REVIEW/SYNTHÈSE

Threat display in birds

Peter L. Hurd and Magnus Enquist

Abstract: The study of threat displays has long been an area in which theory and empirical work have each spurred the other forward. Communication is currently the focus of great interest and effort on the part of modellers. A great deal that classical ethologists have accurately described about threat displays still lacks adequate explanation. Here we review the empirical literature on the use of threat displays by birds competing for small valued resources, both to refocus theoretical attention upon the key characteristics of threat and to assess the degree to which current theory explains these characteristics. We aim to demonstrate that threat displays communicate information about aggressive motivation, but are not handicaps. Handicap models predict a single graded display, while the vast majority of studies report repertoires of about four to six discrete threats for any given species. These displays vary with motivational and strategic considerations, and may be demonstrated to rank consistently on a scale of willingness to escalate, thus providing information about aggressive motivation. We conclude by identifying those features of avian threat displays that have not been adequately explained, in the hope that this reexamination of empirical data will help focus theoretical attention on these issues.

Résumé : L’étude des comportements de menace est un domaine où la théorie et les travaux empiriques se sont toujours éperonnés mutuellement. Pour les modélisateurs, la communication est un sujet de choix qui a suscité de leur part de nombreux travaux. Beaucoup des descriptions détaillées des comportements menaçants par des éthologistes classiques nécessitent toujours des explications satisfaisantes. Nous procédons ici à une révision des données empiriques de la littérature sur le rôle des comportements menaçants utilisés par les oiseaux lorsqu’ils se font compétition pour des ressources limitées mais qui leur sont précieuses, à la fois pour réorienter l’attention vers les caractéristiques importantes des comportements de menace et pour évaluer à quel point les théories actuelles expliquent ces caractéristiques. Nous voulons démontrer que ces comportements transmettent de l’information sur la motivation de l’agressivité, mais qu’ils ne constituent pas des handicaps. Les modèles de handicap prédisent un comportement en une seule phase graduée, alors que la majorité des travaux de recherche décrivent, pour toute espèce donnée, des répertoires de quatre à six comportements distincts. Ces comportements varient selon des considérations de stratégie et de motivation et on peut démontrer qu’ils sont toujours ordonnés en fonction de la volonté de les mener à bout, ce qui transmet de l’information sur la motivation qui sous-tend l’agressivité. En terminant, nous identifions les caractéristiques des comportements de menace des oiseaux qui doivent encore être expliquées adéquatement, dans l’espoir que ce nouvel examen des données empiriques permettra de recibler la recherche théorique dans ce domaine.

[Traduit par la Rédaction]

Introduction

Over 35 years have passed since the publication of Andrew’s (1961) review of aggressive communication in birds, and the study of communication has gone through some great changes during this time. Early quantitative studies of threat (e.g., Moynihan 1955; Hinde 1970) focussed on which displays corresponded to which motivational drives. Current theoretical and empirical interest focusses on the strategic aspects, the balancing of costs and benefits for different displays.

In this paper we will examine the empirical literature on the use of threat display by birds. We will limit our attention to conflict over resources of small value, such as feeder or perch access, club territories (small areas held within aggregations of nonbreeding individuals, typically located at the edge of a breeding colony), and the like. Contests over more valuable resources are expected to be resolved through more escalated contests, in which fighting ability will be more important (Enquist and Leimar 1987). When contested resources are smaller, the relative costs of even a short fight are relatively large. In this situation individuals should be more reluctant to fight, and signals providing information about whether the resource is worth fighting over ought to be more valuable.

Threat displays are seen in almost all agonistic interactions. Many species have but one or two such displays, while others, such as tits and gulls, make use of rich repertoires of

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threat displays. Threat displays are of great theoretical interest because of the apparent benefits of deception. Two highly influential hypotheses have been advanced to explain the evolutionary stability of threats. The first is that threat displays are not actually threats, i.e., that they do not actually communicate information about attack (Caryl 1979). The second is that threats, and all other signals, entail inherent costs, or handicaps, which make it unprofitable for "cheaters" to use them (Zahavi 1975, 1977). A third alternative is that threat displays are conventional signals; they provide information about aggressive motivation without being inherently costly. The latter view corresponds most closely to traditional ethological views of threat displays.

The first hypothesis may be tested empirically by looking for informative variation in display use by animals. If the variables that influence the choice of agonistic display are relevant to receivers for the purpose of judging the future actions of signallers, then they communicate information about intent. The second hypothesis may be tested by examining whether variation in signals varies with the signalled trait as predicted by handicap models (e.g., Grafen 1990), that is to say whether signals tend to be graded or discrete, and whether signal use varies with changing seasonal benefits. The fixed cost of a handicap will be less worth paying when resources are plentiful, while the socially mediated costs of conventional signals mean that a set of signals can be used to communicate a range of motivations on a relative scale. Conventional signals should communicate across seasonal fluctuations, while handicaps ought not to.

We shall first characterize the form of threat displays, then proceed to examine which factors determine their use by signallers, and what their effects on receivers are. Finally we shall describe the properties of whole interactions and contrast these observations with the assumptions of current theoretical models. The costs and benefits of these signals are a function of their influence on receiver behaviour, rather than mere handicapping costs inherent in the production of the signal.

There is a great deal about threat displays that has yet to be fully explained. We hope that this reexamination of empirical data will help focus theoretical attention on these very real issues.

What do threats look like?

Displays are acts "specially adapted …to subserve social signal functions" (Moynihan 1960). These displays are distinct behaviours used across types of agonistic encounters: however, while the aggression context may vary, the displays are consistent in form. Researchers have no problems distinguishing between displays, which are stereotyped to the degree that they can easily be named and their performance can be counted as discrete instances. There is a very strong intuitive recognition of displays that contrasts with watching many other behaviours. The highly stereotyped nature of these displays allows each display to be named fairly precisely, unlike most other behaviours, which are stereotyped to a much lesser degree. The appearance of threat displays gives the strong impression of a simple language. A display usually comprises several distinct elements (e.g., wing or tail extension, body angle, head and beak postures, etc.). Early studies (Stokes 1962*a*, 1962*b*; Dunham 1966; Blurton Jones 1968; Andersson 1976; Balph 1977) tended to investigate these display elements rather than the full displays. The trend has been to move away from this, and only consider the full display (but for a recent exception see Wilson 1992).

Stereotyped displays

It has been suggested that threat displays are by nature continuous, or graded, as this allows for more accurate communication of motivation or other underlying states (Brown 1975; Grafe 1995). It has long been noted that graded displays are not used equally over their range of possible expression, but are typically restricted to some discrete levels of expression (Morris 1957). Handicap models predict a continuously varying signal to indicate a continuously varying trait (Grafen 1990; Godfray 1991; but see Johnstone and Grafen 1992; Johnstone 1994, addressed in the Discussion). Conventional signalling models (Enquist1985; Hurd 1997*b*; Hurd and Enquist 1998) predict that discrete, stereotyped signals will be used to signal continuously varying traits such as aggressive motivation (Enquist et al. 1998). This model predicts that there will be a strategic advantage to indicating aggressive intent as an ambiguous range rather than to a maximally informative, precise degree.

Whether a given example is a continuous display or a set of discrete signals may be difficult to decide. The head-forward threat display is ubiquitous amongst passerines (Andrew 1961). Popp (1987*a*, 1987*b*), Dilger (1960), and Coutlee (1967) report that this display consists of discrete levels of expression (amongst Purple Finches (*Carpodacus purpureus*), American Goldfinches (*Carduelis tristis*), Redpolls (*Carduelis flammea*), and American Goldfinches, respectively). They all report escalating versions in which the head is held forward at the lowest level, a mid-intensity version in which the head is held farther forward and the wings are partially extended with the beak opened wide, and a high-intensity version in which the wings are fully extended. Martin (1970) describes the head-forward display of the Varied Thrush, *Ixoreus naevius*, as a single "graded series" containing variation of beak open or closed and wings spread or folded.

Continuously varying elements may be used discretely; one example is wing extension in the Fulmar, *Fulmarus glacialis*, in which it is the rare exception that the wings are not held at one extreme or the other (M. Enquist, unpublished data). Crest raising in Steller's Jay, *Cyanocitta stelleri*, is often cited as a genuinely continuous signal. The distribution of degrees of crest elevations, however, is significantly different from random ($\chi^2_9 = 243$, $P < 0.001$), with a distinct tendency for overuse of the extreme forms of the display (Fig. 1). The modal angle is either the most extreme, or next to the most extreme, in all seven of the behavioural contexts in which its use has been analysed (Brown 1975).

Animals changing from one display to another will have to pass through some transitional postures that may be thought of as graded (Tinbergen 1959). Any discrete signal will also have some aspect to them that is quantifiable on a continuous scale: a discrete posture will be held for some continuous period of time, a discrete vocalisation will have a continuously variable volume and dominant frequency, and a raised crest will have a continuously variable physical size and brightness. Given that all of these continuous measures of signals can be obtained, it is all the more relevant that distinctly different signals are used. To conclude that any set of displays is a graded display, one has to test the distribution of signals to ensure that there is not actually a set of discrete signals on an underlying continuous scale.

There is no real relevance to variation in components of displays if the displays themselves do not have a variable character. For instance, while Andersson (1976) ranks beak and neck postures as one of three degrees, this does not mean that the gradation of neck posture varies within a single display.

Graded acoustic threats have been demonstrated in at least two species of birds (Nelson 1984; Capp and Searcy 1991). In the Willow Warbler, *Phylloscopus trochilus*, Järvi et al. (1980) demonstrated communication of the probability of attack through the proportion of songs containing a particular note, but, contrary to Grafe (1995), this is not a truly continuous signal. The use of the note in question is undoubtedly discrete (the note is either used or not, a discrete event); it is the experimenter's analysis that converts the discrete signal into a continuous variable.

Repertoire size

One of the most striking things about watching birds during aggressive interactions is the wide range of behaviours used. Table 1 lists the numbers of discrete threat and fighting behaviours of 32 species counted in 26 studies. The methodology and nomenclature vary considerably between the studies listed in Table 1, and the data are not all strictly comparable (note that the three studies of Great Tits, *Parus major*, are not in perfect agreement). Nonetheless, it is clear that repertoires of 5 or 6 discrete ritualised displays are not at all unusual.

In summary, the consistent result is that threat displays have discrete properties which cannot be explained by attempting to abstract them onto a continuous scale. Repertoires of 3–5 discrete displays are the norm, single graded displays are not.

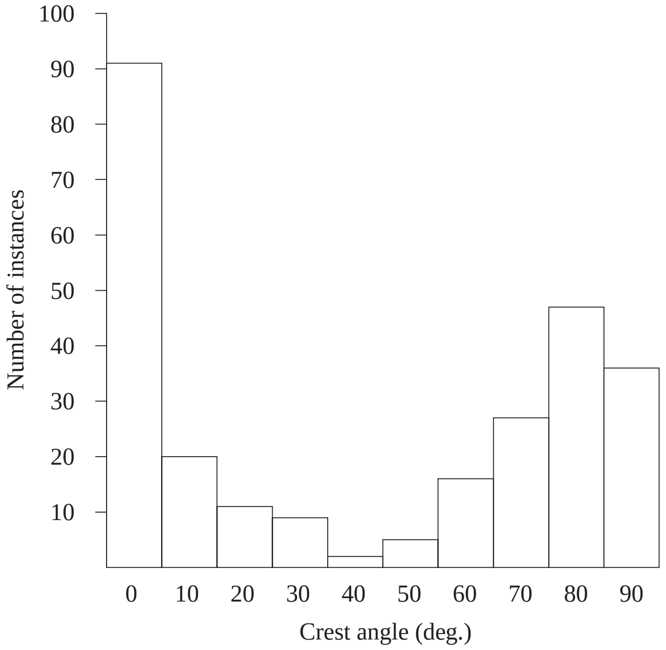
The use of displays: signaller behaviour

Factors influencing choice of display

What factors determine which display an individual will use? Empirical studies have shown several variables that correlate with the choice of threat display. Data about such variation in choice of behaviour come from three distinct sources: experimental manipulations, observational studies, and motiational analyses. The first two correlate the frequency of display use with various factors, while motivational analyses examine variation in signaller behaviour following the use of a display to infer a common causative state for the display and behaviours.

Observational studies have linked variation in choice of aggressive display to season (Stokes 1962*a*; Popp 1987*b*), length of ownership of a resource (Enquist et al. 1985), relative dominance (Popp 1987*b*), signaller sex (Popp 1987*b*; Wilson 1994), receiver sex (Wilson 1994), and behavioural context (e.g., feeder vs. nonfeeder) (Wilson 1992). Wilson (1992) provides an involved principal component analysis of attributes observed to influence choice of display in Great Tits, including season and the bird's age, territorial status, sex, body mass, relative familiarity with the site, and frequency of interaction with the opponent. Experimental studies have demonstrated changes in the use of aggressive display in response to food deprivation (Popp 1987*b*; Wilson 1994) and manipulations of relative dominance and familiarity (Wilson 1994).

Fig. 1. Distribution of crest elevations in Steller's Jay (*Cyanocitta stelleri*) across seven behavioural contexts: combat, aggressive sidling, displacement acts, sidling and circling, in hand, raise back, and courtship feeding. Data are from Brown (1975); we combined all seven histograms on page 305 into a single plot. There is a distinct tendency toward overuse of the extreme forms of the display.



Of these factors, season, length of ownership of a resource, and food deprivation most likely affect choice of display through variation in the value of victory to different individuals. We call these motivational variables internal factors, since an internal state such as hunger may be posited to exist for each.

Relative dominance, receiver sex, and familiarity are all factors that are more likely to affect choice in display strategically, through changes in the anticipated costs of an interaction that result from variation in opponent state. We call these external factors, since they are relational, i.e., their values cannot be properly quantified without knowledge of who the receiver is. In the case of internal factors, we may be imagine some absolute value internal to each individual.

Investigation of internal states through "motivational analysis"

The motivational analysis (Smith 1977) is a common method for identifying the internal factors behind the selection of displays. By considering the behaviour that follows a display we can infer a common state which caused both the display and the ensuing behaviour (Moynihan 1955; Hinde 1970). For instance, if an animal commonly follows a given display with a physical attack, the conclusion is drawn that

Table 1. Agonistic display repertoire sizes and numbers of discrete threat and fighting behaviours for 34 species of birds competing for resources of small value (club territory, access to food, water, perches, etc.) that were counted in 28 studies.

	No. of visual-display elements	No. of ritualized visual displays	No. of calls	No. of other agonistic behaviours	Repertoire size	Study
Heard Island Shag, *Phalacroorax nivalis*		3	2	1		Green 1997
Fulmar, *Fulmarus glacialis*		5		6		Enquist et al. 1985
Bald Eagle, *Haliaeetus leucocephalus*		4		5		Hansen 1986
Ruddy Turnstone, *Arenaria interpres*		2				Groves 1978
Great Skua, *Stercorarius skua*	13*	15	4			Andersson 1976
Lorikeets						
Trichoglossus haematodus					19	Serpell 1982[†]
T. mitchellii					13	Serpell 1982[†]
T. weberi					15	Serpell 1982[†]
T. capistratus					16	Serpell 1982[†]
T. moluccanus					14	Serpell 1982[†]
T. ornatus					20	Serpell 1982[†]
T. chlorolepidotus					10	Serpell 1982[†]
T. flavoviridis					12	Serpell 1982[†]
T. versicolor					5	Serpell 1982[†]
European Jay, *Garrulus glandarius*				2		Bossema and Burgler 1980
Great Tit, *Parus major*	6					Stokes 1962*b*
	6	3	2	8		Blurton Jones 1968
	12			3		Wilson 1992
Blue Tit, *Parus caeruleus*	9	8				Stokes 1962*a*
	6					Stokes 1962*b*
	9	9[‡]		8		Scott and Deag 1998
Marsh Tit, *Parus palustris*	6					Stokes 1962*b*
Black-capped Chickadee, *Parus atricapillus*		4	1			Popp et al. 1990
Varied Thrush, *Ixoreus naevius*		3	4	3		Martin 1970
Starling, *Sturnus vulgaris*		5	2	5		Ellis 1966
Grosbeak, *Pheucticus ludovicianus*	5		3	3		Dunham 1966
Dark-eyed Junco, *Junco hyemalis*	33	5	7	2		Balph 1977
Siskin, *Carduelis spinus*		4				Senar 1990
American Goldfinch, *Carduelis tristis*		5	1	4		Coutlee 1967
		3				Popp 1987*b*
Redpoll, *Carduelis flammea*		6	1	2		Dilger 1960
Purple Finch, *Carpodacus purpureus*			2	2		Popp 1987*a*
Silvereye, *Zosterops lateralis*	7	2	2	3		Kikkawa 1961
	4		2	4		Wilson 1994

Note: Values in the "visual-display elements" and "calls" columns are a direct tally of behavioural elements or calls that the authors listed as being used in aggressive interactions. If it was not possible to determine whether or not the element or call was used in aggressive interactions it was included, but a note (*) was made to this effect. The "ritualised visual displays" column lists the number of behaviours that we felt intuitively seemed to qualify as such; they were often frequently co-occurring sets of elements analysed as single units by the original authors. The "other agonistic behaviours" column includes such things as pecking, landing on the opponent, and other aggressive acts that are commonly occurring categories of behaviour but do not fit the "calls" or "ritualised visual displays" categories.

*This study included non-agonistic behaviours and elements, such as feeding or courtship behaviour.

[†] The study did not report anything more than repertoire size; the repertoire was composed of both ritualised and unritualised behaviours.

[‡] The authors present data supporting their view that each of these elements is a ritualised display unto itself.

the display was caused by a high level of aggressive motivation, perhaps resulting from a high subjective resource value, e.g., hunger. We can examine behaviour subsequent to a display for statistical information about the internal state of the signaller. This traditional ethological analysis is common to all four of the papers reanalysed by Caryl (1979). The original form of this analysis considered only the subsequent action of the signaller without regard to the intervening response from the receiver; a more recent variation on this technique is the trifactorial analysis of contingency (TFA), which will be discussed in the section on sequences. There are several problems inherent in such analyses, the most widely recognised being the successful-threat problem (Stout 1975; Smith 1977; Hinde 1981):

Table 2. Summary of prediction of attack and escape by displays for all displays analysed in nine studies.

Attack		Escape		Correlation		
Median	Range	Median	Range	r_s	N	Study
0.216	0.09–0.36	0.022	0–0.09	0.40	4	Moynihan 1955
0.175	0–0.48	0.205	0.10–0.94	–0.76	8	Stokes 1962*a*
0.23	0–0.80	0.37	0–0.81	–0.56	11	Dunham 1966
0.029	0–0.18	0.12	0.015–0.22	–0.58	12	Blurton Jones 1968 (live opponent)
0.016	0–0.14	0.045	0.006–0.18	–0.50	14	Blurton Jones 1968 (stuffed opponent)
0.19	0–0.42	0.15	0–0.80	–0.29	15	Andersson 1976
0.11	0.04–0.3	0.25	0.12–0.58	–0.35	11	Paton and Caryl 1986 (estimated)*
0.04	0–0.09	0.32	0.26–0.39	–1.0	3	Popp 1987*b*
0.073	0.007–0.17	0.032	0–0.048	0.20	4	Senar 1990

Note: Median and range refer to the strength of prediction of attack and escape for different displays in the repertoire. Correlations of the prediction of attack and escape for different displays are consistently negative. Data for Moynihan (1955) were restricted to displays not associated with attack or escape and displays before or during attack and escape. Displays shown by attackers immediately after attack and displays used by attacked birds immediately after attack were discarded from the data set.

*Numerical values for Paton and Caryl's (1986) data are estimates (see the Appendix); rank orders are unambiguously provided in their Fig. 1. The rank-order statistics presented in this table will be unaffected by errors in the numerical estimates.

> If a certain display indicates that attack is likely, it is quite possible that this information alone would suffice to cause the withdrawal of an intruder without actual attack being necessary. Thus, the association of a display with subsequent attack does not provide a reliable indicator of the information provided by the display.
>
> (Stout 1975)

The problem proves to be quite difficult to resolve, even for the TFA; we will discuss this issue further when examining sequences of behaviour.

A less serious problem arises when the results of different studies are compared. The operational definition of "attack" has varied as the theoretical basis of these studies has changed. If displays are expressions of conflicting drives, then it makes some sense to view approach toward the opponent as an expression of a tendency to attack.

> Attack: actual moving forward on the feeder or in the air to the other bird's position. A slight inching towards an opponent was not considered as attack, although undoubtedly was an intention movement of attack.
>
> (Stokes 1962*a*)

> Attack is used in this paper to mean any intensity of advance by one bird in an agonistic encounter, but especially hopping, sidling or flying toward the second bird from an initial position about 15 to 30 cm from it.
>
> (Dunham 1966)

Contrast the latter with behaviour D—"Use of the bill".

> D. Use of the bill. A bird may open the bill and move rapidly toward another bird, biting at the nearest part of the opponent, which is sometimes the bill if the second bird is similarly motivated.
>
> (Dunham 1966)

This would probably be defined as an attack in a current study (note, though, that Wilson (1994) uses a similar "movement-towards" definition for attack). This approach definition may still have great validity, however, as seems to be the case in the Great Skua, *Stercorarius skua*.

> It may be argued that running or flying towards another bird is not necessarily attack. However, all running or flying birds which reached the other individual did peck, pull, or in other ways fight it.
>
> (Andersson 1976)

As Hinde (1981) notes, prediction of attack can exceed chance long before Caryl's (1979) arbitrary 50% threshold is reached.

Despite these problems, motivational analyses have produced some consistent results. Two clear trends can be seen in the the data from such studies (Table 2). The first is that "escape" is better predicted than attack; this is true both for the high end of the range (the best predictors of each) and the median prediction displays. The second clear effect is that the probabilities of attack and escape following any given display are negatively correlated. Figure 2 shows the percent prediction of escape for displays of high, medium, and low probability of attack. There is a consistent trend toward an increasing probability of escape as the probability of attack decreases. This communicates a consistent message to receivers about the signaller's likely subsequent act, presumably reflecting a lower level of motivation when both the likelihood of attack falls and the likelihood of leaving rises. The two exceptions to both these trends are Moynihan's (1955) data on Black-headed Gulls, *Larus ribidundus*, and Senar's (1990) data on Siskins, *Carduelis spinus*. Both exhibit very low levels of escape (the Siskin data set is odd in having low rates of both attack and escape), meaning that lots of displays are used before a contest is resolved, and these displays are taken from a small repertoire (4 displays for each).

Subsequent actions are not limited to attack and escape; the other possibilities are all lumped into "stay." Figure 3 shows the probability of stay as the next act by the signaller

Fig. 2. Prediction of escape according to the probability of attack. Displays are divided into three groups based on their ranking of predicting attack. Displays that were left after the division into the three groups were placed in the "medium" category; when the threshold was straddled by a set of displays of equal ranking, the members were placed in whichever of the two categories gave the most equal final distribution of displays amongst the categories. Studies, with sample sizes (high, medium, and low categories), are as follows: (*a*) Moynihan 1955 (1, 2, 1); (*b*) Stokes 1962*a* (3, 3, 2); (*c*) Dunham 1966 (3, 5, 3); (*d*) Blurton Jones 1986, live opponent (4, 4, 4); (*e*) Blurton Jones 1986, stuffed opponent (4, 6, 4); (*f*) Andersson 1976 (6, 4, 5); (*g*) Paton and Caryl 1986 (3, 5, 3); (*h*) Popp 1987*b* (1, 1, 1); (*i*) Senar 1990 (1, 2, 1). See Table A1 for quantitative estimates of Paton and Caryl's data.

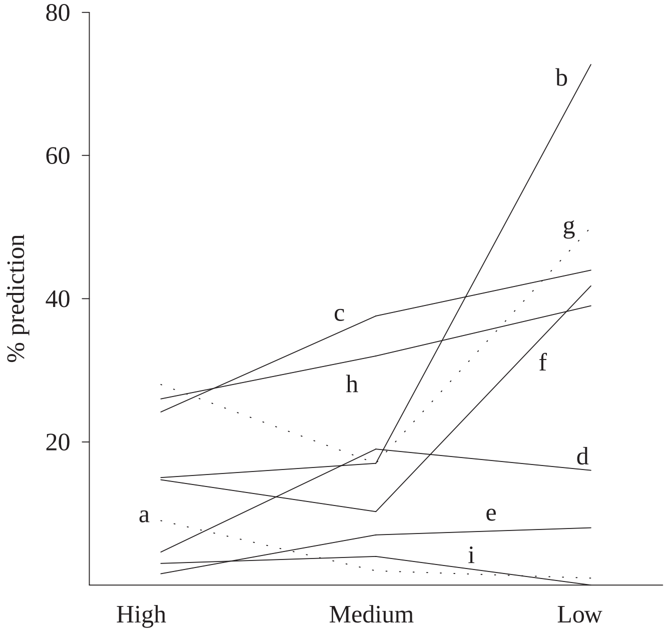
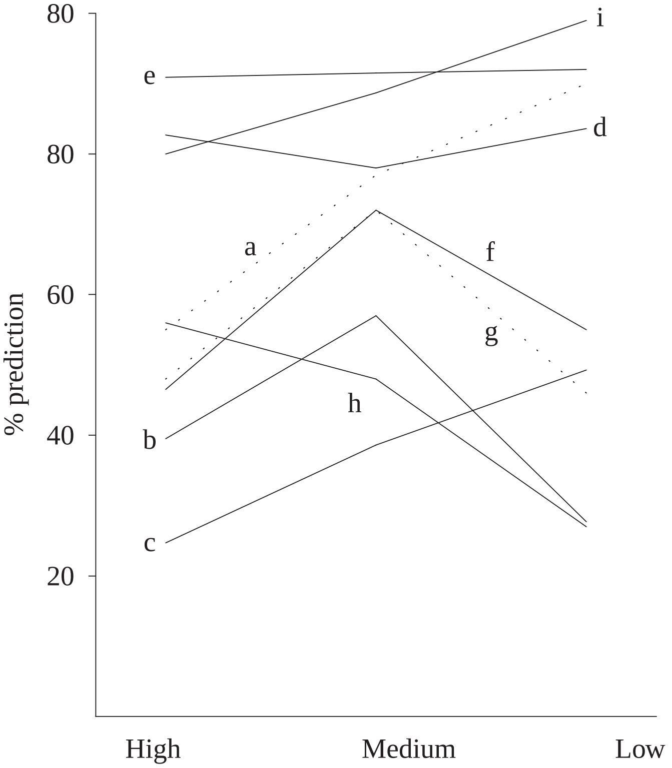


Fig. 3. Prediction of stay based on the probability of attack. For general technique and sample sizes see Fig. 2.



as a function of the aggressiveness of the display. No clear trend emerges from the data. Some studies show that the tendency to stay is highest at intermediate probabilities of attack, while others show a trend toward either an increase or a decrease.

The data are consistent with the interpretation that the signaller is communicating not so much an intent to attack as the motivation to attack if need be (Hinde 1981). The distinction between signalling an immediate attack and signalling motivation to do so may appear trivial, but it is of great relevance to understanding the apparent variation in the meaning of a signal between samples.

Consistency in time and space

It has been suggested that the use and meaning of displays vary greatly over time and space (Andersson 1980; Paton and Caryl 1986). Andersson (1980) suggested that displays which predict attack are evolutionarily unstable and replace each other cyclically as rarer ones become more effective, are then exploited as bluffs, and subsequently decline in their effectiveness and use. Evidence against this view comes from studies such as Tinbergen (1959) and Stokes 1962*b*) which find that similar displays in related species have very similar rankings of escalation. We shall investigate the empirical literature for evidence against the consistent meaning, or use, of threat displays over time and space. For a threat display to have a consistent "meaning" it is necessary that the rules which signallers use to choose displays, and receivers use to interpret them, be constant.

The actual percentage of different signaller actions is expected to change following a signal, owing to variations in external factors. For instance, in times of low resource availability we may expect more aggression in response to all signals. A differential probability of attack or escape over the course of a year is to be expected. Both the receiver's reaction and the signaller's subsequent action will change with changing levels of need or resource availability elsewhere. Signallers may adjust their behaviour in anticipation of a relatively escalated response to any given signal, but what we do not expect to find is that the ranking of the displays changes: their relative meaning should remain consistent.

Stokes (1962*a*) found that the predictive power of particular behavioural elements changed throughout the seasons: for example, "… the horizontal body was a good indicator of attack in Period I [Jan. 26 – Feb. 4 -PLH] (.72) but only a very poor one (.25) by Period IV [March 12 – 15 -PLH]." This has been taken by some (e.g., Paton and Caryl 1986) to mean that the meaning of the display is variable.

While the raw proportion of displays followed by attack and escape may fluctuate, it does not follow that the association of differing displays with differing relative probabilities of attack is lost. Indeed Stokes (1962*a*) states,

> From these observations one can conclude that 1) the probability of a particular postural element leading to attack, escape, or staying may change with season; but, 2) *the occurrence of a particular element always indicates the same motivation (e.g., increased aggressiveness) regardless of season*" [emphasis added].

In contrast, Paton and Caryl (1986) present data demonstrating large variation in the meaning of displays between locations, and between years at those locations. They compare five samples collected at different sites and years and conclude that variation among samples in both the absolute and relative probability of attack after different displays was so great that no information is transmitted.

The data presented in Paton and Caryl's (1986) Tables 3*a*, 4*a*, and 5*a* provide comparisons of display predictions between sites and years. Correlations in prediction of attack are listed in Table 3*a*, correlations in prediction of escape in Table 4*a*, and correlations in prediction of attack or stay Table 5*a*. Tables 4*a* and 5*a* are redundant, since attack, escape, and stay are the only options. The one value that differs between Tables 4*a* and 5*a* is either an omitted "–" in Table 4*a* or an accidental one in Table 5*a* (Noss 78, Fair Isle 79); we assume the former and use this modified Table 4*a*. Of the 30 correlations in Tables 3*a* and 4*a*, 21 are positive, demonstrating a consistent trend toward agreement in the meaning of displays across sites and dates.

The degree to which the data sets agree in their prediction of attack is greatly dependent upon the size of the individual data sets. There is a large positive correlation between the summed numbers of displays in each pair of data sets (Table 1*a* in Paton and Caryl 1986) and the agreement between that pair of data sets in predicting attack (Table 3*a* in Paton and Caryl 1986) ($r_{s\ 9} = 0.94$, $P < 0.01$), suggesting that if all samples were as large as the largest two, their agreement would be just as good ($r_s = 0.966$). While sample sizes ranging from 356 to 2501 displays may seem quite large, the number of attacks observed may still be too small to allow for statistically powerful discrimination between the probability of attack following different displays. The median number of expected attacks for each display in each data set (calculated using Table 1 in Paton and Caryl (1986) and Fig. 1; see the Appendix for estimated numerical values) is less than five (4.8), and less than one for about 18% of the cases.

In summary, signallers choose which display to use on the basis not only of factors that are internal to the signaller (e.g., hunger or sex), but also external factors (e.g., the opponent's dominance status or sex), which suggests that strategic as well as motivational considerations are a factor. The patterns of use are consistent within a repertoire, while absolute levels of prediction of attack and escape fluctuate with seasonal changes in motivational factors. This is consistent with the view that signallers are indicating the motivation to attack if need be, rather than a certain fixed probability of attack as Caryl (1979) implies.

Communication: receiver behaviour

Evidence for communication

Having addressed the question of variation in the signal, i.e., what factors determine which display an animal will use, I will address the second central question: whether threat displays and other behaviours are actually used to communicate during aggressive interactions. In other words, what evidence exists that variation in the signaller's behaviour affects the behaviour of the receiver? This, and not motivational analysis, is the true test of the existence of communication. Evidence for such communication comes from two types of studies: experimental manipulations and analyses of behavioural sequences.

The most unambiguous evidence that displays influence a receiver's behaviour comes from experimental studies which present models of different postures, or use audio playback to present different calls. In a series of model-presentation experiments on Glaucous-winged Gulls, *Larus glaucescens*, Stout and co-workers showed that by changing the posture of a dummy they could influence the behaviour of the receiver (Stout and Brass 1969; Galusha and Stout 1977; Amlaner and Stout 1978). In a similar study they obtained similar results for different calls played during presentations of the same model (Stout et al. 1969).

Evidence for communication can also be obtained from analyses of natural behaviour sequences. Here the studies are more numerous (listed in Table 3) and generally provide evidence for communication via threat displays. The basic statistical technique is simply to show that the response of the receiver is not independent of the signal given prior to the response (e.g., Colgan and Smith 1978).

Analysis of behaviour sequences also reveals that the effects of overt behaviour such as orientation, distance to the opponent, and locomotion have signal value (Andersson 1976; Hayward et al. 1977; Bossema and Burgler 1980; Enquist et al. 1985). Behaviours such as attacking or fleeing also influence subsequent receiver behaviour. Table 3 lists studies in which analyses of behaviour sequences have been used to demonstrate an effect of interindividual distance or signaller behaviour, orientation, or speed of approach on receiver behaviour during aggressive interactions.

A potential drawback to these studies is the lack of controls for correlated variables. It may be that large, or dominant, individuals perform the most threatening displays, and that the receivers are responding to the size or dominance position of the signaller rather than to the display per se. For instance, Popp (1987*b*) compared the reactions to different American Goldfinch displays; while dominance did explain some of the variation in reply, choice of behaviour had an independent effect on receiver action. These effects can be partialled out, or comparisons may be restricted to within individuals or classes; ideally, studies should control for individual effects. None have thus far.

Sequences

Another striking property of aggressive interactions between birds is their relatively protracted nature. Not only do individuals make use of a range of displays, but they often use several of them in the same interaction. Enquist et al. (1985) found an average of 4.1 alternating acts (range 1–22) amongst Fulmars. Nelson (1984) found that Pigeon Guillemots, *Cepphus columba*, used a median of 7 alternating displays, with 25% of interactions exceeding 14 such "steps." Scott and Deag (1998) found that Blue Tits, *Parus caeruleus*,

Table 3. Studies that demonstrate agonistic communication in birds, i.e., an effect of signaller behaviour on receiver behaviour in birds contesting small valued resources.

	Signal	Effect on receiver	Study
Fulmar, *Fulmarus glacialis*	Behaviour and orientation	Frequency of attack/flee	Enquist et al. 1985
Great Skua, *Stercorarius skua*	Speed and proximity of approach	Frequency of attack/stay/escape	Andersson 1976
	Behaviour	Frequency of attack/stay/escape	Andersson 1976
Pigeon Guillemot, *Cepphus columba*	Behaviour	Frequency of behaviour	Nelson 1984
Great Skua, *Stercorarius skua*	Behaviour and distance	Probability of escape	Paton 1986
Little Blue Penguin, *Eudyptula minor*	Behaviour and Δdistance	Frequency of behaviour	Waas 1990
European Jay, *Garrulus glandarius*	Behaviour and distance	Probability of retreat	Bossema and Burgler 1980
Great Tit, *Parus major*	Behaviour	Frequency of attack/escape/stay	Stokes 1962*b*
Blue Tit, *Parus caeruleus*	Behaviour	Frequency of attack/escape/stay	Stokes 1962*a*
Blue Tit, *Parus caeruleus*	Behaviour	Probability of winning or losing	Scott and Deag 1998
Grosbeak, *Pheucticus ludovicianus*	Orientation	Frequency of attack/escape/stay	Dunham 1966
Dark-eyed Junco, *Junco hyemalis*	Behaviour, locomotion	Frequency of attack/escape/display	Balph 1977
Siskin, *Carduelis spinus*	Behaviour	Frequency of attack/display/flee, etc.	Senar 1990
American Goldfinch, *Carduelis tristis*	Behaviour	Frequency of display/peck/flee	Popp 1987*b*
Purple Finch, *Carpodacus purpureus*	Behaviour	Frequency of display/peck/flee	Popp 1987*a*
Silvereye, *Zosterops lateralis*	Behaviour	Frequency of attack/flee	Wilson 1994

used 6 (±1) alternating acts, Popp et al. (1990) found that Black-capped Chickadees, *Parus atricapillus*, used more than 5 displays (range 1–21) in an average interaction, and Waas (1991) found aggressive interactions amongst Little Blue Penguins, *Eudyptula minor*, to be typically 8–13 behaviours in length.

These sequences are not mere repetitions of the same display, but are dynamic exchanges, with both individuals changing their behaviour and making use of several different displays. Such structure allows for a large number of distinct possible interactions, each comprising a unique series of displays. The choice of display is based not just on their opponent's most recent behaviour (Nelson 1984; Popp 1987*b*; Senar 1990; Senar et al. 1989; see previous section and Table 1), but on length of resource ownership (Enquist et al. 1985), dominance relationship (Popp 1987*b*; Senar 1990), and signaller's sex (Popp 1987*b*).

Analysis of these display–counterdisplay–response exchanges requires a trifactorial (signal × receiver's reaction × signaller's action) analysis of contingency (Colgan and Smith 1978). This allows one to test for the effects of signal, reply, and interactions of signal and reply on subsequent behaviour. While this goes some way toward addressing the successful-threat problem, a few problems remain.

One problem is that of variation in the receiver. Receivers are not all identical, and it is possible that the signallers tailor their original signal to the type of receiver they are facing. For instance, when resources are scarce, a signaller who may be in an identical physiological state to a signaller during a plentiful season may not behave the same, the behaviour being a function of different expected replies from the receiver. The appropriate control is either to use model presentations (e.g., Blurton Jones 1968) or to add another factor to the analysis.

A bigger problem is the analysis of behaviour triplets out of temporal context; many studies (e.g., Nelson 1984; Popp 1987*b*; Senar 1990; Waas 1991) have analysed behaviour triplets without reference to whether these are the first three in an interaction or the last three of many. Displays and responses occurring late in an interaction may be chosen as a result of actions that occurred earlier in the interaction, leading to artefactual results. Analysing behaviour triplets also produces several data per interaction that may pseudo-replicate each other.

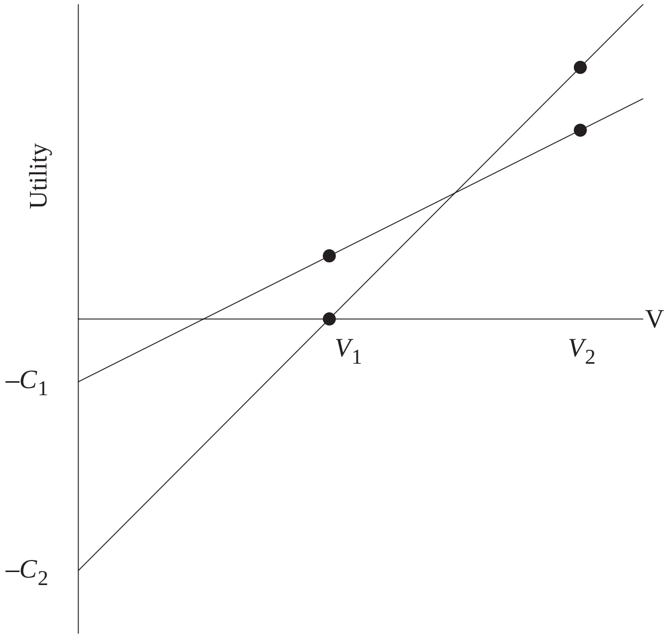
Lastly, the TFA is inappropriate for motivational analyses. Though it does deal statistically with cases in which the receiver flees, it cannot correct for the change in signaller state that presumably occurs when the receiver has withdrawn (Moynihan 1998). That signallers are not seen to redirect attacks against other stimuli following a successful threat highlights the difficulty in rigorously testing the motivational hypothesis. It should be noted that some care is required in defining the subsequent actions of signallers for use in a TFA analysis. If a category is defined for behaviour that follows a successful threat, some cells in the TFA table will be unreachable. A significant TFA says very little other than that communication is taking place; further analysis will be required to provide any understanding about the properties of the communication system. Recently, this additional analysis has been directed at the trade-offs between different signals and the costs and benefits of alternative behaviours. A “tree” analysis, which treats the interaction as an extensive form game, is more appropriate for this sort of data (e.g., Enquist et al. 1985).

That being said, TFA analyses do provide some convincing evidence for signalling of aggressive motivation. The proportions of Senar's (1990) Siskins who stayed without submitting to an actor's initial display and were then attacked were 5.0, 25.5, 17.1, and 61.1% when the actor's display was D1 through D4, respectively ($\chi^2_3 = 21.9$, $P < 0.005$). No receiver who submitted ($N = 216$) was attacked.

Risk and effectiveness

Enquist et al. (1985) proposed a simple model of threat displays which predicted that the effectiveness of a fighting strategy will correlate with its cost (Fig. 4). They supported their model with data obtained from Fulmars fighting over food. The major cost of fights over such small resources is almost certainly the risk of injury. It should be noted that the

Fig. 4. Correlation of cost and effectiveness. The utility of two different strategies at two different levels of subjective resource value, V, is shown. The utility of strategy i is $U_i = p_iV - C_i$, where p_i is the probability that strategy i will lead to a victory and C_i is the cost of strategy i. Note that the slopes of the lines are equal to p.



model makes no assumption about the source of the costs; they could be either handicapping signals or conventional displays. The relative costs of different strategies can easily be quantified as the probability that the given strategy will lead to physical fighting. This produces socially mediated costs, consistent with conventional signalling.

Enquist et al. (1985) also demonstrated lower levels of aggression when owners had been feeding longer, owing to declining relative resource value as predicted by the model. Several subsequent studies (Popp 1987*a*, 1987*b*; Senar et al. 1989; Waas 1991) have shown a positive correlation between risk and effectiveness of avian fighting behaviours. It is worth noting that most of these results (Popp 1987*a*, 1987*b*; Waas 1991) are not explicitly predicted by the original model, which compares the relative costs and benefits of alternative strategies (as in a “tree” analysis; see the next section), rather than actual behaviours (as in a TFA-style analysis). While correlations between the risk and effectiveness of displays taken out of sequence in this manner do not yet have a solid theoretical explanation, the result is not surprising.

The somewhat more complicated relationships between risk and effectiveness found in some studies (Senar 1990; Wilson 1994) are likely to be due to the extended nature of social relationships within stable flocks. If the costs and benefits of various behaviours are not limited to the current interaction, but are part of more complicated social relationships, then it will be much more difficult to test theories about fighting behaviour.

Analysis of sequences

In analysing sequential data one should compare only behaviours that are truly alternatives and consider consequences beyond the receiver’s immediate response. Tree-based analyses seem to be the most appropriate method. Transition matrices (Popp 1987*a*, 1987*b*) and lag analysis (Waas 1991) may be used to compare behaviours that are not alternatives, but allow the use of smaller data sets.

The analysis used by Senar (1990) is a principal-components-style analysis of TFA data for the first three behaviours in each interaction. The results are as complicated as the analysis, making a simple interpretation difficult. Senar concludes from his results that reactors who continue with their previous behaviour are acting submissively, while those that counter-display are acting more aggressively. A simple-minded analysis of the data shows that of those reactors who continued their previous behaviour, 6.3, 44.8, 22.2, and 71.4% were attacked (for actor displays D1 through D4, respectively), whereas counter-displaying reactors were attacked 0, 22.9, 7.1, and 54.5% of the time (for actor displays D1 through D4, respectively). The power of Senar’s analysis comes from comparing the effects of other parameters upon the TFA. Analyses of this style on tree nodes, comparing equivalent nodes on trees compiled from interactions of subsets of data rather than TFA tables, would correct for the problems inherent in TFA-style analyses.

Wilson (1992) also uses a principal-components-style analysis, but analyses display elements as either used or not used over the course of the interaction. This removes almost all information about the original sequence. This analysis would be more useful if it had been performed on data situated in time (or restricted to the initial behaviour as in Wilson 1994). The analysis of elements, rather than whole displays, also makes interpretation more difficult.

In summary, demonstrating variation in receiver behaviour as a function of signaller display is the correct test of communication. Explaining variation in receiver reply requires adequate controls for the effects of receiver type on the original signal. Signals and replies are often chained in dynamic exchanges of display, and correct identification of alternative strategies, by means of “tree” analyses, is required. Such analyses show that a trade-off between effectiveness in repelling opponents and the risk of provoking an escalation underlies threat displays. This is consistent with the view that signallers are indicating motivation to attack if need be, rather than a specific probability of attack (Hinde 1981; Hurd 1997*a*; Scott and Deag 1998).

Discussion

The classical ethological view that threat displays communicate aggressive intent has been in disfavour for some decades (Dawkins and Krebs 1978; Caryl 1979; Hinde 1981; Krebs and Dawkins 1984). The game theoretical models, most prominently the “war of attrition” (Bishop and Cannings 1978; Bishop et al. 1978), that led to this change have not themselves produced any great insights into avian threat displays. It seems that a great deal of what the classical ethologists described about threat displays, their discreteness and number, their tendency to provoke a range of escalating responses, and their temporal sequencing, still lacks adequate explanation.

Models of the classical ethological view (e.g., Maynard Smith and Riechert 1984) do not model strategic choice of threat. The initial models of strategic communication (e.g., Grafen 1990; Godfray 1991) focussed on the inherent costs of signals, and made two predictions that do not agree well with the use of threat displays by birds. Firstly, threat displays appear to be conventional to the observer; different displays do not obviously impose different inherent costs. Instead it appears that the costs and benefits of using different displays derive from the different responses they elicit. Secondly, rather than forming a continuum of increasing cost, indicating a continuous underlying motivation or fighting ability, threat displays seem to be quite discrete in their form. A recent model of conventional signalling of aggressive motivation makes these predictions (Enquist et al. 1998).

One handicap model (Johnstone and Grafen 1992; Johnstone 1994) does predict discrete displays, if receivers make errors in perceiving displays. The conventional signalling model predicts a strategic advantage for signallers who employ ambiguous displays rather than positing errors. This result is supported by models from economics, which predict discrete displays when communication between players in conflict uses costless signals (Crawford and Sobel 1982), whereas a similar interaction with costly signals would produce a signalling equilibrium with handicapping signals (Spence 1973). This model also demonstrates an increasing number of displays as the degree of conflict increases (Crawford and Sobel 1982).

Another difference between conventional-signalling (Enquist et al. 1998) and discrete-handicap (Johnstone and Grafen 1992; Johnstone 1994) models is that the conventional-signalling model assumes an interaction in which both individuals signal and act, as occurs in aggressive interactions, whereas the handicap model assumes that only one player may signal, while the other merely chooses an adequate response, a situation that is more representative of mate choice. Conventional signalling is the more parsimonious explanation for discrete displays.

We conclude from our survey that threat-display repertoires which consist of a single graded display are highly atypical, if they exist at all. Repertoires of 5 or 6 discrete displays are more representative. As a rule these displays occur in sequences of signals and replies that are dynamic exchanges, each animal's behaviour influencing its opponent's response. Threat displays are chosen on the basis of internal factors, such as hunger or sex, as well as external factors, such as the opponent's sex or dominance status. This means that both motivational and strategic considerations determine agonistic signals, and there is no good reason for believing that signallers are somehow constrained to use the one signal they do (i.e., these signals are not performance displays; Hurd 1997*a*). These displays rank consistently on a scale of willingness to escalate that reflects a variable level of motivation combined with a strategic assessment of probable opponent motivation and ability. Patterns of varying use with season suggest that signallers are not indicating a specific probability of attack, but rather the motivation to attack (Hinde 1981). Analysis of alternative strategies shows that a trade-off between effectiveness in repelling opponents and risk of provoking an escalation underlies threat displays. All of these observations are consistent with the view that threat displays are conventional signals rather than handicaps, whose costs and benefits are a function of their influence on receiver behaviour.

Threat displays are a truly distinctive phenomenon; birds fight over seeds give a strong impression of a simple language at work. Game-theory models have drawn attention to the fact that something very interesting must be happening when animals threaten each other. Strategic-handicap models of fighting ability or resource value (Grafen 1990; Johnstone and Norris 1993; Adams and Mesterton-Gibbons 1995) have yet to model interactions in which more than one individual may signal. Evolutionary stable strategy models of aggressiveness (Kim 1995) and models of conventional signalling (Enquist 1985; Hurd 1997*b*; Enquist et al. 1998) have yet to model sequences of alternating display.

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Appendix

Table A1. Quantitative estimates of attack and escape probabilities from Fig. 1 in Paton and Caryl (1986).

	Behaviour		
Posture*	Attack	Escape	Stay
a	0.05	0.58	0.37
b	0.04	0.37	0.59
e	0.3	0.25	0.45
g	0.18	0.36	0.46
h	0.25	0.23	0.52
i	0.115	0.28	0.605
j	0.1	0.18	0.72
n	0.11	0.12	0.77
o	0.095	0.13	0.775
p	0.17	0.14	0.69
q	0.041	0.54	0.419

*Letters refer to postures described in Paton and Caryl (1986).

Table A2. Expected number of attacks following each display in each data set.

		Study sites				
Posture	Density*	Hoy 1979 (N = 356)	Hoy 1980 (N = 1045)	Noss 1978 (N = 493)	Fair Isle 1979 (N = 2501)	Fair Isle 1980 (N = 2191)
a	0.0173	6.14	18.0	8.50	43.1	37.8
b	0.00154	0.548	1.61	0.759	3.85	3.37
e	0.00495	1.76	5.17	2.44	12.4	10.9
g	0.0419	14.9	43.8	20.68	104.8	91.9
h	0.00613	2.18	6.40	3.02	15.3	13.4
i	0.00191	0.679	1.99	0.94	4.77	4.18
j	0.00335	1.19	3.50	1.65	8.37	7.34
n	0.00219	0.779	2.28	1.08	5.47	4.80
o	0.0202	7.20	21.1	9.98	50.6	44.3
p	0.00928	3.30	9.70	4.58	23.2	20.3
q	0.000194	0.06	0.20	0.095	0.484	0.424

*Calculated from the relative distribution of displays given in Table 1*b* in Paton and Caryl (1986).