

Horse signals: the sounds and scents of fury

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Summary

During contests animals typically exchange information about fighting ability. Among feral horses these signals involve olfactory or acoustical elements and each type can effectively terminate contests before physical contact becomes necessary. Dung transplant experiments show that for stallions, irrespective of rank, olfactory signals such as dung sniffing encode information about familiarity suggesting that such signals can be used as signatures. As such they can provide indirect information about fighting ability as long as opponents associate identity with past performance. Play-back experiments, however, show that vocalizations, such as squeals, directly provide information about status regardless of stallion familiarity. Sonographs reveal that squeals of dominants are longer than those of subordinates and that only those of dominants have at their onset high-frequency components.

Keywords: communication; combat; fighting ability; individual identity; signals; information; assessment; displays

Introduction

Combat and communication are inextricably related since contests involve assessment and are settled by differences among individuals in fighting ability, resource valuation, or both (Maynard Smith, 1976; Parker and Rubenstein, 1981). From the earliest moments when two rivals meet, information about fighting ability is transmitted and often prevents contests from escalating to damaging levels. Understanding of how such information is encoded in displays is, however, not yet complete.

During contests between wild animals two different mechanisms have been identified for acquiring information about an opponent's ability. In one, typified by the roaring of red deer (Clutton-Brock and Albon, 1979) and the breast stripe of great tits (Jarvi and Bakken, 1984), signals display status (Rohwer, 1975) or the ability to fight fiercely if challenged. In the other, typified by the plumage markings of wintering turnstones (Whitfield, 1987), or the calls of pikas (Conner, 1985), signals simply indicate identity (Collias, 1943), which can be used to extract information about fighting ability as long as individuals are able to associate an opponent's signature with the outcome of a previous encounter. Here we present the first evidence of both types of signalling occurring during agonistic encounters. In feral horses, vocalizations encode information about status whereas odours provide information about identity.

Signalling and fighting in horses

Most contests among feral stallions inhabiting Shackleford Banks, a barrier island off the coast of North Carolina, are settled quickly with one individual retreating when approached by another;

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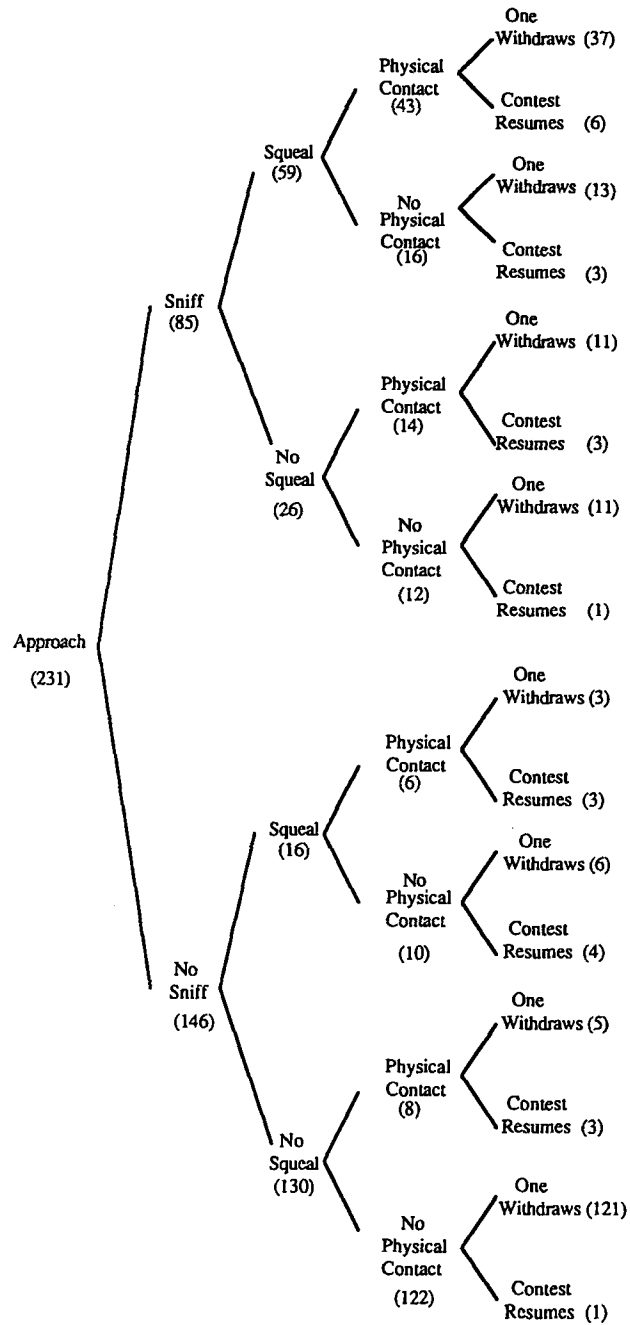


Figure 1. Bifurcating tree showing the sequence of events during a sample of 231 agonistic encounters among stallions when females of a resident stallion were at risk of being lost to an approaching stallion. The numbers in parentheses indicate the number of contests that proceeded from the previous stage.

of a sample of 310 male–male interactions involving 21 stallions during one breeding season, dominance was determined solely by an approach in 53% of the contests. In the remaining agonistic interactions stallions remained within 1 m of each other and displayed or fought; of a sample of 231 interactions in which stallions could have lost females from their breeding groups, hence making the costs of losing extremely high, 43% of such interactions involved olfactory or vocal signalling, and 35% involved either moderate (pushing) or intense (biting, kicking, or rearing) physical contact (Fig. 1).

Contests typically follow a ritualized sequence. Approaches are followed by the sniffing of faces, genitals, or defecations, which in turn is followed by vocalizing. If close-contact contests are not resolved after these signalling stages, and 58% are not, pushing or rubbing ensues, and if these actions also fail to settle the dispute biting, kicking and even rearing on the hind legs occurs. Nineteen per cent of contests follow the sequence from beginning to end and, of those interactions that escalate to physical contact ($n = 71$), 61% do so with both olfactory and acoustical signalling, whereas only 11% do so without either; 28% involve one form of non-contact assessment.

Physical aggression is effective in settling disputes since 80% of the contests that involve combat ($n = 71$), and 88% that involve intense combat ($n = 35$), terminate with one or both contestants withdrawing from the fray with dominance having been clearly established. Yet, displays by themselves are also very effective; 79% of the encounters ending after sniffing or vocalizing ($n = 30$) do not begin anew (Fig. 1). Clearly, assessment plays a frequent and effective role in peacefully settling horse contests without recourse to physical contact, but how each signal achieves its success is unclear.

Signals and meaning

Rationale

The feral horses inhabiting Shackleford Banks have a population and social structure which makes it possible to determine experimentally how information about fighting ability is encoded in acoustical and olfactory signals. Approximately 100 horses reside on this 15 km island, with the breeding adults living in 16 single-male, multi-female groups (harems). Although there are no extreme topographical barriers on the island, two sub-populations exist. Each consists of eight breeding groups and associated sub-adult or 'bachelor' males, and a clearly defined linear dominance hierarchy exists among these stallions (Rubenstein, 1986). If signals operate only as *status indicators* then sounds and scents of dominants (top half of the hierarchy) should elicit a different behavioural response from those of subordinates (bottom half of the hierarchy), irrespective of familiarity. Signals that act as *signatures* should also enable individuals to identify those that are familiar from those that are not. Thus if signals serve only as signatures then sounds and scents of familiar (same sub-population) and unfamiliar (different sub-population) individuals should elicit different behavioural responses, irrespective of dominance status.

Methods

These possibilities were tested by recording squeal vocalizations from typical fights and collecting fresh samples of dung from two dominant and two subordinate stallions from each sub-population. These signals were then presented to males in each sub-population following a $2 \times 2 \times 2$ factorial design: signals from dominants and subordinates were presented to both familiar and unfamiliar, dominants and subordinates. Presentations were made between and among categories because rank differences between two dominants or between two subordinates were always less than between a dominant and a subordinate. A total of 55 vocalizations were

Table 1. Responses to squeal play-backs and dung presentations. Head-up and sniff responses are derived from experiments using a $2 \times 2 \times 2$ factorial design: squeals and dung collected from dominant and subordinate stallions were presented to both familiar and unfamiliar, dominants and subordinates. The rank of the responding stallion had no significant effect on the responses, and none of the two-way or three-way interactions were statistically significant. As a result, only the means and (standard errors) from the two critical main effects are displayed. Significant positive effects are shown in the notes. The contingency analysis was performed on approach frequencies.

Type of signal	Type of response	Characteristics of signalling stallion			
		Dominant	Subordinate	Familiar	Unfamiliar
Sound	Head-up (s)	42.7 (9.5)	98.7* (17.9)	70.4 (14.6)	75.6 (16.9)
	Approach (%)	44	77**	58	67
Scent	Sniff (s)	9.9 (1.2)	10.3 (1.4)	7.9 (0.8)	13.3*** (1.9)

* $F_{1,47} = 6.54, p < 0.02$.

** $\chi^2 = 5.19$ (with Yates Correction), $n = 55, p < 0.01$.

*** $F_{1,38} = 7.43, p < 0.01$.

transmitted from a loudspeaker hidden no more than 70 m away, and the stallion's response was noted: For how long did he lift his head and did he approach the speaker? A total of 46 scent samples were presented by placing a few pieces of fresh dung 50 m in front of an approaching group, and the intensity of the stallion's response was measured by the length of his sniff.

Results and discussion

Table 1 shows that the squeals of subordinate stallions elicited significantly greater responses than those of dominants. Stallions, regardless of their own dominance status, kept their heads elevated for almost twice as long when they heard the call of a subordinate and they were much more likely to approach the squeal if it came from a low-ranking male. Stallions, however, showed no significant difference in their response to squeals of males they encounter regularly and those they never meet. Exactly the opposite pattern of responses occurred for olfactory cues (Table 1). Stallions were able to discriminate among dung samples on the basis of familiarity, whereas they showed no difference in their response to scents of dominant and subordinate stallions. The dung of unfamiliar stallions was likely to be examined for nearly twice as long as that of familiar males.

These experiments show that two different stages of contests contain information about fighting ability, but in different sensory forms and encoded in different ways. Since scents are being used to discriminate among individuals on the basis of familiarity, they can potentially be used as signatures to identify individuals. Their reliability as indicators of fighting ability will depend, however, on how frequently individuals encounter each other and how rapidly fighting ability changes. In horses, home range overlap is extensive among breeding males and rank changes little during one breeding season (Rubenstein, 1981; Berger, 1986; Duncan, 1983). Consequently, during a fight associating the odours of an opponent encountered frequently with the scent and outcome of previous encounters should provide an accurate, if somewhat dated, estimate of an opponent's ability. Moreover, even for interlopers, such as the 'bachelor' males

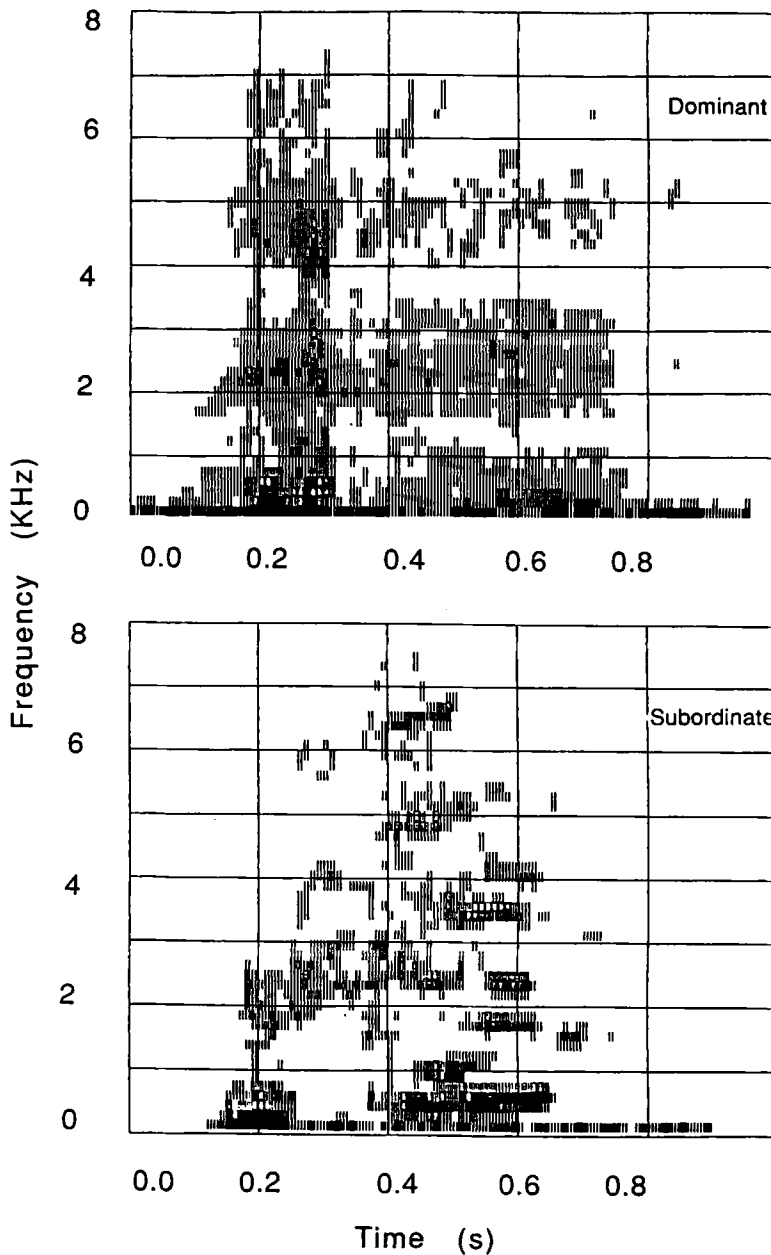


Figure 2. Sonograms of dominant and subordinate squeals. Spectral analyses of three dominant and three subordinate calls were recorded digitally and 'average calls' were computed, and digital displays made, at the Rockefeller University courtesy of Peter Marler and his laboratory. Louder sounds appear as darker squares.

who rarely interact with the breeders, being able to compare the scent of an opponent with memorized scents of dung piles, should facilitate assessing an opponent's status early in a contest (Gosling, 1982). Since stallions defecate most frequently in core areas where critical resources are located (Rubenstein, 1986), a match between an opponent and a frequently encountered scent

should tell an interloper that he has met the area's dominant resident who values the area highly. Thus unless the interloper is itself of superior ability, it is not likely to win, and any attempt at escalating or even acquiring more current or accurate information would be energetically wasteful and risky (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981). The fact that dung piles persist for months may explain why such an indirect method of assessing ability occurs first in close-contact contests; 85% of such encounters involve sniffing first (Fig. 1).

As status signals, squeals could provide instantaneous indications of tenacity if correlated with physiological ability at withstanding escalated fighting. At least for Shackleford horses this appears to be the case since the sonograms of the dominant squeals and those of subordinates are fundamentally different (Fig. 2). Those of dominants are about 20% longer than those of subordinates ($t_6 = 6.25$, $p < 0.001$), and they contain high-frequency sounds at the beginning of the call that are absent from those of subordinates. Moreover, the squeals of dominants maintain three strong broad sound energy bands to the end, whereas those of subordinates have narrower ones in the same region. Such a pattern implies that dominants are able to squeal more forcefully and for longer than subordinates, and suggests that lung capacity, or the strength of the thoracic musculature, is better developed in dominants. The alternative possibility that the shorter and 'thinner' sounding squeals of subordinates highlight inferior ability – such as 'Don't worry about me' – seems less likely since subordinate squeals hold the attention, and are actually more likely to attract the responder than those emitted by dominants (Table 1).

While other studies on anurans (Davies and Halliday, 1978; Ryan, 1985; Robertson, 1986), birds (Rohwer and Rohwer, 1978; Krebs, 1982), and mammals (Clutton-Brock and Albon, 1979; Conner, 1985) have shown that assessment occurs during the early stages of contests, none has shown that a redundant signalling system is operating. Perhaps horses are special in that home ranges of groups are large, yet overlap considerably, and both olfactory and acoustic senses have been heightened because of reproductive and anti-predator requirements. Alternatively, many other species may actually be employing different sensory modalities to encode information about fighting ability in different ways as a means of enhancing honest signalling in large populations where groups are only moderately stable.

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