songs (*z*soft) and rate of flights (*z*flight).

Table S3. Rates of soft songs (*z*soft) and closest approach (*z*closest).

Table S4. Model selection table for Cox-regression analysis.

Table S5. Averaged model for the Cox-regression.