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Author for correspondence:
Andrew N. Radford
e-mail: andy.radford@bristol.ac.uk

After the fight: post-contest acoustic signalling

Andrew N. Radford, Amy Morris-Drake and Josh J. Arbon

School of Biological Sciences, University of Bristol, Bristol, UK

ANR, 0000-0001-5470-3463; AM-D, 0000-0003-4243-4651; JJA, 0000-0002-8509-4362

Animal contests often involve acoustic signals at different stages, but empirical work has primarily focused on usage before and during antagonistic interactions. Far less attention has been paid to post-contest acoustic signals (PCAS): those occurring after the outcome is decided. We begin by describing three main functions of PCAS—showcasing winning, minimizing costs of losing and repairing/affirming relationships—illustrating our ideas with taxonomically diverse examples involving resource defence and within-group social conflict. We also highlight additional contexts where PCAS are likely produced and how to test between different functions, providing specific predictions about acoustic characteristics, signaller behaviours and receiver responses. We then focus on the two signalling parties. First, we discuss environmental, social and contest factors that might drive interspecific and intraspecific variation in signaller production of PCAS. Second, we consider the varied types of information within PCAS, how their value can decay or accumulate, and how that affects their importance and reliability to receivers over different timeframes. We finish by suggesting future studies to expand our understanding of PCAS and how this, and manipulating PCAS, can provide deeper knowledge not just about contest consequences but also animal conflict, information use, communication, social interactions, behavioural flexibility and cognition more generally.

1. Introduction

Conflict is rife in the natural world and contests often involve considerable acoustic signalling. Animals come into conflict for myriad reasons, including food, mates, breeding sites, collective decisions and individual contributions to cooperative behaviours [1,2]. Conflict occurs between territorial rivals, among family members, and both within and between social groups [1,2]. A core component of many agonistic interactions (hereafter 'contests') is signalling. Signalling aids assessment and decision-making about retreat, individual levels of participation in contests and post-contest engagement with former protagonists, including in relation to mate choice, subsequent challenges, appeasement and consolation [3–5]. Contests and associated signalling are therefore widespread throughout the animal kingdom and pertain to many aspects of behaviour and life history. In numerous species across taxa, acoustic signals have evolved to aid these processes, though the core principles that we discuss here apply across sensory modalities. While an extensive body of empirical work exists on the use of acoustic signals *before* and *during* contests, far less attention has been paid to those occurring *after* contests have ended [6–8], leaving an important gap in our understanding of acoustic signalling and animal conflict.

Post-contest acoustic signals (PCAS) are likely to be important for several reasons and their function can be readily tested experimentally. Contests take time and energy, carry the risk of injury or death, and can disrupt social relationships [2,9,10], so post-contest signals that reduce these costs will

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have selection benefits [7]. Such signals can also have longer-term influences on social dynamics and social network structure [11,12]. Post-contest signals can therefore aid researchers in determining who has won and lost, in understanding contest consequences, and in assessing how protagonists and bystanders minimize costs and maximize benefits arising from contests. Acoustic signals may be particularly valuable as they are effective even when lines-of-sight are limited (e.g. at night, in dense vegetation, underground). Moreover, acoustic signals offer the opportunity for long-distance, multi-directional communication with many individuals; the audience size is often greater than with other sensory modalities [4]. Finally, the use of playback experiments is a well-established and logistically feasible method allowing testing of ideas relating to the use of and response to PCAS.

In this prospective review, we begin by describing three main functions of PCAS: showcasing winning, minimizing costs of losing and repairing/affirming relationships. We illustrate our ideas with empirical examples involving resource defence and within-group social conflict, as the most-commonly studied contest scenarios, from a broad range of taxa. We also highlight additional contexts where PCAS might be produced and what is needed to test between different potential functions, providing specific predictions relating to acoustic characteristics, associated signaller behaviours and receiver responses. We then focus on the two signalling parties in turn. First, we discuss interspecific and intraspecific variation in signal production, considering ecological and social factors, as well as the characteristics of individuals and contests themselves, that affect when and how PCAS are given. Second, we explain how PCAS contain information that can be used by receivers over different timeframes, how different pieces of information can decay at different rates and/or accumulate, and how that affects their value and reliability. We finish by suggesting how future studies could profitably expand our understanding of PCAS and how this, and manipulating PCAS as a powerful experimental tool, can provide deeper knowledge about contest consequences themselves, as well as animal conflict, information use, communication, social interactions (within and between species), behavioural flexibility and cognition more generally.

2. Functions of post-contest acoustic signalling

In principle, post-contest acoustic production could simply result from elevated arousal arising from a conflict situation. However, we will focus on potential adaptive explanations for PCAS. These functions are not necessarily mutually exclusive and a given post-contest signal may be directed at more than one audience [7,13].

(a) Showcasing winning

Acoustic signals are often produced specifically by winners of territorial and social contests. While there are anecdotal accounts of these ‘victory’ or ‘triumph’ displays from a range of birds, anurans and invertebrates (e.g. [14–16]), the best examples come from studies explicitly quantifying aspects of the signal or conducting experimental manipulations. For instance, staged contests between male mangrove crabs (*Perisesarma eumolpe*) resulted in stridulation (sound production by rubbing together body parts) only by winners and after fights had ceased [17]. Similarly, in two cricket species, *Teleogryllus oceanicus* and *Gryllus veletis*, winners produced more aggressive songs after staged contests than during them [18,19]. Following a territorial dispute, victorious male song sparrows (*Melospiza melodia*) exhibited increased song rates compared with losing males and non-competitors [7], while little blue penguins (*Eudyptula minor*) produced stereotyped displays with a vocal component after winning contests [20]. PCAS are not restricted to interactions between individuals: following simulated territorial intrusions, winning pairs of tropical boubous (*Laniarius aethiopicus*) sang particular duets, whereas losing pairs remained silent [21]. The boubou post-contest songs had unique characteristics—they were longer, had higher frequencies and involved more overlap of male and female notes [21]—suggesting a specific function, rather than simply a continuation of the same vocalization used during the contest. Although not yet demonstrated, we suggest that winners may produce PCAS in group-territorial species where three or more individuals combine their vocalizations into choruses when competing with rivals, as in lions (*Panthera leo*) and green woodhoopoes (*Phoeniculus purpureus*) [22,23].

Winners are suggested to advertise victory with post-contest signals for two main reasons (figure 1), both of which have been shown to be evolutionarily stable through mathematical modelling [24]. First, winning displays may decrease the likelihood of future conflict with the previous antagonist, by reinforcing the winner’s dominance and discouraging the loser (‘browbeating’ hypothesis [7]). Reducing the number of contests lessens the energetic cost, minimizes the injury risk and leaves more time for other activities (e.g. foraging and mating). It also lowers the mortality risk because contest participants are more vulnerable to predators through distraction [25]. Experimental support for the browbeating hypothesis was provided in *Teleogryllus oceanicus* field crickets, where surgical muting of winners prevented the reduction in subsequent fighting between male antagonists that occurred when post-contest acoustic communication was possible [19]. Likewise, following staged contests between mangrove crabs, losers were three times less likely to initiate another fight if the winner gave a stridulation victory display [13]. The second proposed function of winning displays is as a signal of quality or resource ownership to the wider network of potential mates and rivals, increasing perceived attractiveness to the former and decreasing the likelihood of attack by the latter (‘advertisement’ hypothesis [7]). This may be particularly important if there is a need to signal the outcome to those who have not witnessed the contest itself. In support of the advertisement hypothesis, male *Gryllus veletis* (another field cricket species) produced more PCAS—in the form of victory display behaviour—in the presence of a male audience (i.e. individuals who might be future competitors) compared with no audience or one composed of females [26]. A field experiment found that playback of contest winners, as opposed to losers, increased the stress level of rival male little blue penguins, but not that of their mates [27]. Moreover, male penguins were less likely to threaten winners than losers using vocal signals during

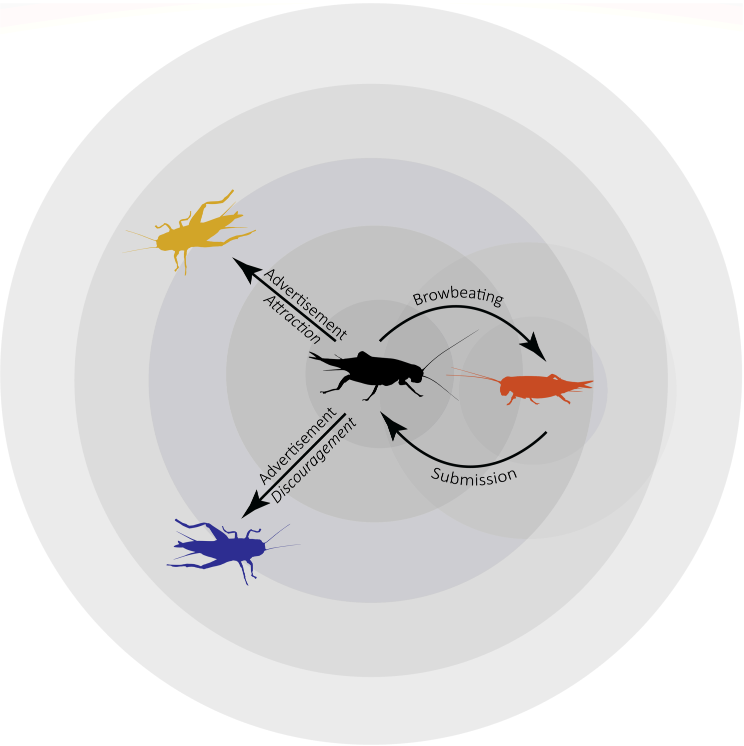

Figure 1. Winners and losers produce post-contest acoustic signals (PCAS) for a variety of reasons. Illustrated is a contest between two male Pacific field crickets (*Teleogryllus oceanicus*). Concentric rings represent the spread of information (i.e. active space) from PCAS produced by the winner (black individual) and the loser (orange individual), with acoustic attenuation in space. Each arrow links a signaller with a potential receiver and indicates the reason for targeting that audience. Losers may produce signals with acoustic features (e.g. higher frequency and lower amplitude) that restrict the likely audience to the other antagonist. By contrast, winners may produce signals with acoustic features (e.g. louder and lower-pitched) that broadcast information more widely, including to other potential male competitors (blue individual) and female mates (yellow individual).

a simulated challenge [27], providing evidence that victory displays modify the behaviour of audience members in favour of contest winners.

Further experimental work is needed to determine the reason for winning displays in many cases; the browbeating and advertisement hypotheses are not exhaustive nor mutually exclusive. Considering behaviour associated with the production of PCAS may prove useful: for example, displaying from higher perches may indicate an attempt to extend the range over which the signal is broadcast, and thus the likely audience size [21], supporting the advertisement hypothesis. Differences in acoustic characteristics of the signal might also be expected depending on the reason for production. For instance, winning vocalizations intended for a wider network might be louder, less modulated and overlap less with the natural background noise than those targeted at just the loser, as these acoustic characteristics enhance sound transmission [28]. Additionally, there is a theoretical suggestion that the intended audience of winning displays (i.e. losers versus bystanders) depends on the reproductive advantage of winning [24]. That is, when the reproductive advantage is high, as in species showing defence polygyny, then victory displays are likely more about intimidating former opponents [16] as there is a clear gain to dominating those individuals who might otherwise obtain matings at the winner's expense [24]. By contrast, when the reproductive advantage of winning is low, as in monogamous birds [21,27], victory displays should be targeted more towards bystanders than losers as there is little value in dominating a recent opponent [24]. Interspecific, phylogenetically controlled comparisons would be useful to test this idea, but there are currently data from insufficient species to generate an adequate sample size.

(b) Minimizing costs of losing

PCAS are also produced by contest losers, although there are fewer documented examples than those by winners. This difference in recorded prevalence is likely, in part, because the marginal cost of signalling is lower for winners than losers; winners are likely of higher quality than losers and thus can better afford to produce signals [29]. We know of only one empirical example of a losing display related to territorial behaviour: male black-capped chickadees (*Poecile atricapillus*) were more likely to produce a post-contest song if they lost a contest (as indicated by being pitch-matched) and if they were socially subordinate [30]. Examples of vocalizations by losers of within-group contests are more common, including gorilla (*Gorilla gorilla*) 'grumbling', rhesus macaque (*Macaca mulatta*) lip-smacking, chimpanzee (*Pan troglodytes*) pant-grunting, ring-tailed lemur (*Lemir catta*) yipping and dwarf mongoose (*Helogale parvula*) squealing [31–35]. But experimental investigation of the function of these signals in social species is still needed.

Contest losers may display in the aftermath for a variety of reasons. One potential function is to reduce the likelihood of further attacks, either by the previous opponent (figure 1) or others. Preventing further attacks is important both to minimize inherent contest costs and because losers are more likely to lose again due to winner-and-loser effects [36,37]. In some cases, the signal by losers could be one of submission: ritualized behaviours indicating acceptance of a contest loss, inducing a reduction in aggression from the victor, commonly occur both at the end of contests and in the aftermath [4,38]. As with many post-contest signals, these could include vocalizations or other acoustic displays such as the teeth chattering and belly slapping observed in primates [31]. Submissive signals are expected to be maximally different from those of aggression to minimize ambiguity [38]: submissive vocalizations are, for example, often higher-pitched and more tonal, whereas aggressive ones are low in frequency and broadband [4]. An alternative explanation to submission is that losers are signalling their continued motivation and that they are sufficiently strong to engage in further contests; this is the suggested reason for the post-contest song of losing black-capped chickadees [30]. The target audience would then be not just the recent opponent but also other group members (in the context of social conflict) or potential territorial rivals (when contests are about resource ownership). Moreover, in social species, losers of within-group contests often show aggression towards bystanders in the aftermath [39]. As well as reducing the physiological costs of a contest loss, this 'redirected' aggression may minimize the risk of further aggression from individuals that perceive them to be in a weakened state. Redirection can be a particularly noisy affair—such interactions disproportionately often include vocal elements compared with equivalent bouts at other times—which is likely to increase the audience size [39].

As with winning displays, a greater focus on the responses of receivers and the acoustic properties of signals will help to shed light on the intended audience and likely functions of those produced by losers. For instance, if the goal is to appease a recent antagonist but simultaneously minimize wider knowledge about a loss, signals of relatively high frequency, low amplitude and high modulation might be favoured [28]. Theoretical modelling has indicated that submissive signals should be more frequent when, for instance, there are limited opportunities for safe retreat by the loser, there can be relatively accurate estimation of the difference in resource-holding potential by the protagonists, and the costs of escalated fighting are greater [8]. These provide testable predictions for future empirical studies and comparative work, when sufficient data exist from different species. Finally, one generally overlooked potential function of low-amplitude vocalizations (e.g. those produced by some contest losers) is autocommunication or self-stimulation [40,41]. Call production may have a positive effect on an individual's endocrine system and/or act to soothe the signaller following a recent contest [41], but this needs testing in the context of PCAS.

(c) Repairing and affirming social relationships

In stable social groups, PCAS can aid friendly reunions ('reconciliation') between former opponents [11,42] (figure 2). Groupmates obtain a range of behavioural and fitness benefits from maintaining strong social bonds [43,44], so the breakdown of valuable relationships due to aggression has led to the evolution of post-contest reconciliation in many species, including chimpanzees, olive baboons (*Papio anubis*), spotted hyaenas (*Crocuta crocuta*), bottlenose dolphins (*Tursiops truncates*), wolves (*Canis lupus*) and ravens (*Corvus corax*) [42,45–49]. As well as reducing the likelihood of further attacks and associated anxiety (see also §2b), reconciliation can help to restore the opponents' relationship to pre-contest levels (reviewed in [9]). Social relationships within groups were traditionally considered to be maintained by physical interactions such as grooming and preening. However, vocalizations are effective at longer distances, can engage more than one partner at a time, are less time-consuming, carry less risk (as they can be produced away from the proximity of potential aggressors) and can occur simultaneously with other tasks [50]. Vocalizations have therefore been suggested as a means of 'grooming-at-a-distance' [50], and there is empirical evidence that they can function generally in this regard [51–53]. For example, ring-tailed lemurs vocally responded the most to playback of groupmates whom they frequently groom [52]. In bottlenose dolphins, whistle exchanges occur more frequently between core allies that spend less time together, by contrast to the physical bonding seen between those who are more often in close proximity [53]. PCAS might therefore act to strengthen or repair social bonds affected by conflict.

Acoustic signals aiding reconciliation can be produced by both winners and losers, either in conjunction with other affiliative behaviours [45,54,55] or alone [11,56]. For example, dominant female chacma baboons (*Papio cynocephalus ursinus*) grunt to their former (more subordinate) victims during post-contest reunions; after playback of grunts from an aggressor, victims approached them and tolerated their approaches more often than during control conditions [57]. By contrast, in Japanese macaques (*Macaca fuscata*) it is the losers of contests that are more likely to vocalize afterwards, likely in an attempt to restore their relationship with the aggressor [54]. Beyond the protagonists, close relatives of the aggressor can act as mediators, vocally reconciling with the victim on behalf of their relative (figure 2). For instance, when compared with hearing the playback of a control female, recently threatened wild chacma baboon females were more likely to tolerate the proximity of the original aggressor when they heard the friendly grunt of its relative, simulating kin-mediated vocal reconciliation [58]. Further research is required to assess the occurrence of vocal reconciliation in non-primate species, especially where within-group contests are common and friendly reunions have evolved to repair relationships (e.g. in ravens, bottlenose dolphins and spotted hyaenas [46,47,49]). There would also be value in considering additional social scenarios where vocal reconciliation might be important. For instance, vocal reconciliation following contests between territorial neighbours might be expected to facilitate the maintenance of dear-enemy relationships with familiar foes [59,60]. Moreover, where reconciliation occurs between species, such as following conflict in the mutualistic relationship between *Labriodes dimidiatus* cleaner wrasse and their clients [61], the role of acoustic signals offers a fruitful avenue for future research.

Beyond reconciliation, PCAS might serve other functions related to the maintenance of social relationships. For example, there is some evidence that bystanders may 'console' groupmates after involvement in a contest [62]. This consolation could be achieved through vocal communication as seen in Asian elephants (*Elephas maximus*) responding to group members in distress [63]. Alternatively, post-contest vocalizations may be used to solicit consolation (figure 2), as appears to be the case in bonobos (*Pan paniscus*) [55]; whimpering in dogs may also enhance the likelihood of receiving affiliative behaviour [64], though this remains to be tested explicitly. Another potential within-group function of PCAS is the reaffirmation of alliances: individuals

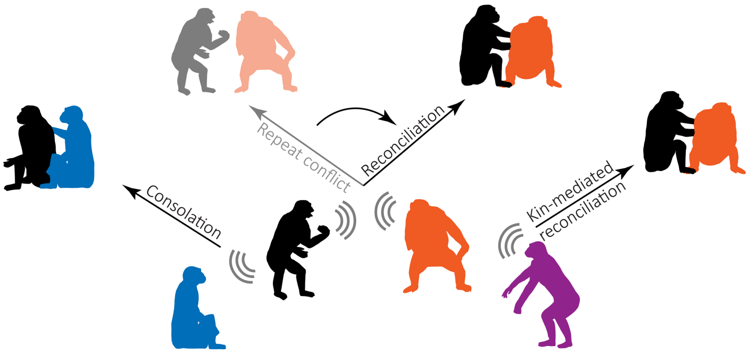

Figure 2. Post-contest acoustic signals can shape multiple future interactions within social groups. Illustrated is a contest between two bonobo (*Pan paniscus*) group members (black and orange individuals in the centre). Each arrow indicates an outcome of post-contest acoustic signalling. Clockwise from the top: preventing of repeat contests and promoting of reconciliation behaviour between the protagonists; promoting of reconciliation between protagonists by kin of the aggressor (purple individual); and soliciting of consolation from a bystander (blue individual) by a former protagonist.

who have combined forces in a contest may strengthen their mutual bonds, while non-participant allies might reaffirm strong bonds with a contest participant afterwards [65]. Finally, we propose that PCAS might be used in social species to mitigate the effects of conflict with out-group rivals; that is, outsider individuals or groups seeking reproductive opportunities, resources or territories [10,66]. Out-group threats and interactions with rivals can lead to subsequent increases in within-group affiliation, typically grooming, preening or other physical contact [67–70]. However, the use of acoustic signals could overcome the challenges associated with these physical interactions (see above), with vocal exchanges between groupmates functioning to reduce anxiety; responding vocally to the calls of particular individuals could also act as a reward for engagement in an out-group contest [10]. Detailed observations following naturally occurring out-group interactions (as in [71]) or the simulated presence of rivals (as in [67,70]) are needed to test this possible function of PCAS.

3. Signallers and receivers

As with all communication, PCAS entail transfer of information from signallers to receivers. In this section, we consider the process from the perspective of each party in turn, including the broader themes to which such signalling pertains.

(a) Signaller perspective: variation in post-contest acoustic signal production

As it is becoming clearer that PCAS are widespread, consideration can turn to variation in their use. Investigation of the individual, social and ecological factors that drive interspecific and intraspecific variation in signal production is a topic of wide interest among those studying communication and information use across sensory modalities. Interspecifically, the evolution of PCAS is most likely, and more intense displays are predicted, in species where contests regularly escalate to physical aggression [29]. For example, a comparison of four cricket species showed that winning displays of male competitors had more components in the two species with more aggressive contests compared to the two where contests were less fierce [72]. A similar prediction can be made in relation to PCAS used to promote reconciliation among groupmates: such signals are expected to be more prevalent following contests over valuable resources, which are likely to be more intense than those over less valuable resources. For instance, disagreements over food often occur in many species but the consequences may be small—the simple loss of a common food item or foraging position does little to damage the relationship between protagonists—thus, we would predict little need for post-contest reconciliation. By contrast, if a food source is only rarely available, such as is the case with fruiting trees [73], we would expect PCAS to be more prevalent.

The extent to which post-contest signalling behaviour is acoustic should depend, at least in part, on how likely it is that intended receivers are in sight. For example, if contests are themselves acoustic, occurring with the protagonists some distance apart, then post-contest signals are also likely to be acoustic. Acoustic signals would be expected in species living in habitats where it is difficult to convey information visually, such as dense forests. Similarly, acoustic information transfer should be more common in nocturnal species than those active in the day, although data are scarce because of the logistical difficulties of nighttime research. Acoustic signals should also be favoured when group members are widely scattered and non-protagonists are an important audience, as in the large foraging troops of some primates. All of these ideas need empirical testing. Additionally, social system is likely to affect the occurrence and prevalence of PCAS. In principle, acoustic signals—which do not require signallers and receivers to be in close proximity—should be favoured in species with greater variety in potential relationships and less predictability in contest outcomes, which result in more uncertainty between groupmates. For instance, we would predict that PCAS are more likely in more fluid societies, such as those exhibiting fission–fusion dynamics (especially those with despotic rather than egalitarian structures), compared with more rigid social structures such as fixed-group cooperative breeders. That is because there is less alignment of interests in the former, as well as less certainty in information on potential competitors.

In general, because acoustic signals tend to increase the spatial range of information transfer compared with other sensory modalities, they are more open to eavesdropping by both conspecifics and heterospecifics. Eavesdropping is increasingly recognized as a valuable way for animals to gather information in a variety of scenarios, including mating, foraging and predation, and it affects the occurrence, form and content of acoustic signals in non-contest contexts [74]. Much is also known about social eavesdropping on acoustic signals produced during animal contests: as one example, subsequent male fighting decisions and female mating decisions can be influenced by information overheard when songbirds compete vocally [75]. This in turn can exert selection pressure—if social eavesdropping carries costs for signallers, quieter and higher-pitched vocalizations that reduce sound transmission would be favoured. More widely, acoustic signals may be eavesdropped on by heterospecifics; some interspecific eavesdropping may carry no cost [76] but interception by predators and parasites, for example, can be to the detriment of signallers who become prey or hosts [28,74]. In such cases, there will be selection for a range of counter-adaptations, such as reduced calling or altered acoustic characteristics, to reduce the risk [41,77]. In the first instance, there need to be experimental studies testing how PCAS attract eavesdroppers and at what distances they can be detected, thus providing some indication of the audience size. Recent advances in higher-order network approaches that allow the modelling of non-dyadic systems [78]—systems such as broadcast communication networks—could then help to generate further testable predictions about the prevalence and characteristics of PCAS.

In species where PCAS have evolved, we would expect context-dependent variation in their use due to differences in external factors (e.g. seasonality and bystander audience), contest characteristics (e.g. intensity and duration), the protagonists' relationship (e.g. familiarity and value) and individual condition (e.g. nutritional state). To date, there has been relatively little work empirically testing these ideas, but we highlight some exceptions. In terms of external factors, the presence and type of bystanders affected the post-contest displays of *Gryllus veletis* field crickets: more victory displays were produced with a male audience compared with no audience [26]. Bonobo group members also appear to adjust their post-contest signalling flexibly depending on audience size and composition [55], although those signals are multi-modal so the importance of the vocal elements has not been isolated. There is often seasonal variation in the costs and benefits of contests within and between groups, relating to food availability or breeding period [79,80]. This might be expected to affect the use of PCAS too—for instance, if there is a greater need to avoid future contests when resources are scarce and so energy levels are lower—but, to the best of our knowledge, this has not been investigated. As with interspecific comparisons, post-contest signalling within a species is predicted to be more prevalent the longer and more intense the contest [29], although it could be argued that intense contests mean protagonists have little energy left for subsequent signalling. The empirical evidence to date supports the former hypothesis, as winning mangrove crabs that fought more intensely were more likely to produce stridulation signals afterwards [17], losing black-capped chickadees were more likely to display following highly aggressive interactions [30], and the production rate of PCAS by *Gryllus veletis* males was positively influenced by both the intensity and the duration of the contest [18]. The relationship between protagonists is also likely to influence post-contest behaviours. For instance, non-contact behaviours (such as acoustic signalling) are expected to be used more when the opponent is less familiar and thus less predictable, minimizing the chances of physical harm. Empirical support for this hypothesis comes from hamadryas baboons, mandrills and Japanese macaques [54,81,82]. These ideas have mostly been considered with respect to contests between individuals (e.g. mating rivals or group members). However, equivalent predictions could be made in species where territorial pairs and groups form relationships with and/or develop different levels of familiarity with rivals; for instance, with neighbours and strangers [60,83] or with groups from which current group members originated versus those with no prior connection [84]. Finally, the condition of the signaller is likely important; for example, dietary intake (whether particular nutrients or their balance) may well influence PCAS production and use [85], but empirical work is lacking.

(b) Receiver perspective: information use over different timeframes

PCAS can contain a variety of information that may be acted on by receivers over different timescales. Investigating how animals respond to individual signals, balance competing and complementary information, and assess honesty and reliability are all important for our understanding of cognitive abilities and social decision-making. One key piece of information in PCAS is the current state of the signaller. This information is likely to decay quickly in reliability as competitors return to a baseline physiological state or recoup the energetic costs of competing: for instance, shore crabs (*Carcinus maenas*) returned to baseline heartrate within an hour of a contest [86]. Moreover, winner-and-loser effects—where winners of recent contests are more likely to win subsequently, while losers are more likely to lose—can also be short-lived [36,37]. Thus, information about a recent contest often possesses a crucial temporal component and requires relatively rapid action. For example, it may pay to avoid an individual that has just won a contest as it will be in an elevated 'winner' state, although the protagonist might also be energetically compromised; animals need to balance the probability of these competing processes across short timescales. Responding to losing signals is likely more clear-cut: a recent loser might be both low in energy and in a depressed 'loser' state, indicating an ideal time to attempt to take advantage (figure 3). In social groups, individuals that are subordinate to losers may also use such signals to facilitate the avoidance of any potential redirected aggression; losers might seek to attack bystanders to pre-empt subsequent challenges from the former aggressor or other group members [39]. The need to respond soon after a contest will also be similar for individuals looking to provide consolation to recent antagonists [87], to maximize the benefits of consoling before other social partners intervene or those who competed return to baseline stress levels [88]. As PCAS likely reflect characteristics of the contest itself—for instance, more exaggerated victory signals following more intensive or prolonged contests (see §3a)—this additional information should affect the immediate behaviour of third parties (figure 3). For example, bystanders might be expected to engage protagonists who appear to have been involved in more costly contests, as their energetic reserves may be lower.

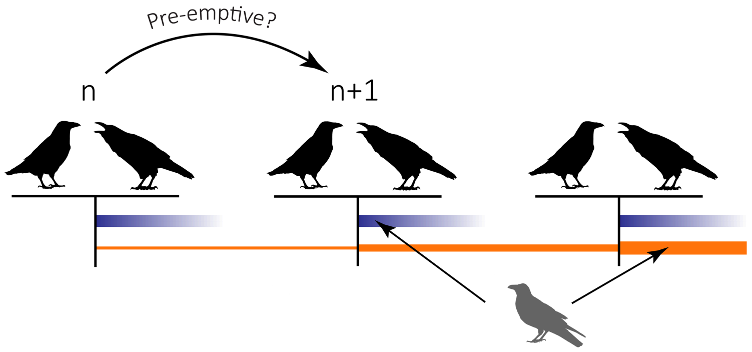

Figure 3. Post-contest acoustic signals (PCAS) can provide several pieces of information to receivers. Illustrated is a series of contests between the same two ravens (*Corvus corax*). In addition to learning which individual won or lost, bystanders (such as the grey individual) can gather rapidly decaying information about a competitor's state (indicated in blue). Moreover, they can obtain information that is more reliable over longer timescales and that can be accumulated across multiple contests (which may be separated by minutes, hours or days), such as the quality of specific individuals (indicated in orange) and their relationships to others (e.g. dominance rankings). Thickness of bars represents information quality, while colour intensity represents its reliability; arrows from bystander indicate the times that using the different types of information will be most adaptive. The arrow between contests n and $n + 1$ highlights how PCAS given after contest n can be considered pre-emptive signals given before contest $n + 1$.

Information provided after contests may not always be acted on immediately by receivers. This could be due to a lack of opportunity: subsequent interactions with signalling individuals may be hours or days in the future. For instance, animals integrating information from post-contest signals into mating decisions may have to wait until the cessation of a conflict period before they can act. In species with specific mating systems such as lekking or rutting, there can be inherent delays between the contests among potential mates and mating opportunities themselves [89,90], while information gathered outside of a breeding season will have to be carried forward to influence mating decisions. Similarly, contests over ephemeral resources might only occur sporadically: a raven attracted to a carcass by the sounds of conflict [91], for example, may have to wait until it finds itself at another carcass with the protagonists before it can make use of any gathered information about their dominance. Certain behaviours may also have specific diel cycles that affect when information about contests can be used to inform behavioural decisions. For instance, dwarf mongoose group members may engage in foraging disputes throughout the day, but it is at the sleeping burrow in the evening when vocal information about the contests translates into reduced grooming of aggressors [35]. Instead of a lack of immediate opportunity, a different reason for later use of information from PCAS is increased reliability. While state-based information from post-contest signals decays quickly, information about the dominance of winners and losers is likely more temporally stable [92] and therefore more reliably carried forward by receivers into future behaviour, including in subsequent contests (figure 3). Consistency in relationships between individuals (e.g. as characterized in dominance hierarchies [92]) can be used to generate indirect assessment of potential competitors through transitive inference, an ability demonstrated in various species such as pinyon jays (*Gymnorhinus cyanocephalus*), *Polistes dominula* and *Polistes metricus* paper wasps, and rhesus macaques [93–95]. Receivers can also integrate signals following multiple contests which increases the reliability of inferences [96]; the most recently acquired information is the most accurate and therefore would be expected to be weighted most heavily. Hearing the outcome of multiple contests could therefore be a low-risk way of maintaining knowledge about relationship with others, over extended timeframes, without paying the costs of participating or observing at close quarters. The different requirements to acquire, process and retain information from PCAS therefore provide an opportunity to investigate selection on social cognition within and between species, and the abilities that evolve to solve these social dilemmas.

The potential for responses to occur across different timeframes means that PCAS could be temporally multi-purpose. For example, a browbeating display may indicate to others both that the victor is in a winner state in the short term and that it is likely dominant in the longer term. Moreover, the same PCAS could have multiple receivers who use the signals over different timeframes. For instance, a contest loser may be suppressed from re-engaging with the victor in the short term, while the same signal could also prime the protagonists and their audience for subsequent contests. This highlights a more general conceptual point: contests rarely occur in isolation because the outcomes often feed forward to influence future interactions [37,92]. As demonstrated when victory signals decrease the likelihood of future challenges by rivals [13], signals given after contest 'n' can also be conceived as signals given in preparation for contest '$n + 1$' (figure 3). This potential for signals to be pre-emptive—produced in anticipation of future contests—blurs the lines of what constitutes pre- and post-contest and warrants future empirical and theoretical consideration.

4. Future research

Most simply, more experimental studies of PCAS are required in a broader range of contexts and species. To date, most empirical work has focused on contests over resources, such as those between territorial rivals or groupmates; broadening to include disputes over, for instance, cooperative contributions and collective decisions (e.g. [97]) would be beneficial. There are also taxonomic biases in the empirical evidence currently available. As one example, clear-cut cases of winning displays exist for various invertebrates and birds [7,17–21], but not for mammals, amphibians or fish. Moreover, most studies so far have focused on contests between two individuals. Given the prevalence of pair-bonded and group-living species in which there is duetting and chorusing in intergroup contests, or the potential for subsequent within-group vocal communication (even if contests are entirely physical) [22,23,98], this is likely a rich area for future research. Similarly, in many social species, individuals form alliances or coalitions which compete against other members of the same group [99,100]. Learning how multiple winners and losers from the same (polyadic) contest use PCAS will generate valuable insight into the dynamics of groups and coalitions, but careful experimentation is needed to allow clear identification of receivers and quantification of benefits to signallers.

Existing work on PCAS has revealed the need for experiments to resemble conditions found in the wild as closely as possible. While this is a general principle in animal behaviour research, the potential for PCAS to be influenced by both social and environmental factors highlights this more distinctly than in many cases. For instance, Bertram *et al*. [18] include a note of caution about their findings in spring field crickets because the research was conducted in small arenas [18]. That set-up prevented losers from moving away fully following a contest as they might in natural conditions, which could influence the use of PCAS. Similarly, wild individuals should preferentially be used in experiments: a subsequent study of PCAS in the same cricket species revealed that field-captured males were more responsive than laboratory-reared ones to the social environment [26]. Ultimately, increasing the number of studies on a broader range of contexts and species opens up interspecific, phylogenetically controlled comparisons as a means of answering questions such as those posed in Box 1.

Box 1. Example questions (with predictions in italics) about post-contest acoustic signals (PCAS) that could be answered with interspecific comparative work.

What factors drive the evolution of PCAS? *PCAS likely evolve in response to environmental conditions (e.g. more likely when competition is over scarce resources and other sensory modalities are less useful, such as at night or in dense vegetation). PCAS are likely also affected by social factors (e.g. where there is less certainty between individuals about the responses to conflict and when the risks from heterospecific eavesdroppers are low)*.
When should losers signal? *Losing and submissive signals should be more prevalent in species where safe retreat is difficult, accurate estimation of protagonist differences in resource-holding potential is feasible (e.g. in social species with regular interactions between the same individuals), and there are greater costs of escalated fighting (e.g. in animals with longer lifespans and dangerous weapons)*.
How do the acoustic characteristics of PCAS and associated behaviours differ depending on the intended receivers? *If the signal is meant primarily for the former antagonist, sounds should be of relatively high frequency, low amplitude and high modulation, and delivered from near the ground, to minimize the transmission distance; the opposite is true if the signal is intended for a broader network of receivers*.
Do PCAS systematically differ from acoustic signals given within contests? *If PCAS are simply the result of elevated anxiety, the same acoustic signal might be heard during and after a contest, whereas if PCAS have clear functional value, distinct signals should have evolved. Compared with during contests, when both protagonists likely use the same signalling, PCAS may be more diverse as winners and losers have different information to convey and potentially different audiences*.

Beyond expanding empirical work on the functions of PCAS and contextual variation in their use, more is needed on underlying theory and mechanism. Currently, the mathematical modelling of post-contests signals has focused just on victory displays, with separate models for browbeating and advertisement as the two main hypotheses [24,29,101], although there is some modelling of submissive signals given during contests [8]. For mathematical tractability, existing modelling has also been restricted to consideration of just three individuals, but there are often situations with many more participants or audience members. Other aspects of contest behaviour have received far more detailed theoretical attention ([102] provides a review of the last 50 years of such work), so there is both a clear foundation and scope for expansion. Similarly, there has been very little research on the mechanisms (for instance, hormonal or neural) that underpin post-contest signalling or how PCAS might help return contest-induced elevations in hormones (such as cortisol) to baseline levels before they become costly [38]. In a recent paper, Potegal [103] provides an overview of physiological processes and neural circuits that are important in the termination of aggression in non-human animals (as well as anger in humans) [103]. But they also emphasize that far more is currently known about the initiation and persistence of aggression than about its cessation. The tractability of PCAS, relative to other post-contest signalling and behaviours, offers a timely opportunity to close this gap through the integration of behavioural, hormonal and neuronal research.

In addition to increasing our understanding of post-contest signalling, playbacks of PCAS can be a powerful tool in expanding our knowledge about social behaviour and cognition more generally. For instance, they could be used to manipulate apparent contest outcomes and thus to investigate the perception of relationships both within and between groups, while reducing the potential stress that can be caused by simulating contests directly. Staggered playbacks of PCAS across one or more days would allow testing of how receivers integrate social information from different events. Recent field experiments have demonstrated that animals can, for example, monitor multiple actions of groupmates from vocal cues—tracking cooperative contributions as well as conflict involvement—and alter subsequent behaviour towards specific individuals depending on a perception of their cumulative earlier behaviours [35,104]. Investigating how long different pieces of information are retained and how they are weighted depending on recency would generate insight into cognitive processes and capacity across species.

There is also a growing appreciation that vocalizations play a crucial role in the social network structure of many species; Xie *et al*. [105] found 14 papers that have investigated interactions between social dynamics and vocal networks, and 12 of these were published in the last decade [105]. However, to understand specifically how vocalizations can underpin relationships requires experimental manipulation in addition to the building of networks based on natural exchanges. New wearable tag technologies allow the simultaneous recording of movements and vocalizations, with the possibility to fit them to all members of the same group and thus continuously monitor social and vocal interactions [106]. Additionally, while most research on social networks focuses on within-group interactions, there is an increasing awareness that those between a broader range of conspecifics can be important. For instance, recent work has shown that third-party observers may gather information during intergroup contests [107], and that interactions between groups may not always be conflict-driven but can have cooperative elements too [108]. PCAS provide a tractable way of expanding our understanding of what drives the dynamics of these out-group social networks. Finally, many contests are ritualized [2] but relatively little is known about how animals might learn to give the correct signals related to these contests. Much like gestures in primates [109], acoustic signals could be culturally inherited. This is true of signals at all stages of the process—before, during and after—so PCAS offer the opportunity for broader knowledge development about the role of social learning in contest signalling.

5. Conclusion

Conflict pervades all aspects of animal life, including our own; as with any social behaviour, communication is a key aspect of contests. Our goal with this review is to stimulate a greater interest in the acoustic signals that occur after contests have finished, and thus gain a fuller understanding of conflict behaviour, social interactions, information use, communication, group dynamics and cognition. Doing so might also help us to understand human post-contest behaviour; for instance, victory displays include sporting laps of honour to military parades [110], as well as signals of pride and shame [111]. While acoustic communication has long been a topic of wide research interest, we argue that there would be great value in deeper consideration not just of signals given before and during contests but those in the aftermath too.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.N.R.: conceptualization, funding acquisition, project administration, writing—original draft, writing—review and editing; A.M.-D.: writing—original draft, writing—review and editing; J.J.A.: conceptualization, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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