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Reviewed work(s):
Source: *Behaviour*, Vol. 74, No. 3/4 (1980), pp. 284-293
Published by: BRILL
Stable URL: http://www.jstor.org/stable/4534064

COMMUNICATION BY AGONISTIC DISPLAYS: A DISCUSSION

by

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(Acc. 10-III-1980)

THE PROBLEM

In an earlier issue of this journal CARYL (1979) posed the question: "Is information about the probability of attack an important component of the message conveyed by an aggressive display?" (pg. 136). He discussed the predictions of the "War of Attrition" model (MAYNARD SMITH, 1974), comprising that information about the probability of attack should be concealed. He further re-analysed the data published in a number of papers (STOKES, 1962a, b; DUNHAM, 1966; ANDERSSON, 1976). These papers were originally presented as evidence for the traditional ethological view: threat displays have been evolved to serve communication about intentions (*e.g.*, MOYNIHAN, 1955; CULLEN, 1966; SMITH, 1977). Nevertheless CARYL concluded that in none of these cases communication about attack readiness could be proved. In two cases (blue tit: STOKES, 1962a; great skua: ANDERSSON, 1976) information about the escape probability appeared to be conveyed. The "War of Attrition" model, however, predicts neither transfer of information about attack, nor about escape. The finding that information about escape was transferred, and a few other peculiarities in the data compelled CARYL to be careful in his interpretation. He emphasized the explanatory power of the "War of Attrition" model, and considered it as a good, but not necessarily the best, model for explaining behavioural data (pg. 166).

The previous paper in this issue (BOSSEMA & BURGLER, 1980) clearly shows that in captive jays information about the probability of attack is conveyed by subtle actions. For this case the "War of Attrition" model is certainly not fitting. One might therefore wonder to what extent BOSSEMA

1) I would like to thank Professor G. P. BAERENDS, Dr I. BOSSEMA, Miss M. K. CARLSTEAD, Dr P. G. CARYL, Professor J. P. KRUIJT, Mr J. SCHILSTRA and Mr R. VODEGEL for their comments, Mrs H. LOCHORN-HULSEBOS for typing the manuscript, and Mrs G. BAEYENS for correcting the French résumé.

& BURGLER's material differs from that investigated by CARYL. I want to consider three possible sources for these opposite results:

1. the jays made use of individual recognition in the settlement of conflicts, while the animals in the work cited by CARYL possible did not,
2. BOSSEMA and BURGLER only considered subtle actions, while the other authors mainly considered elaborate and, at least for the human observer, conspicuous action patterns, and
3. BOSSEMA and BURGLER used different methods for measuring the probability of attack than the other authors.

In this paper I further want to discuss two topics which are of current interest as a consequence of the application of game-theory to the evolution of fighting behaviour (MAYNARD SMITH & PRICE, 1973; MAYNARD SMITH, 1974; PARKER, 1974; MAYNARD SMITH & PARKER, 1976; DAWKINS & KREBS, 1978; MAYNARD SMITH, 1979):

1. bluff, exaggeration of features which are used by opponents to estimate the potential danger by the bearer of these features, and
2. graded signals, indicating different levels of the attack readiness of the performer of these signals.

It is probable that individual recognition influenced the evolution of bluff and graded signals in a way which has (until now) hardly been considered in the game-theory models. BOSSEMA and BURGLER's data will be of great help in developing ideas about how "bluffers" may be selected against, and how "graded signals" may evolve.

INDIVIDUAL RECOGNITION

The jays in BOSSEMA and BURGLER's experiments certainly knew their group members personally. VAN RHIJN & VODEGEL (in press) showed that, if individual recognition is involved, it would be a good strategy (under certain conditions) to exchange honest information about the readiness to attack. It might therefore be suggested that CARYL (1979) did not find this exchange of information, because the animals he referred to did not recognize their opponents individually. I want to consider this suggestion by a careful examination of the papers cited by CARYL.

STOKES (1962a, b) studied the interactions between titmice at a winter feeding station. It has been shown (BRIAN, 1949; DRENT, in prep.) that at feeding stations stable dominance hierarchies exist in tits. In view of the large amount of evidence provided by the latter authors, it is likely that these hierarchies are based on individual recognition.

DUNHAM (1966) made his observations on six hand-reared grosbeaks, kept together in a group. Unfortunately he gave no information about individual behaviour. I would expect clear differences in behaviour between the six group members. Under DUNHAM's conditions I presume perfect individual recognition.

ANDERSSON (1976) analysed the behaviour of skuas in a club. PERDECK (1960, p. 133) remarks that in this species a "club is not a haphazard gathering of birds". In the central part of the club PERDECK observed many birds close together. The individuals were not very aggressive in this central part, and not attached to a distinct spatial position. In the peripheral part (obviously where ANDERSSON collected most of his data) the birds were highly aggressive and defended temporary club-territories. The territory-holders often attacked intruders. To me it is not very clear how frequently neighbouring territory-owners attacked each other, but it seems to be likely that an individual has a large number of aggressive encounters with each of a few neighbours, and perhaps only a few encounters with each of the intruders (perhaps many individuals). So, it is certainly possible that the skua uses information about earlier conflicts with the same opponent. At any rate, ANDERSSON (pers. comm.) has the strong impression that his animals made use of individual recognition in the settlement of conflicts.

Summarizing, the suggestion that CARYL did not find an exchange of information about attack readiness because the animals did not recognize their opponents individually can be repudiated.

SUBTLE ACTIONS AND ELABORATE ACTION PATTERNS

The dominant communicators in BOSSEMA & BURGLER's experiments mostly performed only a very subtle action (monocular or binocular looking at a long or a short distance). CARYL's paper mainly concerns elaborate and conspicuous action patterns (often called: "ritualized displays"), on which most ideas about communication about aggressiveness were based (*e.g.*, MOYNIHAN, 1955; BLURTON JONES, 1968; GALUSHA & STOUT, 1977).

VAN RHIJN & VODEGEL's (in press) simulations demonstrated that, if individual recognition is important, an animal should (under certain conditions) give a warning before attacking a known opponent. They did not differentiate between simple gestures and elaborate action patterns as warnings. It is easy to see, however, that the only demand made upon a warning is that it is likely to be understood by the opponent. One might therefore expect that, if the intentions of an animal can be conveyed by simple gestures, natural selection will work against the development of elaborate (energy consuming) action patterns as warnings. This implies that CARYL could be right in his suggestion that "information about the probability of attack" is *not* "an important component of the message conveyed by an aggressive *display*" (CARYL used the word "display" here in the sense of elaborate action pattern). In fact the use of the term "aggressive display" is reprehensible in this context. It indicates that information about intentions *is* displayed.

A considerable part of the information conveyed by elaborate action patterns during conflicts seems to concern the quality of each of the contestants. MAYNARD SMITH (1979) makes a clear distinction between information about intentions (or motivation), and information about the "resource-holding potential" or "RHP" (strength, size, ownership, *etc.*: PARKER, 1974). He claims that during contests mainly information about RHP is transferred, because it affects the outcome of an escalated contest (while intentions can easily be exaggerated). I expect that information about intentions will be transferred if there is a clear asymmetry between both contestants (and if this asymmetry is known to them), and if liars about intentions can be detected. On the other hand, information about RHP will be transferred if a possible asymmetry is not yet known to both contestants. In these cases the animals have to evaluate each other's RHP before risking a dangerous fight with a — perhaps — stronger opponent. There are several examples of elaborate action patterns containing information about strength. It seems to be impossible to exaggerate this information, because the strength of the performer is a causal factor for the pitch, the form, or the duration of that display (DAVIES & HALLIDAY, 1978; CLUTTON-BROCK & ALBON, 1979; VAN RHIJN, in prep.).

Symmetric contests are very rare. In many cases, however, existing asymmetries are partly or wholly unknown to the contestants. One might therefore expect that in many aggressive conflicts both information about RHP and information about intentions is transferred. One might even imagine that many signals used in aggressive situations contain both kinds of information. This idea is supported by the fact there is no sharp boundary between subtle actions and elaborate action patterns: the distinction is artificial. Consequently I presume that, if liars about intentions can be detected, even elaborate action patterns may contain some information about the intentions of the performer. This presumption is not in accordance with the results of CARYL's re-analysis.

METHODS FOR MEASURING THE ATTACK READINESS

BOSSEMA and BURGLER's paper demonstrates that it is possible to consider "standard situations" under (semi)natural conditions. The "standard" is the reaction of the opponent. For each "standard" BOSSEMA and BURGLER determined to what extent the different actions were followed by attack. Although the absolute measures for the attack readiness differed strongly in the different "standard situations", the measure for the different actions relative to each other were similar to a great extent.

The methods used in the papers cited by CARYL are certainly less powerful. In all papers the measurement of information about attack and escape was based on the probabilities that the different displays of the actor were followed by attack or escape by the actor, irrespective of the behaviour of the reactor. In both BOSSEMA and BURGLER's and my opinion this procedure is incorrect. I shall illustrate this with an example. Suppose that a given display of a dominant animal is always followed by attack if the subordinate does not retreat within a short period. Consequently, during the display of the actor, the probability of the reactor retreating is high, and thus, after the display the probability of attack by the actor is low. If this last probability would be used as a measure for information about attack, the conclusions could be completely wrong.

CARYL also considers this possibility, and argues that in that case there would be an inverted U-shaped relationship between the observed probability of attack and the actual level of the readiness to attack. I doubt whether some kind of relationship can be assumed between these variables. For instance, one might also imagine that during a display indicating a very high level of readiness to attack, an opponent will often have no time to retreat before the actor starts its attack. CARYL further argues that if the probability to attack is influenced by the opponent's behaviour, one should expect more attacks towards a stuffed opponent, which can not retreat, than towards a live one. He quotes BLURTON JONES (1968) to show that this is not the case for the great tit. CARYL concluded from this that the probability of attack is not influenced by the opponent's behaviour. On the other hand BLURTON JONES shows that there is an influence of the opponent because the transition probabilities differ between situations with a stuffed opponent and with a live one. Furthermore, I doubt whether CARYL's expectation (more attacks towards a stuffed opponent) is valid, since the stimulus characteristics of a stuffed opponent are certainly not equal to those of a live one. I feel confident that Caryl underestimates the influence of the reactor's behaviour on the probability to attack of the actor. Consequently, the fact that he failed to find communication about the attack readiness could be attributed to defective methods in the original papers.

ON BLUFF

The behaviour of the jays in BOSSEMA and BURGLER's experiments is best comparable to the "Threat-dominance" strategy proposed by VAN RHIJN & VODEGEL (in press). In short, this strategy implies that in confrontations the dominant individuals always warn and subsequently attack if the subordinates do not retreat, and that the subordinates mostly retreat, but occasionally perform behaviour like dominants. In agreement with this strategy were the facts (BOSSEMA, pers. comm.) that (1) attacks were — in the majority of the cases — preceded by a warning, and (2) subordinate individuals sometimes provoked attacks of dominants. The following features, occurring in the behaviour of the jays, were not taken into account in the description of the "Threat-dominance" strategy: (1) pursuits by dominants rarely continued for a long period and seldom led to injuries (not to mention serious injuries), and (2) subordinates never attacked a dominant individual. It becomes clear, that the strategies used in the simulations (VAN RHIJN & VODEGEL) are simplifications of many real strategies.

One might wonder why the jays spent a considerable amount of time and energy in these short lasting, not very dangerous pursuits. In the situations considered by VAN RHIJN and VODEGEL the "Threat-dominance" strategy never appeared to be the most successful. They, however, did not believe that it was a nonsense strategy. They were convinced that if the strength of an individual is not constant over time, a situation which they did not consider, and if the dominance hierarchy can be adapted in the course of time, the "Threat-dominance" strategy must be the most successful under certain conditions. In the jays, however, the dominance hierarchy is very stable. It is difficult to see that the animals would spend such a large investment for extremely rare changes. I therefore think that there is a second factor (which may even be more important than the previous one), namely the testing of the honesty of the signals of the opponent. VAN RHIJN and VODEGEL asserted that, if individual recognition plays a role, bluff can hardly evolve, because bluffers shall mostly be recognized. They did not indicate in detail by what mechanism bluffers would be recognized. I presume that a modified "Threat-dominance" strategy (with short provocations of submissives, which seldom led to injury, and no real attacks of subordinates against dominants) offers an excellent mechanism to prevent bluff about intentions (in situations with stable dominance orders). To prevent bluff about RHP during the settlement of the dominance hierarchy, a similar strategy (with longer retaliations and infrequent attacks against animals which seemed to be dominant in earlier conflicts) might be the most effective.

GRADED SIGNALS

BOSSEMA and BURGLER distinguished four different threat categories by the dominant: monocular or binocular looking at a long or a short distance. These categories were clearly associated with different levels of the attack readiness, and may thus be treated in an analogous way as graded signals. It may be questioned why a dominant individual uses threat categories indicating different levels of attack-readiness in order to intimidate subordinates. It could be argued that a dominant should be successful after any signal indicating its interest in a resource which is (or could be) exploited by a subordinate. The phenomenon of "graded signals" also posed a problem to DAWKINS & KREBS (1978).

VAN RHIJN and VODEGEL did not consider the possibility of graded signals. On the basis of their simulations, however, it is not very difficult to see that there may be a successful strategy in which different warnings with increasing strengths are given before a real attack occurs. In cases with perfect knowledge about strengths VAN RHIJN and VODEGEL made plausible that the superiority of the "Threat-right" strategy (attacks preceded by a warning, only from dominants towards subordinates) over the "Attack-right" strategy (a similar strategy, but without a warning before attacking) was due to differences in the costs of a warning and an attack. It must therefore be possible to demonstrate that, in certain conflicts, it would be adaptive for a dominant to signal first with a warning costing almost nothing, then, if the submissive does not react in the desired way, signal with a warning costing a little bit more, etcetera, before performing a real attack with the highest cost. There are indications (BOSSEMA, pers. comm.) that this phenomenon occurs in the jays.

Graded signals could also be important in the weighing of interests (for a given resource) of different animals against each other. The individual with the greatest interest can be expected to be prepared to invest more than another individual in a contest with the resource concerned at a stake. A contest may therefore easily be settled without escalation in favour of the animal which signalled with a higher intensity than its opponent. However, there must be a mechanism preventing an animal signalling with an intensity which is more than a reflection of its actual interests. It has been discussed already in the previous section how bluff can be opposed by means of individual recognition and regular testing of the opponents. In that situation, however, opponents also have knowledge about each other's strengths, being another predictor for the outcome of an escalated fight. One might therefore imagine that in groups of animals in which the individuals know each other (and each other's strengths), conflicts are settled by means of a process of heterogeneous summation of the strength-difference (known to the individuals) and the interest-difference (indicated by the signals). This process is analogous to the processes involved in the summation of different characteristics of the same stimulus situation (*e.g.,* DAWKINS, 1969; BAERENDS & KRUIJT, 1973), and in the summation of motivational factors and external factors (*e.g.*, BAERENDS, BROUWER & WATERBOLK, 1955). In the jays there are only slight indications for the hypothesis that graded signals play a role in a process of heterogeneous summation. One indication is that submissive individuals take greater risks if the dominant individual signals only weakly. In these cases they might more often succeed in stealing food from a dominant. However, there are not yet indications that submissive jays try to supplant dominant individuals if the interests are strongly different (BOSSEMA, pers. comm.). Nevertheless, I presume that this phenomenon does occur in many vertebrate species.

SUMMARY

This paper discussed the information content of threat signals. It was an attempt to explain the inconsistencies between the points of view of model-builders using game theory as a tool (represented in a paper by CARYL in 1979 in this journal), and of the (mainly field-) ethologists spending a considerable part of their time observing animals in groups (expressed for instance in the paper by BOSSEMA & BURGLER in this issue).

Arguments were presented for the transfer by threat signals of both information about intentions (motivation), and information about "resource-holding potential" (strength, ownership, *etc.*). Individual recognition was expected to be associated with honest signals about intentions. CARYL's deviating findings could not be attributed to an absence of individual recognition in the animals he considered. His findings could also not be explained very well by the fact that he hardly considered subtle signals, although the present paper argued that information about intentions is mainly given by subtle signals, and information about resource-holding potential by elaborate action patterns. Imperfect methods in the papers cited by CARYL were considered as the most important source for the deviations.

Finally it has been discussed to what extent observational data as presented by BOSSEMA and BURGLER help in solving problems raised by the model-builders. The occurrence of frequent, short escalations has been suggested as a mechanism for preventing bluff. The evolution of graded warning-signals could be related to (1) the low cost of a warning as

compared to an attack, and (2) the settlement of a conflict on the basis of differing motivations. This paper considered the possibility of heterogeneous summation of (already known) information about the resource-holding potential of an opponent, and the information about its intentions (from the displays).

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RÉSUMÉ

Cet article discute le contenu d'information des signaux menaçants. Il essaie d'analyser les inconsistences entre les constructeurs de modèles, faisant usage de la théorie des jeux (représenté par CARYL en 1979 dans ce même périodique), et les éthologistes (travaillant principalement sur le terrain) consacrant beaucoup de temps à observer des animaux en groupes (par example exprimé dans l'article par BOSSEMA & BURGLER dans cette livraison-ci).

On a raisonné que les signaux de menace transfèrent de l'information concernant les intentions (motivation) et le pouvoir de maintenir des resources ("resource holding potential": la force, la possession *etc.*). La reconnaissance individuelle était supposée d'être associée avec des signaux honnêtes concernant les intentions. Les résultats déviants de CARYL ne pouvaient pas être attribués à l'absence de la reconnaissance individuelle entre les animaux qu'il a considéré. Aussi, ses résultats ne peuvent pas totalement être expliqués par la négligence de signaux subtils, quoique cet article-ci a argumenté que l'information concernant les intentions est transferée principalement par des signaux subtils tandis que l'information concernant la puissance de maintien de ressources se fait par des signaux élaborés. On a argumenté que l'origine principale des déviations se trouve dans les méthodes défectueuses dans les articles cités par CARYL.

Enfin, on a discuté la mesure dans laquelle les données d'observations, comme présentées par BOSSEMA et BURGLER, contribuent à la solution des problèmes posés par les constructeurs de modèles. Le phénomène des combats courts mais fréquents est suggéré comme étant le mécanisme pour empêcher d'être trompé. L'évolution des signaux menaçants d'intensités différentes est relatée (1) aux dépenses basses d'un advertissement en comparaison avec elles d'un assaut, et (2) au règlement d'un conflit selon les motivations différentes. Cet article a considéré un addition hétérogène, notament de l'information concernant la puissance de maintien de ressources (étant connu par l'adversaire), et de l'information concernant les intention (se rélévant par l'intensité du signal).