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Research in the past decade has established the existence of consistent individual differences or 'personality' in animals and their important role in many aspects of animal behaviour. At the same time, research on honest signalling of aggression has revealed that while some of the putative aggression signals are reliable, they are only imperfectly so. This study asks whether a significant portion of the variance in the aggression-signal regression may be explained by individual differences in signalling strategies. Using the well-studied aggressive signalling system of song sparrows (*Melospiza melodia*), we carried out repeated assays to measure both aggressive behaviours and aggressive signalling of territorial males. Through these assays, we found that aggressive behaviours and aggressive signalling were both highly repeatable, and moreover that aggressive behaviours in 2009–2010 predicted whether the birds would attack a taxidermic mount over a year later. Most significantly, we found that residual variation in signalling behaviours, after controlling for aggressive behaviour, was individually consistent, suggesting there may be a second personality trait determining the level of aggressive signalling. We term this potential personality trait 'communicativeness' and discuss these results in the context of honest signalling theories and recent findings reporting prevalence of 'under-signalling'.

1. Introduction

In the last decade, many studies on animal behaviour have converged on the conclusion that animals exhibit stable individual differences in suites of behavioural traits; these have been termed personality or behavioural syndromes [1–4]. Aggressiveness is one of the individually consistent traits that has received greatest attention since it is readily quantifiable in the field and would seem to have obvious fitness consequences for individuals. A number of studies on a variety of species have also found aggression levels not only to be individually consistent over time (see [5] for a review), but also correlated with several other aspects of behaviour such as exploration [6–8] or boldness [9,10]. Some studies have also found that the consistent individual differences in aggression have fitness consequences [5,11,12], bringing personality research into the forefront of behavioural ecology.

Despite the burgeoning interest in personality, the relevance of such individual differences to issues in animal communication has gone mostly unexamined. This omission is particularly significant given the extensive research, both theoretical and empirical, on animal communication. On the theoretical side, there is a large literature devoted to evolutionarily stable strategies of signalling in animal contests, starting with Price and Maynard Smith's classic work [13–16]. Most models of aggressive signalling have focused on the question of whether signals can be honest on average, and how the problem of cheating (over-signalling for a given level of aggressive intent or fighting ability) can be overcome [17,18]. Although some of these models have considered the possibility of variability in the form of errors in production or assessment of signals [19,20], they have not considered the possible role of consistent individual differences in signalling (see [21]; for an exception).

Empirical research on aggressive signalling has similarly focused on its honesty or reliability. In these studies, the researchers generally elicit signalling from animals and correlate signalling levels with concurrent or subsequent aggressive behaviours [22–26]. A key point for this research is that in these earlier studies,

aggressive behaviour and aggressive signalling have been operationalized separately. For instance, in songbirds aggression is usually measured in terms of flights and close approach to the playback speaker or taxidermic mount, and aggressive signalling in terms of vocal and visual threat displays, with the question being do the latter predict the former? Although these studies have found that some putative threat signals are indeed correlated with concurrent or subsequent aggressive behaviour, the relationship between signalling levels and actual aggression is far from perfect. For example, in our recent study on song sparrows (*Melospiza melodia*), we found that while the level of low amplitude ('soft') songs on average reliably predicted whether or not a song sparrow would attack a taxidermic mount later in the trial, a substantial number of birds that signalled at a high level did not attack, whereas others that signalled at a low level (or not at all) did attack [27], see also [22]. Soft songs and wing waves were able to correctly predict only 66.7% and 62.3%, respectively [27]—significantly different from chance, but far from perfect. The fact that aggressive signals predict aggression only imperfectly suggests that other uncontrolled factors may also be affecting aggression and aggressive signalling. Although there has been a tendency to assume that this 'partial reliability' simply reflects experimental noise, to our knowledge no study to date has examined the question of whether some of the variation in signalling is due to variation in an individually consistent trait, i.e. whether some individuals simply signal consistently more or less than others of similar aggression levels.

As mentioned above, previous research in our study species and others [28,29] has established that personality differences in aggressiveness is an individually consistent trait that is correlated with boldness [9,10] or exploration [6,8], and thus constitutes a behavioural syndrome or a personality trait. Although aggressiveness is a well-studied personality trait and potentially drives expression of both aggressive behaviours and aggressive signalling by itself, it would not be sufficient to explain partial reliability of signalling. We hypothesized the presence of a second, independent source of variation, a hitherto unexamined individual trait we call tentatively 'communicativeness'. We operationalize communicativeness in our situation as the tendency to signal consistently more or consistently less than expected given the animal's level of aggressiveness.

Several hypotheses relating aggressive behaviour and aggressive signalling are illustrated in figure 1. Figure 1a is the null hypothesis that no individual traits underlie variation in aggressive behaviours and aggressive signalling. Under this scenario, neither aggressive behaviours nor aggressive signalling should be repeatable across individuals. Figure 1b illustrates the first alternative hypothesis, that a single personality trait, aggressiveness, drives both aggressive behaviours and aggressive signalling. There is some residual variation in both aggressive behaviours and signalling but this is simply owing to random error. The implication for partial reliability is that once an individual's aggression level is taken into account, the residual variation in signalling is random and not individually consistent. Finally, under the second alternative hypothesis (figure 1c), aggressive signalling is driven by both the aggressiveness and the communicativeness of the individual. The effect of communicativeness in this scenario would manifest itself as individually consistent residual variation in signalling behaviour once the level of aggressive behaviours of individuals has been taken into account. For instance, some individuals would show consistently negative
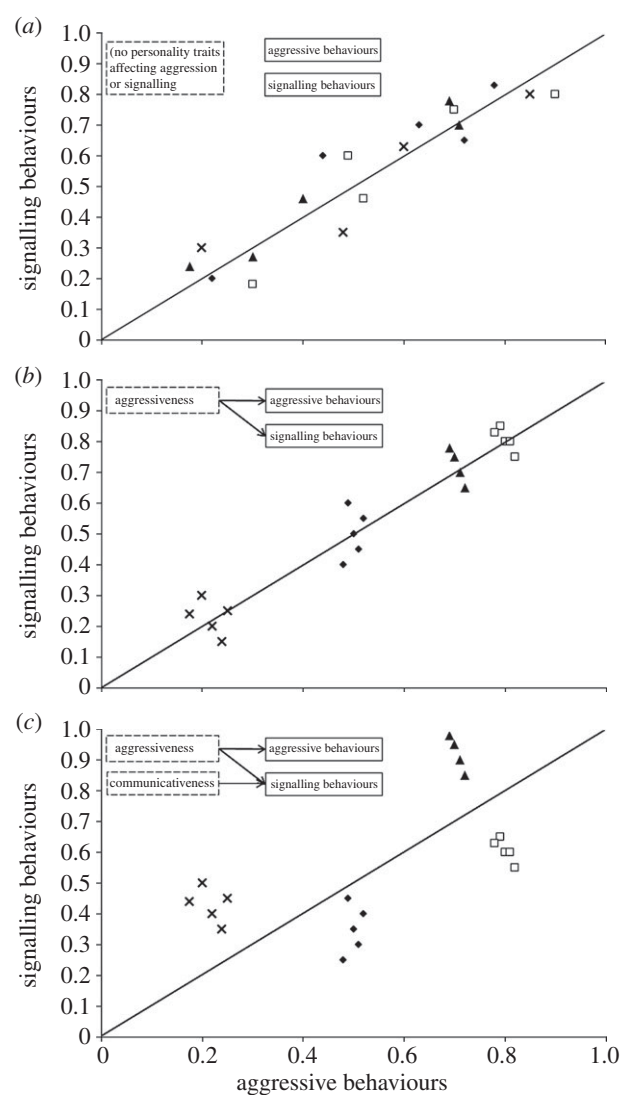
Figure 1. Three hypotheses on the relationship between personality traits (dashed boxes) and aggressive behaviours and signalling (solid boxes). The hypotheses are illustrated in the respective scatterplots of four hypothetical individuals marked by the different symbols. The diagonal line is $x = y$ and is meant to illustrate a hypothetical relationship between signalling and aggression. (a) Represents the null hypothesis that there is no personality trait influencing aggressive behaviour or signalling behaviours, although these two are correlated with each other (i.e. signalling is honest). (b) Represents the first alternative hypothesis where aggressive and signalling behaviours are influenced by a single personality trait, aggressiveness. In this hypothesis, residual variation in signalling behaviours once aggressive behaviours are taken into account is not individually consistent. (c) Represents the second alternative hypothesis where signalling levels are influenced not only by aggressiveness but also by a second personality trait which we term communicativeness. The presence of the second personality factor is inferred from whether the residual variation in signalling levels—once aggressiveness is controlled for—is repeatable.

residual signalling levels (lower than expected for their level of aggression), whereas other individuals would show consistently positive residual signalling levels (higher than expected levels of signalling for their aggression levels).

In this study, we used repeated playback experiments on the same males to assess the level of individual consistency in aggressive behaviour and aggressive signalling. We focused on the well-studied aggressive communication system of male song sparrows, and in particular on two signalling behaviours, soft songs and wing waves, which have been shown to reliably predict subsequent attack [22]. The repeated assays permit us to:

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(i) assess the stability of aggressive phenotypes over a long period; (ii) assess the reliability of an aggressive signalling system by taking into account individual consistency; and (iii) ask whether there are consistent individual differences in communicativeness, i.e. in a bird's tendency to signal at higher or lower intensity for a given aggression level.

2. Material and methods

(a) Subjects and stimuli

We tested 69 colour-banded male song sparrows holding territories in autumn 2009 and spring 2010 in Discovery Park, Seattle, WA, USA. We recorded each male's repertoire before the experiments using a solid-state recorder and a shot-gun microphone (Marantz PMD 660 and Sennheiser ME66/K6). For each male, we picked two of the bird's own songs from his repertoire (self-song) to be used as stimulus songs based on the quality of recording. Prior studies showed that song sparrows give the same behavioural responses to self-song and stranger song [30,31], and self-song has the additional benefit of being equally matchable by all of the subjects, thus avoiding individual differences in matching rates owing to similarity of a matching stranger song to the bird's own version.

We attempted to test each male five times: in autumn 2009 (September and October), and in winter and spring of 2010 (January, February and April), although sample sizes in each month varied owing to temporary or permanent disappearance of subjects. Fifty-eight subjects were tested at least twice (13 subjects were tested two times, 12 subjects three times, 19 subjects four times and 14 subjects five times) for a total of 219 trials. The average inter-test interval was 67 days (range: 20–214 days), the average interval between the first and last test was 174 days (range: 21–248 days). For each playback song, we created a 15 s wave file using SYRINX (www.syrinxpc.com, John Burt) that included the song (about 3 s) and a silent period (about 12 s), making for a playback rate of four songs per minute.

For 34 of the 69 subjects, we had information on their age because they were banded either as a nestling, in juvenile plumage before their first moult, or singing plastic song in their first autumn. The rest of the birds were banded in adult plumage and singing adult song, therefore we did not have precise age information on these birds. Age was defined by calendar year so that a hatch year bird would be considered 1 year old, a second-year bird would be considered 2 years old, etc. The mean age in 2009 was 3.71 years with a range of 2–7 years.

(b) Design and procedure

For playbacks, we used a Pignose speaker connected via a 20 m cable to an iPod Touch (Apple, Inc.), with the playback amplitude set to normal singing amplitude of song sparrows, approximately 80 dB SPL measured at 1 m with a Radio Shack 33–2055 sound metre. The playbacks were carried out in the approximate centre of the territory for each bird and each successive playback was done from the same location on the territory (with the exception of a few cases where the subject had moved significantly from the previous trial). Each trial lasted 10 min, with playback of one self-song type for the first 5 min and a switch to the second self-song type in the second 5 min. Two observers stood about 20 m from the speakers at different angles so as to be able to keep the subject in sight at all times. One of the observers recorded the entire trial using the same recording equipment as above, thus capturing both the vocal behaviour of the subject and a narrative of the subject's behaviours.

(c) Response measures

We distinguished between signalling and aggressive behaviours based on the definition of a signal by Otte [32]: 'signals are defined as behavioural, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms' (p. 738). Under this definition behaviours such as flying around the opponent and keeping a close distance, although potentially informative to an observer, do not constitute signalling as they have evolved not because of their signal value but because of the fact they are required for physically dealing with an intruder. Therefore, we defined the following behaviours as aggressive (non-signalling) behaviours: time spent within 5 m of the speaker, number of flights and closest approach to the playback speaker. It is important to note that although we did not have a taxidermic mount in this experiment, the above measures of aggression are a very reliable proxy of whether or not the bird will attack (see below and the electronic supplementary material).

We extracted the following signalling measures: number of soft songs, number of wing waves, number of song types the bird sang and whether or not the bird sang the same song type as the stimulus song (i.e. 'type matched'). Of these four signalling measures, the first two have been shown to reliably predict attack during simulated intrusions with a mount [22,27]. Type matching also has been shown to predict attack, but only in the context of a gradual escalation and not when the simulated intrusion starts from the territory centre [27]. We also recorded the number of broadcast ('loud') songs which are known not to correlate with aggression in song sparrows (or in most songbirds for that matter; review in [33]). Our analyses of signalling strategies therefore focused specifically on the known aggressive signals in song sparrows: soft songs and wing waves.

Twelve of the 69 subjects were tested an additional time in spring 2011, i.e. a year after the latest trials of the main experiment, using a taxidermic mount of a song sparrow in addition to the playback, as part of a separate experiment. Briefly, in the 2011 experiment, subjects were confronted with a playback sequence that started at the boundary of their territory followed by the revealing of a taxidermic mount along with playback at the centre of the territory for 15 min (or until attack). Attacks were defined as landing on or coming within 10 cm of the mount (for details of this experiment see [27]). We used these additional trials to determine: (i) how stable aggression is over this longer time period (more than a year), and (ii) whether our measures of aggressive behaviour did in fact predict attack (i.e. were valid measures of aggression).

(d) Data analyses

We converted each count of behaviour into rates by dividing these with duration of observation (measured from the subject's first flight or song response to the playback to the end of the trial). The rates of soft song and wing waves were highly correlated with each other and therefore we carried out a principal component analysis (PCA) on these two measures. The first component of the PCA (PC1) explained 68.3% of the variance and was taken as the signalling score. Similarly, the measures of aggressive behaviour (rates of flights, closest approach and proportion of time spent within 5 m) were also highly correlated with each other. The first component of the PCA on these measures explained 67.9% of the variance and was taken as the aggression score (see the coefficients in the electronic supplementary material, table S1). Both PCA analyses were carried out on all the trials ($n = 219$ trials).

Repeatability (the intraclass correlation coefficient) is the ratio of the between-subject variance to the sum of between- and within-subject variance [34,35]. We first calculated simple repeatabilities in R [36] using the 'rpt.aov' function in package rptR [35] for aggressive response scores, signalling scores and loud song rates, and 'rpt.poisGLMM.multi' function for number of types sung during the trial and number of song type matches (both count variables). For analyses on type matching, we only included trials where the subject sang at least one loud song ($n = 170$ trials).

To assess the repeatability of signalling scores while controlling for aggression scores, we took two parallel approaches. In

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the first approach, reported below, we regressed the signalling scores on aggression scores and took the standardized residuals from this regression [37]. We then calculated the repeatability of these residuals using the 'rpt.aov' function. In the second approach, reported in the electronic supplementary material, we ran a linear mixed model (LMM) to partition the variance in signalling scores and calculate the adjusted repeatability of signalling scores controlling for aggression scores as suggested by Nakagawa & Schielzeth [35]. Although the latter approach has the benefit of being more general, we believe the residual analysis is more transparent and therefore we report it in the main text and the LMM in the electronic supplementary material. The repeatability estimates from the two approaches were in good agreement (see Results).

We assessed the overall reliability of the signalling system focusing on the average aggression and signalling phenotypes of individuals. To that aim, we took the average of the aggression and signalling scores of each individual across all the instances the individual was tested, including only individuals that were tested at least in three trials ($n = 45$). We chose the three-trial minimum as a trade-off between getting a reliable estimate of the average scores and having an adequate overall sample size. This procedure gives us a single average score for an individual's aggressiveness and for his signalling level. Note that taking the average scores across several trials approximates the information that would be available to an opponent having repeated interactions with this individual, as would happen if they were neighbours. To ask whether signalling scores reliably predicted aggression scores, we then carried out a linear regression of the average aggression scores on the average signalling scores. We expected that the regression with average scores would yield a higher estimate of signal reliability (i.e. a high portion of variance in average aggression scores would be explained by average signalling scores). As a comparison, we also carried out linear regressions on aggression and signalling scores for samples of one randomly selected trial for each subject (using the same subset of subjects as above) for 10 000 iterations. We then compared the distribution of R^2 from these regressions to the R^2 from the average scores.

Finally, to address a point raised by a reviewer, we carried out additional analyses to answer the question whether individual differences in signalling and aggression scores can be mostly or solely attributed to age effect. These analyses were carried out on the subset of 34 males that we had age information about. Briefly, we carried out adjusted repeatability analyses with the LMM approach cited above to control for the effect of age in estimating repeatabilities. Because the results of these analyses closely replicate the findings with the entire dataset, we report them in the electronic supplementary material. All analyses were carried out in R, except the PCA analyses which were carried out in SPSS 14.0.

3. Results

We found that both aggression scores ($r = 0.48$, 95% CI: 0.35, 0.62, $p < 0.0001$, $n = 219$ trials, 69 subjects) and signalling scores ($r = 0.57$, 95% CI: 0.45, 0.70, $p < 0.0001$, $n = 219$ trials, 69 subjects) were significantly repeatable across seasons. So were rates of loud song ($r = 0.37$, 95% CI: 0.23, 0.51, $p < 0.001$ $n = 219$ trials, 69 subjects), number of song types ($r = 0.50$, 95% CI: 0.28, 0.64, $p < 0.001$ $n = 219$ trials, 69 subjects) and number of song type matches ($r = 0.18$, $p = 0.005$; the confidence intervals given by rptR were unreliable for type matches, $n = 170$ trials, 69 subjects).

The average aggression scores in 2009–2010 were predictive of attack in the mount trials carried out for 12 of these subjects in spring 2011. The subjects who attacked the mount ($n = 7$) had higher aggression scores than subjects who did not attack ($n = 5$) in spring 2011 trials; $t_{10} = 2.84$, $p = 0.017$
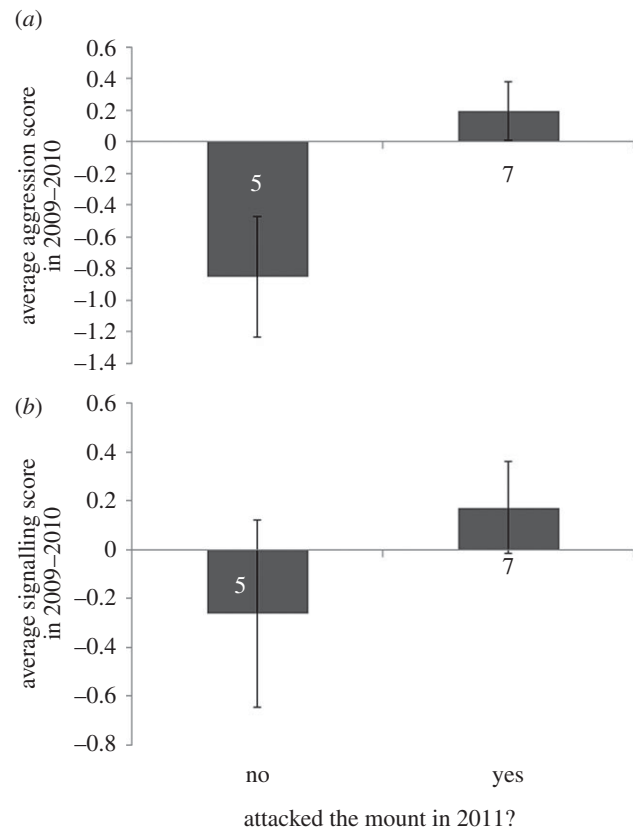
Figure 2. (a) Average aggression and (b) signalling scores in 2009–2010 of subjects that attacked the mount in an experiment in 2011 [27].

(figure 2a). Attackers also tended to have higher signalling scores than non-attackers in 2011 (figure 2b); $t_{10} = 1.93$, $p = 0.08$. These findings indicate that our measure of aggression is a valid predictor of actual aggression and is able to predict an attack in an experiment carried out a year later. Given the intervening time, this finding also indicates aggressiveness is highly stable over at least consecutive springs.

When average signalling scores were regressed onto average aggression scores for individuals that had at least three trials ($n = 45$ subjects), there was a strong positive relationship between these two ($\beta \pm$ s.e. $= 0.74 \pm 0.10$; $t_{43} = 7.58$, $p < 2 \times 10^{-09}$), with the model explaining 57.2% of variance (figure 3). In separate regression analyses carried out on single, randomly selected trials for each of these individuals, variance explained by signalling scores were on average 35.9% (s.d. $= 0.09$, 10 000 iterations). The R^2 from the average scores (57.2%) lies in the 99th percentile of this distribution of R^2.

Finally, using the entire dataset, we regressed the signalling scores on aggression scores and took the residuals of signalling scores ($\beta \pm$ s.e. $= 0.54 \pm 0.06$, $t_{217} = 9.47$, $p = 2 \times 10^{-16}$). The residuals of signalling scores were significantly repeatable ($r = 0.36$, 95% CI: 0.214, 0.51, $p < 0.00001$, $n = 219$ trials). We found a similar repeatability coefficient ($r = 0.44$) using the LMM approach (see the electronic supplementary material for details of this analysis). This last result indicates that residual variation in signalling behaviours is individually consistent after aggression levels are controlled.

4. Discussion

In this study, we examined the individual consistency of aggressive behaviour and signalling behaviour to identify the
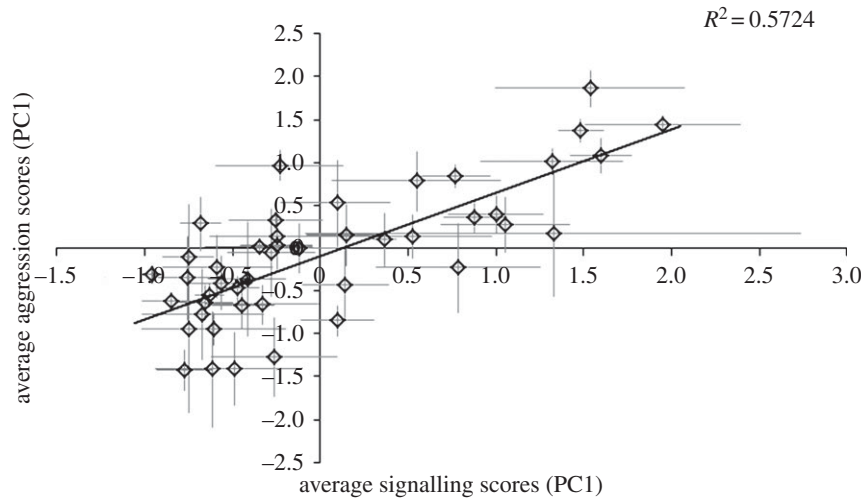
Figure 3. Average aggression and signalling scores of the 45 individuals with at least three trials. Each dot represents an individual and the error bars represent +1 s.e. Although the correlation between average signalling scores and average aggression scores is improved compared to when looking at single trials, there remains a significant portion of variance that is unexplained by this relationship. Individual differences in communicativeness seems to be responsible for at least part of this residual variation.

personality traits potentially underlying them. Our main findings are as follows. (i) Aggressive behaviour and aggressive signalling were each highly repeatable across individuals between autumn 2009 and spring 2010, and the average aggression and aggressive signalling scores of the birds are highly correlated. Furthermore, (ii) aggression scores in 2009–2010 predicted whether or not subjects attacked a taxidermic mount in spring 2011, suggesting that aggressiveness is a stable trait over at least a year. (iii) Aggressiveness was not the only individually consistent trait that determined signalling levels. In particular, individual differences in signalling levels were repeatable even after controlling for the aggression level of the individual, suggesting that a second personality trait besides aggressiveness may affect overall signalling levels. These individual differences were not due to different latencies to respond or the effect of age (see the electronic supplementary material).

(a) Flexibility versus constraint in expression of aggressive behaviour

We found that aggressive behaviours were individually consistent over at least a year. It is important to note that the high repeatability of aggression levels does not mean that expression of aggression is inflexible, especially given that here we tested aggression in a single context. Indeed, it is well known that animals recognize individual conspecifics [38] and respond with different aggression levels to different individuals, such as to neighbours versus strangers [39] or to aggressive versus non-aggressive neighbours [40–42]. Thus, expression of aggression is highly context dependent. Nonetheless, even in different contexts, aggression levels can be correlated within an individual. For instance, in a previous study we found that although the level of aggression directed at an aggressive, 'bad' neighbour was significantly higher than that directed towards a non-aggressive, 'good' neighbour, the aggression levels displayed by a particular individual towards the two neighbours were nevertheless correlated with each other [41]. Therefore, differences in aggressive personalities of individuals can be best described as individual differences in behavioural reaction norms [43,44].

(b) Individual differences in communicativeness and partial reliability

Although previous research has shown that some aggressive signals correlate with aggressive response, the correlation is usually imperfect, and some portion of the variance in aggressive signalling is typically left unexplained by aggression levels. Indeed, looking at only a single trial per subject, we were able to detect a significant relationship between signalling scores and aggression scores, with a mean of 35.9% of variance being explained by signalling scores. This percentage grew significantly to 57.2% when we took average signalling and aggression scores across at least three trials.

This finding can be viewed in two not mutually exclusive ways. In the 'glass half-full' view, our finding that reliability of signalling improves when looking at averages of multiple trials suggests that indeed some of the variance unexplained by signalling in most studies is probably owing to transient factors and does not necessarily mean the signalling system is unreliable. To some extent, assaying aggression repeatedly versus at a single point in time simulates two different but biologically meaningful scenarios: the repeated-trial assay approximates the information that would be available to an opponent after repeated interactions (e.g. between long-term neighbours), whereas the single-trial assay approximates the information that would be available to a first-time intruder. In nature, repeated interactions are likely to be more common, as detailed observational studies have shown [45,46]. During these interactions, opponents are likely to gather progressively more accurate information on one other, and so the reliability of signalling should become greater through repeated sampling.

Nonetheless, even when looking at the average scores across several trials, more than 40% of variance in aggression scores was left unexplained by signalling scores, i.e. aggressive signalling was only partially reliable (glass is half-empty). We found that this residual variance in signalling levels, once levels of aggressive behaviours were taken into account, was repeatable across individuals—individuals tended to signal consistently more or consistently less than expected given their typical level of aggressiveness. This finding is especially striking because signalling in this case involves behaviours

(soft songs and wing waves) that cost little to produce and which one might therefore expect to display a great amount of flexibility in expression. We suggest that these individually consistent signalling strategies may be owing to a personality trait that we term communicativeness. It remains to be seen whether individual differences in signalling strategies also drive signalling in contexts other than aggressive signalling or whether it correlates with other behaviours for example exploration, e.g. [6,8], so that it can be justifiably called a personality trait or a behavioural syndrome.

Individually consistent differences in signalling can, in principle, take two different forms in the aggressive context. First, an individual can overstate its aggressiveness, signalling at a higher level than expected based on the population mean. We refer to this as over-signalling following [47]. This form of signalling strategy is usually viewed as cheating or bluffing and poses a problem for the overall reliability of signalling. Indeed, most models of honest signalling deal with the question of how signal reliability can be evolutionarily stable when there is possibility of cheating.

The second possible form—signalling at a lower level than expected levels, under-signalling [27]—has received much less attention in the literature. Very few empirical studies have paid serious attention to possible empirical examples of under-signalling [27,47–49]. Most relevant are the findings of Searcy et al. [47] and our group [27] that under-signalling (in the form of birds that attack a taxidermic mount with little or no signalling prior to attack) is the more prevalent form of deviation from the population norm in song sparrows. Whether this reflects a general pattern or is unique to the signalling system of song sparrows remains to be seen. Nevertheless, the prevalence of under-signalling raises the question of how this signalling strategy can evolve.

Only a few previous studies, reviewed in [47], have considered a strategy of under-signalling and asked whether such a strategy can be adaptive. These models have found that such a strategy can invade an otherwise honest signalling system in some circumstances [50,51]. For instance, Johnstone & Morris [51] found that a strong individual displaying a small badge (i.e. under-signaller) could invade the population and thus render the badge signal unreliable, unless there was a cost associated with aggression independent of any contests.

More recently, Searcy et al. [47] proposed an adaptive model of under-signalling which suggests that the main benefit of aggressive signalling is realized when an aggressive interaction can be resolved without an actual fight that may incur a net cost on both parties. In this model, signalling is expected to have relatively little benefit for individuals who almost certainly would win the fight without significant risk of physical injury. If one then makes the additional assumption that there is an opportunity cost to signalling (such as not being able to mate guard, forage, etc.), then a high-quality individual who does not stand to lose much from a physical fight may be selected to forego signalling altogether. This 'opportunity-cost' model predicts that under-signalling should be positively correlated with the quality of signaller such that high-quality individuals are more likely to skip signalling before attacking.

In another recent model, Botero et al. [21] considered the possibility that some variance in signalling behaviour (in terms of both over- and under-signalling) may in fact reflect consistent individual differences in signalling codes, similar to what we have termed 'communicativeness'. In a series of simulation models, they found that when there are significant levels of errors in self-assessment of quality as well as in perception of signals, multiple signalling strategies can emerge with some individuals apparently under-signalling given their 'quality' while others are over-signalling. These consistent differences between individuals in how intensely they signal are analogous to our finding that individuals differ in terms of their communicativeness. In the Botero et al. model, however, under-signalling is not necessarily an adaptive strategy but rather arises from errors in production and perception of signals. Thus, unlike the opportunity-cost model above, this model predicts no relationship between under-signalling and signaller quality.

As mentioned above, the possibility of under-signalling as a limit to reliability has been noted only recently [27,47]. Therefore, further empirical work is needed to distinguish between these hypotheses about under-signalling, as well as to quantify the relative prevalence of under-signalling compared to over-signalling in aggressive communication in other systems.

In summary, we found that aggressive behaviour and signalling were both highly repeatable over a long period. We also found that males displayed individual differences in how intensely they signalled for their aggression level, with over- and under-signalling representing the extremes. The presence of such individual differences in communicativeness probably explains the fact that signalling is only partially reliable. Together, these results suggest interesting new avenues of research into the ecology and proximate mechanisms of aggression and aggressive signalling.

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