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**Aggressive vocalizations in feeding guanacos, *Lama guanicoe***

Shieh, Bao-sen, Ph.D.

Iowa State University, 1993

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300 N. Zeeb Rd.  
Ann Arbor, MI 48106



**Aggressive vocalizations in feeding guanacos, Lama guanicoe**

by

**Bao-sen Shieh**

**A Dissertation Submitted to the  
Graduate Faculty in Partial Fulfillment of the  
Requirements for the Degree of  
DOCTOR OF PHILOSOPHY**

**Department: Animal Ecology  
Major: Animal Ecology**

**Approved:**

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## GENERAL INTRODUCTION

The adaptive significance of diverse signals in aggressive interactions has been an important topic in animal communication. Auditory signals can create composite signals in association with other modes of communication, such as visual or chemical signals. In addition, auditory signals have the advantages of greater complexity of temporal coding, simultaneous production with other types of behaviour (such as feeding), and adaptation to quick changes in motivational state (Marler 1967, Kiley 1972). Few studies have been directed towards the aggressive vocalizations within social groups of ungulates.

Graded threat displays and vocalizations are often emitted during aggressive interactions between group members of guanacos (Lama guanicoe) (Franklin 1982, Pilters 1956). The guanaco, a wild species of the South American camelids, is highly social with family groups, male groups, female groups, and solo males in open-arid land environments (Franklin 1982, 1983). In Lama species, studies to date have documented 13 intraspecific vocalizations and 4 interspecific alarm vocalizations (Pilters 1956, Wood 1981, Franklin 1982). Among those 13 intraspecific vocalizations, 8 have been observed primarily in aggressive situations. Franklin (1982) hypothesized that 3 aggressive vocalizations (snort, grumble, and click) are low to mild forms of aggression. Three aggressive vocalizations are common in feeding guanacos: squeak (first described in this study), grumble and spit vocalizations. Beyond these descriptions, aggressive vocalizations in Lama species are poorly understood.

The purpose of this study was to investigate the causation and

functional significance of aggressive vocalizations in feeding guanacos. Aggressive interactions within a captive group of guanacos when feeding on hay were recorded. The causation of aggressive vocalizations, namely, individual and contextual variations, were investigated. Finally, logistic regressions of winning probabilities against difference of rank were used to examine the applicability of an optimal deceit model, based on aggressive interactions and vocalizations in the feeding guanacos.

### Explanation of Dissertation Format

This dissertation is composed of a literature review and 2 papers. Following the explanation of dissertation format, I review game theory models for the functional significance of aggressive signals. Paper 1 investigates the causation of aggressive vocalizations, particularly the individual and contextual variations in feeding guanacos. Paper 2 applies an optimal deceit model to aggressive vocalizations in feeding guanacos, compares observations with predictions and proposes an alternative hypothesis. Papers 1 and 2 are prepared for submittal to Behaviour and Animal Behaviour, respectively. The personal pronoun "we" is used to indicate multiple authorship through both papers. The second author was responsible for supervising the study, providing the subject animals, and editing the papers. Following Paper 2, there is a General Summary followed by references cited in the General Introduction.

## A Review of Game Theory Models for Aggressive Signals

Maynard Smith (1982) stated that evolutionary game theory is a way of thinking about evolution at the phenotypic level where the fitness of particular phenotypes is frequency dependent in the population; that is, the best strategy to adopt depends on what others are doing (Maynard Smith 1976). An evolutionary game can be described by the set of strategies, the possible states of the population (players), and the payoffs (fitness) corresponding to different states of the population (Maynard Smith 1982). A strategy is defined as a specification of what an individual will do in all the situations which it may find itself; it may be pure or mixed (e.g. in situation A, do behaviour x with probability p and behaviour y with probability q) (Maynard Smith 1976, Maynard Smith and Parker 1976).

The aim of most applications of game theory is to determine the evolutionary stable strategy (ESS) for a given set of conditions; the result depends on the available strategies, the cost and benefits they entail, and their frequencies (Archer 1988). An ESS is a strategy such that if all the members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection (Maynard Smith 1982). In addition, behavioural strategies in animals don't necessarily imply conscious decision-making as in humans (Huntingford and Turner 1987), and the ESS is a result of individual selection (Maynard Smith 1976).

Enquist (1985) suggested that the evolutionary game of aggressive signals involves 2 important processes: communication due to choice of



behaviour (strategic game) and communication due to "performance" of a chosen behaviour (signalling game) (Fig. 1). There are 3 possible kinds of information transmitted in signals: information about fighting abilities (strength, status, size, or age), information about intentions, and information about the environment (Maynard Smith 1982, Krebs and Davies 1987). Earlier game models, such as the Hawk-Dove game, have focused on the strategic choice and assumed perfect information about fighting ability and intention. The signalling process and choice of strategy have been both incorporated together in recent models (e.g. Bond 1989, Grafen 1990).

In the following review of models, aggressive signals primarily refer to visual and auditory displays. Environmental constraints on the evolution of those signals such as attenuation and degradation in sounds (Wiley and Richards 1978) will not be considered.

### Strategic Games

Symmetric Games In his classic model of the Hawk- Dove game, Maynard Smith (1974, 1976) assumed that there were random interactions and no individual differences. Subsequent researchers have found those assumptions to be unrealistic, and several revised models have been suggested (Huntingford and Turner 1987, Archer 1988, Toro and Silio 1986). I will first describe symmetric games, which assume that contestants are equal in contests, and then discuss asymmetric games in which individuals are unequal.

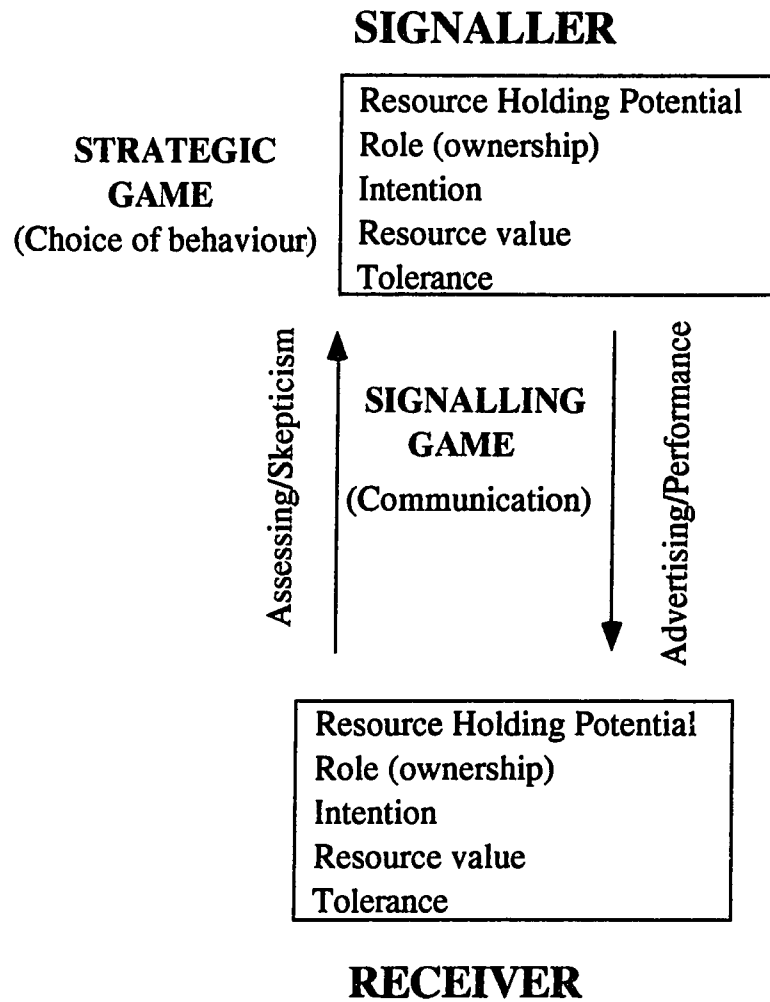


Figure 1. Aggressive signals model.

The ESS in the basic Hawk-Dove game depends on the resource value ( $V$ ) and cost of injury ( $C$ ) (Maynard Smith and Price 1973, Maynard Smith 1982). Animals that play the 'Hawk' strategy would escalate until injured or until opponent retreats. Animals that play the 'Dove' strategy would display, and retreat when opponents escalate. If  $C < V$ , the pure 'Hawk' strategy is an ESS. If  $C > V$ , a mixed strategy is an ESS, where the proportion of hawk adopted is  $P(H) = V/C$ . The mixed ESS may be a genetic polymorphism in a population with  $V/C$  proportion of hawk individuals and  $(1 - V/C)$  of dove individuals, or a mixed strategy of an individual with  $V/C$  of time playing hawk and  $(1 - V/C)$  of time playing dove ((Maynard Smith and Parker 1976, Maynard Smith 1982).

Caryl (1981) revised the basic Hawk-Dove game with the 'Prudent Hawk' which attacks at the same level as a hawk but withdraws after a suitable time even if no injury has occurred, and added the variable, the risk of attack to the value of the resource ( $C/V$  = the risk of escalating). The decision rules of the outcome in Caryl's model (1981) included: (1) hawk and hawk shall fight until one is injured (selected randomly if equally matched); (2) the injured one stops fighting at once; and (3) the injured one pays a cost  $C$ , the victor gets  $V$ , the prize. He concluded that when the risk of escalating ( $C/V$ ) is great, prudent hawks form the majority of the population, and the probability of injury between 2 prudent hawks is  $V/C$ . He also argued that a contest usually stops before serious injury occurs and this model fits better than the original Hawk-Dove model, where all escalated contests ended in serious injury. In a model that allows for a more complex strategy, 'Retaliating' (attacks only if one's opponent does so first)

was the ESS (Maynard Smith 1982, Maynard Smith and Price 1973). In conclusion, for those models of symmetric games, evolutionarily, mixed and 'limited attack' strategies are more stable than the pure Hawk or Dove strategies (Archer 1988).

Asymmetric Games and Assessment Real contests are rarely symmetric. Asymmetries of opponents could be payoff relevant, such as resource holding potential (RHP), resource value, or payoff irrelevant (role of ownership, etc.) (Maynard Smith and Parker 1976).

RHP asymmetry The asymmetries of RHP could involve greater body size, better weapons, more fighting experience, or a history of more winning; however, body size is probably the most important indicator of RHP (Archer 1988).

With RHP asymmetries, assessment of an opponent before beginning a fight is an ESS (Parker 1974, Maynard Smith and Parker 1976). Animals assess reliable indicators of RHP because those indicators are direct and indirect measures of the factors influencing RHP (Parker 1974), or because they are too costly to fake (Zahavi 1977). For example, animals such as toads could use the pitch (frequency) of an individual's call as an indirect cue of its body size (Davies and Halliday 1978). In addition, signals with the largest coefficient of variation (most variable components of displays) should be the best predictors of RHP (Zahavi 1975, 1977). In their game theory model of RHP asymmetries, Maynard Smith and Parker (1976) predicted that animals use behavioural patterns as reliable indicators of

relative RHP early in an aggressive encounter, and opponents assess those indicators to settle contests without escalation. However, other theoretical studies have shown that whether an assessing strategy (escalate if an estimated opponent is smaller, display if an estimated opponent is larger) is an ESS depends on the cost of assessing (Maynard Smith 1982).

If the cost of assessing is less than the cost of losing an escalated fight, assessing is an ESS even when RHP is not a perfect predictor of which animal would win; but if cost of assessing is more costly than escalation, the hawk strategy is shown to be the ESS. That is, assessing is an ESS if assessment is cheap, escalation is dangerous, and body size is a good predictor of victory.

In these early models, it was assumed that information acquisition was perfect and animals made assessments 'before' fighting (Maynard Smith and Parker 1976, Parker and Rubenstein 1981). If information about the asymmetry between the contestants is uncertain, contests could involve a phase of assessment (Maynard Smith 1982). To model this situation, Enquist and Leimar (1983) proposed that information about the difference in fighting ability was accumulated during the fight in a way that can be compared with statistical sampling, and used 'causal factor space' analysis to examine the sequence of behaviour when information was incomplete before fighting. They concluded that if the fighting proceeds in stages with varying intensity, the most informative but also most costly display will take place during the final escalated phase.

Role asymmetry Ownership role is a common asymmetry in animal conflicts. The Bourgeois strategy (an animal should respond like a

hawk when it is the owner and like a dove when it is the intruder) is an ESS in the Hawk-Dove-Bourgeois game (Maynard Smith 1974, 1982). This game assumes that owners always win without a damaging fight, and the result could be reversed for any given pair when ownership is reversed. An escalated fight would occur if both animals perceive themselves to be the owner (Archer 1988). Animals use ownership role to settle the conflict in the situations when they have perfect information about an opponent's role, and the cost of potential injury is relatively high (Maynard Smith and Parker 1976).

If resource value is much smaller than the cost of escalation, ownership may be used to settle a contest even though there is a RHP difference. Bourgeois strategy is also more likely to be the ESS when animals with dangerous weapons are contesting food items (Archer 1988). Although ownership is supposed to be payoff irrelevant, in most situations, resource value may be different for the owner and the intruder, and the owner usually has larger RHP. Payoff relevant factors such as resource value and RHP, are usually confounded with ownership.

Intention asymmetry Maynard Smith (1982) defined intention as what animals attempt to do next. Classical ethologists have believed that animals use a range of actions that could be arranged on a scale of increasing aggressiveness, and they present information about their intention during contests. Animal contests usually start with a low level of aggression and gradually escalate, but may or may not end in physical contact (Maynard Smith 1982). Dawkins and Krebs (1978) argued that

animals should not convey their intention during contests. Hinde (1981) explained that the ambiguity in the meaning of signals is the result of indecision about what to do next in the aggressive interactions ("fight" or "flight"). For predicting the ultimate winner, Caryl (1979, 1982) opposed the idea that animals tell the truth about their intentions, and concluded that displays convey no information about motivation, or about the level to which an animal will escalate.

Whether an animal tells the truth about its intentions by signals depends on the relative costs and benefits of those signals (Huntingford and Turner 1987). Bluffing intentions may be possible and not risky but the cost of lying may be high and outweigh the benefit (Enquist 1985, Zahavi 1977). Besides, revealing intentions could be an ESS in repeated encounters between the same individuals even if intentions are easily bluffed (Van Rhijn and Vodegel 1980, Maynard Smith 1982). It has also been proposed that transmitting information about one's internal state to an opponent is a byproduct rather than the prime evolutionary pressure in developing behavioural displays in aggressive contests (Turner and Huntingford 1986). Moreover, distinguishing the RHP from internal state is usually impossible (Van Rhijn 1980, Moynihan 1982). Although researchers have discussed the question of whether animals should conceal their intention in a conflict or not, little attention has been directed toward modeling the asymmetries of intention and assessment.

More than one aspect of asymmetries    It is hard to prove individuals use particular asymmetric cues to settle contests because one

asymmetric factor usually confounds another, such as previous experience with dominance, or ownership with size or age (Maynard Smith and Price 1973, Maynard Smith and Parker 1976). In a game with asymmetries of resource value and ownership, Bourgeois is usually an ESS when the resource value is greater for the owner than the intruder (Maynard Smith 1982). This result was based on assuming equal RHP between contestants and complete information about resource value (Archer 1988).

When the risk of injury is much greater than the resource value, contests may be settled by ownership (Bourgeois as an ESS) even if a payoff relevant asymmetry exists (RHP or resource value). However, if the payoff relevant asymmetry (ex. RHP) exceeds a critical value, it will be used to settle the contest (Hammerstein 1981). That is, the bigger the difference in RHP, the more likely the contest will be settled by RHP assessment.

The Assessing strategy is an ESS if ownership is associated with a big difference in resource value and injury is relatively serious to the owner ( $V < C$ ). However, the ESS is the Bourgeois strategy if  $V > C$  for the owner and the RHP differences of contestants are below a threshold (Hammerstein 1981). These conclusions are based on assuming that opponents are fully informed about the asymmetric features (resource value, etc.) and the assessment of relative fighting ability is unambiguous and without cost (Hammerstein 1981).

In New Zealand jumping spiders (Marpissa marina), Jackson and Cooper (1991) found that away from nests, larger males tended to win, but at nests, prior residency in a nest was more important than body size. In experimental studies of controlling residency and experience, Turner and



Huntingford (1986) concluded that male mouthbrooders (Oreochromis mossambicus) settled contests on the basis of size in long-term contests while showing intention in their behaviours during short-term contests; that is, intention predicted the outcome in shorter contests, while RHP predicted the outcome in longer contests. Animals should reveal asymmetry (especially the asymmetry of RHP) to settle contests, if little opportunity for bluffing exists (Turner and Huntingford 1986). They also found that the size asymmetry between 2 male mouthbrooders did not strongly affect initial behaviour, but was very important in influencing the end of the contest. This implied that assessment occurred 'during' rather than 'prior to' a fight.

Information is transmitted in the process of a prolonged contest and this changes the cost and fighting intention. Therefore, a contestant may not be able to set maximum cost beforehand (Turner and Huntingford 1986). Enquist (1985) speculated that in shorter contests, the strategic game offers more favorable options with more choices of displays, while in longer contests, assessment of performance becomes more important and favors the repetition of the same displays.

In conclusion, in asymmetric games of animal conflicts, the ESS must be pure and unique whether it is Bourgeois or Assessing strategy. As the asymmetries become more obvious, it is likely that more costly (energy and time or risk of injury) cues will be used for assessment. Escalation occurs when the assumption of perfect information about the asymmetries is violated (Maynard Smith and Parker 1976).

Strategic games have been very useful in understanding the evolutionary process in animal conflicts, and are an essential part of

modeling aggressive signals (Fig. 1). However, to complete the picture, an important part, the signalling process, needs to be added.

### Prisoner's Dilemma

In a signalling game, signallers can choose either an honest or bluffing strategy, and receivers can choose to be either trusting or devaluing (non-trusting). The outcome of this game is similar to the game of Prisoner's Dilemma. Signallers gain a higher payoff by bluffing whether receivers are trusting or devaluing; and, in response to signallers' bluffing, receivers do better by devaluing (Wiley 1983). As a result, bluffing signallers and devaluing receivers are evolutionarily stable strategies against other strategies. However, when signallers bluff and receivers devalue, the payoffs for signallers and receivers are smaller than when signallers are honest and receivers are trusting (Maynard Smith 1982). This is the dilemma: higher payoffs of honesty and trusting are denied without knowing the opponent's next move and by trying to take advantage of one's opponent.

If the game is played repeatedly between 2 opponents with memories of past encounters, Tit-for-Tat (in receivers, trust on the first move and continue to trust if signallers are honest; otherwise, devalue if signallers are bluffing) appears to be the best strategy, and honesty in signalling is an ESS in this iterated game of Prisoner's Dilemma (Wiley 1983).

For social animals, repeated encounters between 2 individuals are unavoidable. Therefore, the conclusions of Tit-for-Tat strategy as the best strategy and honesty in signalling would likely be true in social animals if they have memories of past encounters. However, this Prisoner's Dilemma

game has not considered one important aspect in social animals, the asymmetries of RHP. Especially for animals living in relatively stable groups, dominance status is the most important asymmetry (Van Rhijn and Vodegel 1980).

### Strategic-signalling Game

In the strategic-signalling game, Grafen (1990) modeled the underlying quality of signallers ( $q$ ), signallers' advertising level ( $a$ ), and perceived value ( $p$ ) of signallers' quality by receivers. In Grafen's model, signallers vary in their qualities ( $q$ ), and can advertise their qualities according to a function  $A(q)$ ; receivers assess the advertising value ( $a$ ) and perceive the signaller's quality as  $p$  (the perceived value) according to the function  $P(a)$ . Because this game model allows signallers to choose their advertising level and opponents could have unequal qualities (such as fighting abilities), it could be considered as a strategic game of asymmetry. In addition, this game model incorporates the signalling process that considers how signals are performed and perceived.

Grafen (1990) concluded that honesty was an ESS in this model as Zahavi's handicap principle claimed (Zahavi 1975). High quality animals (such as high fighting ability) don't gain by deception; on the other hand, producing the deceptive signal in low quality animals is costly and may reduce their chances for a successful interaction (by depleting energy) (Grafen 1990). The costs of signals guarantee their honesty and determine the possibility of deception; cues are reliable only if they cannot be faked (Zahavi 1975, Zahavi 1977). Although asymmetries and the signalling

process were considered in the strategic-signalling game, the strategy of signallers was limited to advertising, and the choice of receivers was limited to assessment, allowing no other strategies for the receivers, such as devalue or withdraw.

### Optimal Deception

Manipulation theorists have believed that signals persuade and manipulate the receivers rather than inform them; receivers respond to manipulation by "mind reading" (Dawkins and Krebs 1978, Krebs and Dawkins 1984). As a result of this mutual exploitation, signals in aggressive conflicts should be loud, exaggerated and deceitful (Krebs and Dawkins 1984). However, if the aggressive signals do not provide truthful information about their concealed qualities and evolve to a uniform expression of maximum intensity as manipulation theorists have suggested, these signals will be ignored by the receiver and fail to influence the receiver's behaviours. Herein lies the paradox of manipulation and information: if displays are not truthful, they cannot have been selected for; if they were selected for the purpose of communication, they cannot be truthful (Bond 1989).

Optimal deception was first implied by Andersson (1980). He explained the evolution of diverse threat signals as a result of frequency-dependent oscillation of the effectiveness. Signals indicating high attack probabilities (revealing intention) are subject to bluff, and when those signals are less effective because of receiver's skepticism, other signals with more reliability will replace those more deceitful signals (Andersson 1980).

Those reliable signals will become subject to bluff. Under the circumstance, their use will reach a stable balance because of frequency-dependent selection. Dawkins and Guilford (1991) attributed this stability of bluffing signals to settling contests with cheaper and less reliable cues in order to avoid the high costs of assessment in receivers. It was Bond (1989) who first combined asymmetries of opponents and strategic choice with the signalling process, and modeled optimal deceit in animal conflicts. Bond (1989), in his optimal deceit model, first constructed a 2 by 2 payoff matrix with asymmetries of contestants (signaller either inferior or superior than receiver in fighting quality), and 2 strategies of receivers (challenge or withdraw). Then, he introduced the exaggeration factor, the expected value of disparity between the signal and signaller's true quality value, to generate a Poisson distribution. The model demonstrated that given 3 simple strategies by signaller (truth, 10% deceit, no information), the expected payoff for the signaller was greatest at 10% deceit when the risk of being injured in an escalated fight was low or medium. Only at high risk, was "no information" the preferred strategy. Additionally, an equilibrium level of deceit was converged in the model when the advantages of deceit and the disadvantages of selecting for skepticism in the receiver were simulated; that is, optimal deceit was an ESS.

The basic assumptions of the optimal deceit model were: the opponents had no prior experience with one another, and were equally matched in apparent physical qualities (Bond 1989). In social animals, those assumptions may be unrealistic because of frequent and repeated interactions between group members with unequal physical appearances (size, color,

confirmation, etc.).

### Considerations for Modeling in Social Animals

In a social group, group members are usually unequal in fighting abilities. They interact repeatedly, having prior experience of interactions and preferred opponents. Although group members may compete for resources on a short-term basis, they cooperate as a stable group for long-term advantages.

By applying the communication game of the Prisoner's Dilemma to repeated encounters and considering no asymmetries between opponents, an ESS of honesty seems to be the result of the Tit-for-Tat strategy. When considering only asymmetries of fighting qualities, and assuming no prior experience between opponents, optimal deceit seems to be the ESS. To resolve this difference, both asymmetries and repeated encounters between opponents of social animals need to be considered in a game model.

The above models have all assumed random encounters between opponents. Social members may interact more frequently with particular members in a group, such as 2 steps apart in the dominance hierarchy (Freeman et al. 1992). Toro and Silio (1986) constructed a 2 by 2 strategy game for the assortment of encounters. However, asymmetries and repeated encounters (prior experience) were not incorporated in this game of nonrandom encounters.

In investigating the evolution of fatal fighting, Enquist and Leimar (1990) modeled the value of present and future contesting. They concluded that when the value of present contesting was similar to or greater than the

future value, selection favored strategies of fighting to death; as a result, the assessment on asymmetries of fighting ability and ownership role had little effect on settling the contest. However, in social animals, the advantages of group living such as avoiding predation and securing more food in the future (Krebs and Davies 1987) may outweigh the present value of contesting for food. In this situation, the future value will have greater effect on the present game of conflict.

To meet the real situations in social animals, modeling of repeated encounters, asymmetries, nonrandom encounters, and future value of group living should be emphasized in investigating the functional significance of aggressive signals.

### Conclusions

Different game models have different results on ESS (Table 1). In symmetric games, mixed or limited strategies are evolutionarily stable. In asymmetric games, the ESS is pure and unique, e.g. Assessing or Bourgeois. Symmetric and asymmetric games have focused on the strategic choice in animal conflicts, and both are important in modeling aggressive signals. To complete the picture of modeling aggressive signals, the signalling process needs to be added.

The communication game of Prisoner's Dilemma shows that signals should be deceitful, but by allowing repeated encounters between opponents with memories of past encounters, honesty of signals is evolutionarily

Table 1. A summary of game models suggested for aggressive signals.

Game model	Properties of models		Evolutionary Stable Strategy (ESS)
	Signal <sup>a</sup>	Opponent <sup>b</sup>	
Symmetry	(T)	S	Mixed ESS
Asymmetry	(T)	A	Pure ESS (Bourgeois, Assessing, etc.)
Prisoner's dilemma	(T)	S	Deceit
Strategic-Signalling	(T) (C)	A	Honesty (iterated) <sup>c</sup>
Optimal deceit	(T) (C)	A	Honesty
			Optimal deceit

a: Strategic game (T), Signalling game (C).

b: Symmetry of opponents (S), Asymmetry of opponents (A)

c: If repeated encounters and with memories, Tit-for-Tat is the best strategy and honesty is the ESS.



stable. The strategic-signalling game model and the optimal deceit model investigated both the strategic choice and signalling process but have different conclusions. The strategic-signalling game model concluded that honesty is the ESS, while the optimal deceit model suggested that optimal deceit is the ESS. The different conclusions resulted from different assumptions. The strategic-signalling game model assumed assessment as the only strategy in receivers, while the optimal deceit modeling assumed 2 strategies in receivers (challenge or withdraw). For animals living in social groups, I suggest that 2 important factors, nonrandom encounters and the future value of group living, should be incorporated in game models of aggressive signals.

**PAPER 1.**

**AGGRESSIVE VOCALIZATIONS WITHIN GUANACO FEEDING  
GROUPS: INDIVIDUAL AND CONTEXTUAL VARIATIONS**

**AGGRESSIVE VOCALIZATIONS WITHIN GUANACO FEEDING  
GROUPS: INDIVIDUAL AND CONTEXTUAL VARIATIONS**

by

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## INTRODUCTION

The adaptive significance of diverse signals in aggressive interactions has been one of the most important issues in animal communication. Individuals in a social group have different roles; as a result, the number of signal types increases (MARLER, 1967). Auditory signals can create composite signals in association with other modes of communication, such as visual or chemical signals. Moreover, auditory signals have the advantages of greater complexity of temporal coding, simultaneous production with other types of behaviour, and adaptation to quick changes in motivational state (MARLER, 1967; KILEY, 1972).

To understand the significance of the diverse vocalizations in mammalian aggression, we first need to investigate the causation. Two areas should be addressed: individual and contextual variations. On the individual level, age and social roles (especially dominance rank) are the two main variables affecting the usage and relative rate of diverse calls. It has been shown that the number of call types produced by young animals is often fewer than adults because of developmental limitations of the postnatal structural and functional maturation of the nervous system and vocal tract (EHRET, 1980; KILEY, 1972). Although the relationship between visual displays and dominance has been investigated in many animals (MAYNARD SMITH et al., 1988), little is known about the relationship between vocal signals and dominance within a social group. Individual recognition among group members could be achieved not only by visual and scent communication, but also by individual differences of call structures. The recognition of individual voice pattern is an especially important skill for

individuals in social groups with repeated interactions (LILLEHEI & SNOWDON, 1978).

Context has been increasingly studied in vocal communication because it provides both functional and motivational information (GOULD, 1983). The context of a signal is considered to be the signal itself, all that accompanies it, and the past and present state of the signaller and receiver (SHALTER et al., 1977). MORTON (1977) suggested that motivation-structural (M-S) rules govern the physical structure of sounds used in proximity of other animals in communication. Several studies (SIBER, 1984; AUGUST & ANDERSON, 1987) have been carried out to demonstrate that aggressive motivation is expressed through harsh, nontonal, and low frequency sound, while on the other end, fearful and friendly motivation is expressed through tonal, and high frequency sounds. However, two correlated problems have become apparent in testing M-S rules: (1) operational measures of motivational state were lacking, especially for different degrees of intensity; and (2) M-S rules were tested by comparing the two extreme ends of motivation (aggressive vs. friendly) rather than a continuum as originally emphasized by MORTON (1977).

A series of alternating calls given in the same behavioural context may reflect oscillating states of motivation (EHRET, 1980). Thus, different degrees of aggressive motivation and the behavioural context contribute to eliciting a particular vocalization. In other words, diverse vocalizations used in aggressive interactions may be the combined result of the contextual variations, including behavioural (external) and motivational (internal) stimuli.

Although KILEY (1972) described a wide variety of ungulate aggressive vocalizations, most studies have focused mainly on long-range communication between competing males (CLUTTON-BROCK & ALBON, 1979; GUNDERSON & MAHAN, 1980; HALL et al., 1988). ATKESON et al. (1988) qualitatively studied close-range communication in white-tailed deer (Odocoileus virginianus), describing aggressive vocalizations relative to context and intensity of aggression.

Graded threat displays and different vocalizations are often emitted during aggressive interactions between group members of guanacos (Lama guanicoe) (FRANKLIN, 1982; PILTERS, 1956). The guanaco, a wild species of the South American camelids, is highly social with family groups, male groups, female groups, and solo males that primarily inhabit arid-open land environments (FRANKLIN, 1982 & 1983). In Lama species, studies to date, have documented 13 intraspecific vocalizations and 4 interspecific alarm vocalizations (Table 1). Among those intraspecific vocalizations, 8 have been observed primarily in aggressive situations. FRANKLIN (1982) hypothesized that 3 aggressive vocalizations (snort, grumble and click) are low to mild forms of aggression. In feeding guanacos, there are 3 common aggressive vocalizations: squeak (first described in this study), grumble and spit vocalizations. However, aggressive vocalizations in Lama beyond these descriptions, are poorly understood.

The aim of this study was to investigate the causation of 3 aggressive call types (squeak, grumble, and spit vocalizations) in feeding guanacos by assessing individual and contextual variations. Specific objectives were: (1) to examine the effects of individual variation in age and social rank on the

rates of aggressive displays and call types, and the sonagram structure of the different call types; (2) to classify the contextual variations of aggressive calls by sequential usage and Logistic Discriminant Analysis; and (3) based on the contextual variations and sonagram structures, to test the motivation-structural rule which predicts that these 3 aggressive calls should form a continuum of aggressive intensity from low, mild to high.

## METHODS

This study was conducted on a captive herd of guanacos composed of 10 adult females (>4 years old), 5 subadults (2-4 years old), 3 yearlings (6-12 months old), and 3 juveniles (0-5 months old). Group size ranged from 16 to 18 due to 3 births and 1 death. All animals were ear-tagged for permanent identification and neck collared for easy identification from a distance. There were 5 llamas (*Lama glama*) which joined the group during different time periods. Those llamas were treated like guanacos in collecting data and assigning social rank. However, only observations of guanacos were used in data analysis.

### Data Collection

Sampling began immediately after providing hay in the morning and afternoon. Preliminary observations showed that aggression rates decreased as feeding time increased, sharply dropping after 1 hour of feeding. Therefore, we observed 6 animals in sequential order for 48 minutes (8 minutes per animal) by continuous focal animal sampling (ALTMANN, 1974). In each replication, each guanaco in the herd was first observed by a randomly chosen order and then observed in another order until all guanacos were observed once in order 1 to 6. Ten replications and 135 hours of observations were completed from March to November 1989. Identities of signaller and receiver, aggressive threat displays (FRANKLIN, 1982; WILSON & FRANKLIN, 1985) and aggressive vocalizations from signallers' perspective (Table 2), and subsequent behaviours of signallers and receivers were recorded for each aggressive interaction. Aggressive vocalizations



were defined because they were usually accompanied by signaller's ear threat displays and receiver's reaction of turning away. An aggressive interaction began at the start of the signaller's aggressive behaviours and ended with nonaggressive behaviours, such as feeding, and head or body turned away.

Aggressive vocalizations were recorded from a Sennheiser shotgun microphone that connected to a Nagara III recorder (tape speed: 7.5 ips). The auditory sound was translated into visual sonagrams by a Multigon Uniscan II spectrograph. To produce better visual images of call structures on the spectrograph monitor, the spectrograph frequency ranges were set at 20 kHz for spit (noisy structure), 5 kHz for grumble (pulsed structure), and 2 kHz for squeak (tonal or compound with tonal and noisy structures).

### Sonagram Measurements

Definitions of vocalization structure were adapted from STRUHSACKER (1967) and EISENBERG et al. (1975). A 'syllable' was defined as a temporally uninterrupted tracing on the sonagram. Syllables could be tonal with harmonics or noisy without harmonics. A 'note' (or click) was a extremely brief ( $\leq 0.05$  sec in this study) syllable. A 'phrase' was 1 or more notes separated from another group of notes by a time interval longer than any internote interval within that phrase (see Appendix 1B for average time interval). A 'call' was a phrase or group of phrases and distinctive at the time of hearing. A 'series of calls' was a group of calls (either same or different types) in an interaction.

Variables on sonagrams of squeak, grumble, and spit vocalizations are

described in Table 3. Spit vocalizations had 3 variables (Fig. 1, Appendix 1A). Grumbles were distinguished into 3 subtypes according to the number of phrases on sonagrams: G1 with 1 phrase, G2 with 2 phrases, and G3 with 3 phrases (Fig. 2, Appendix 1B). Four subtypes of squeaks were distinguished: SQ1 with 1 tonal syllable, SQ2 with 2 tonal syllables, SQ3 with 1 noisy syllable, and SQ4 with 1 noisy syllable and 1 tonal syllable (Fig. 3, Appendix 1C).

### Data Analysis

Social rank was assigned by modifying the fighting success index described by CLUTTON-BROCK et al. (1979). The most dominant individual with the highest fighting success index was ranked number 1, while the most subordinate with the lowest fighting success index was ranked number 26. The fighting success index was calculated with the outcomes of all aggressive interactions during the study period: fighting success index =  $(W + \Sigma w + 1) / (L + \Sigma l + 1)$ , where  $W$  = the number of guanacos the subject defeated,  $\Sigma w$  = the total number those defeated guanacos ( $W$ ) defeated,  $L$  = the number of guanacos the subject lost to, and  $\Sigma l$  = the total number those guanacos ( $L$ ) lost to. The winner of an encounter was determined by the opponent displaying a 'head turn away' or 'body turn away'. A tie was determined when both guanacos turned away or neither turned away.

Two kinds of sample units were treated in the analysis: individuals and interactions. First, with individuals as sample units, the differential usage of call types was examined by the Friedman test (HOLLANDER & WOLFE, 1973). For focal animals giving signals, their rates of aggression

(including all aggressive behaviours, see Table 2) and of the 3 call types were transformed according to the Box-Cox method (BOX & COX, 1964; SABIN & STAFFORD, 1990). After transformation, ANOVA was used to test the effects of social rank, age (after removing social rank effect), and observation order. We assumed that the social rank derived from the fighting index indicated the animal's potential fighting strength (body size, experience, etc.), whereas its age class was the representative of development excluding the fighting strength. Individual differences of measurements on sonagrams were analyzed first by nonparametric analysis with the Kruskal-Wallis test (HOLLANDER & WOLFE, 1973). Then, significant variables ( $p < 0.10$ ) of those measurements were transformed according to the Box-Cox method, and the effects of social rank and age (after removing social rank effect) were tested by ANOVA.

Secondly, aggressive interactions were used as sample units under the assumption that they were independent of each other. Logistic Discriminant Analysis was used to discriminate the binary responses from the signaller's perspective, such as the outcomes ('win' vs. 'not win') of interactions ('not win' included lose and tie), calling behaviour ('call' vs. 'not call'), the occurrence of a particular call type ('occur' vs. 'not occur'), and the occurrence of a particular call type in subsequent calling. These binary responses, coded as 1 or 2, were used as dependent variables. Age class and social rank of signallers and receivers, and behaviours of signallers were used as explanatory variables (Table 2). Stepwise logistic regression with 0.25 as the entered and removed probability was used to select models. Then, for those selected explanatory variables, different combinations of

variables were used in logistic discriminant functions, and the logistic discriminant function with the highest correct rate in predicting the 'occurred' or 'win' events was chosen as the end result. 'Sensitivity' from the computer output is interpreted as the probability of correctly classifying the 'win' or 'occur' observations, while the 'specificity' is the probability of correctly classifying the 'not win' or 'not occur' observations. For each aggressive interaction, the fitted logistic discriminant model produced an estimator of the probability that the aggressive interaction is a 'win' or 'occur'. When this estimated probability is larger than the specified critical probability, the aggressive interaction is classified as a 'win' or 'occur'. As the critical probability is increased the sensitivity tends to decrease and specificity tends to increase. The critical probability in discrimination was initially set at 0.5 and then substantially changed to achieve a good compromise for high levels of correct rate and sensitivity. The analysis was done using the Logistic procedure of SAS software (SAS INSTITUTE, 1989).

## RESULTS

Guanacos feeding close together used 3 aggressive call types: squeak, grumble, and spit vocalizations. Spit vocalization was the loudest when an animal suddenly released a burst of air, saliva, or food from its mouth. Squeak and grumble were subtle and only heard from a close distance to the signaller. The squeak, first being recorded in this study, sounded similar to 'en' or 'em'. Guanacos grumbled without opening their mouth, and the grumble sounded similar to 'glu-lu'.

### Individual Variations

#### Call type usage

The number of aggressive call types used by juvenile guanacos was smaller than all other age groups (Table 4). Spit vocalization was the only call type used in all age groups. Juveniles did not use the squeak and grumble vocalizations. Although yearlings produced all 3 call types, the number of subtypes used was less than half that of subadults and adults. The number of the squeak and grumble subtypes was the same in subadults and adults. G1 was the most frequently used subtype (75%) of grumbles, and SQ1 was the most common subtype (55%) of squeaks (Table 4).

#### Rates of aggression and vocalizations

The effect of social rank on the rates of aggressive displays and aggressive vocalizations was significant (natural logistic transformation of aggression rate:  $F_{1,16}=129.47$ ,  $p<0.05$ ; inverse transformation of squeak rate:  $F_{1,16}=15.43$ ,  $p<0.05$ ; inverse transformation of grumble rate:

$F_{1,16}=24.99$ ,  $p<0.05$ ; inverse transformation of spit rate:  $F_{1,16}=14.52$ ,  $p<0.05$ ). As guanacos increased in social rank, their rates of aggression and usage of the 3 aggressive call types increased (Fig. 4).

Social rank and age were highly correlated (Spearman rank correlation coefficient  $r=0.89$ ,  $p<0.05$ ): older guanacos were dominant over younger ones. With removal of the rank effect, only the rate of aggression showed a significant age effect (natural logistic transformation of aggression rate:  $F_{3,16}=3.87$ ,  $p<0.05$ ) (Fig. 5).

After the initial feeding of hay to guanacos, the rates of aggression and spit vocalization significantly declined (significant order effect on natural logistic transformation of aggression rate:  $F_{5,80}=2.83$ ,  $p<0.05$ ; and inverse transformation of spit rate:  $F_{5,80}=2.61$ ,  $p<0.05$ ). Both rates of aggression and spit vocalization were particularly higher in the first 8 minutes (order 1) (Fig. 6). Although the rates of grumble and squeak were higher in the first 8 minutes, the order effect was nonsignificant (Fig. 6).

### Sonagram structures

Appendix 1 summarizes variables of sonagrams for the 3 aggressive call types and their subtypes. For those variables showing significant differences among individuals by the Kruskal-Wallis test, we further transformed them according to Box-Cox method and examined the individual difference (  $df = n1-1$ ,  $n2-n1$  in Table 5), social rank and age effects (social rank effect with  $df = 1$ ,  $n1-4$ , and age effect with  $df = 2$ ,  $n1-4$  if only 3 age groups used the call type; or social rank effect with  $df = 1$ ,  $n1-5$ , and age effect with  $df = 3$ ,  $n1-5$  if all 4 age groups used the call type) on

those transformed variables by ANOVA (Table 5). Social rank had a significant effect on 4 variables: 3 variables of G1 subtype (75% of all grumbles) and duration of the spit vocalization. In addition, all 4 variables showed that as the guanacos became more dominant, the duration of those sonagram measurements increased (Fig. 7).

None of the variables examined showed a significant age effect after removing linear rank effect. Additionally, 12 variables showed significant individual differences without significant rank or age effects (Table 5): 1 on spit vocalization, 2 on G1 subtype, 4 on G2 subtype (21% of all grumbles), 1 on G3 subtype (4% of all grumbles) and 4 on SQ4 subtype (13% of all squeaks).

### Contextual Variations

#### Winning, calling and call types

We classified the contextual variations of aggressive interactions relative to the outcomes of winning vs. not winning. Guanacos who initiated aggressive interactions (as signallers) won 78% of the time (2308 of 2949). For signallers, winning interactions could be predicted correctly 97% of the time based on the occurrence of spit vocalization, third ear threat display (E3), head turned toward (HTT), physical contact (CONTACT), moving toward to the receiver (CLOSE), the age class and dominance of the signaller, and the social rank of the receiver (Table 6).

We classified the contextual variations of eliciting vocalizations by discriminating the occurrence of calling or not calling. Calling occurred in 37% of aggressive interactions (1095 of 2949). Those calling interactions

could be correctly predicted 51 % of the time based on the signaller's social rank, age class, and associated behaviours. Aggressive calling most likely occurred when the signaller had neither physical contact nor its head turned toward the receiver. The receiver's age class or social rank did not significantly increase the sensitivity and total correct rate (Table 6).

Among the 1095 calling interactions, we further classified the contextual variations of each call type by discriminating their occurrence. Although the occurrence of squeak and spit vocalizations could be predicted by the absence of other call types (sensitivity of the occurrence of squeak = 65%, and of spit vocalization = 64%), none of the signaller's aggressive visual displays, age class or social rank of the signaller and receiver improved the sensitivity and total correct rate (Table 6). However, the sensitivity for predicting grumble could be increased (up to 87%) by including the signaller's ear display (FET) and signaller's rank (SRTOTAL) in the model; guanacos grumbled more when not giving FET ear displays and when they were higher social rank.

### Sequential calling

Among 1315 aggressive interactions with calling (the sample size included interactions without knowing the identity of receivers or other displays), 76% of those calling aggressive interactions had only a single call, 19% of them had a series of 2 calls, and 5% of them had a series of 3 or more calls. All age classes of guanacos had a series of 2 calls in an aggressive interaction. All age classes except yearlings used a series of 3 calls in an aggressive interaction. Feeding guanacos showed significant



preference in the usage of the 3 call types (Fig. 8). For the first call in an aggressive interaction, squeak was used significantly less than grumble and spit vocalization among 20 individuals ( $S'=15.2$ ,  $k=3$ ,  $n=20$ , Friedman multiple comparison,  $p<0.05$ ). For the second call in an aggressive interaction, spit vocalization was used more than squeak among 19 individuals ( $S'=12.5$ ,  $k=3$ ,  $n=19$ , Friedman multiple comparison,  $p<0.05$ ). For the third call in an aggressive interaction, spit vocalization was also used more than squeak among 10 individuals ( $S'=9.8$ ,  $k=3$ ,  $n=10$ , Friedman multiple comparison,  $p<0.05$ ).

To predict the subsequent call types and classify their occurrences, we discriminated the occurrence of a particular call type as the second and the third calls in a series of calling. The occurrence of particular call types used in the second aggressive call was less predictable (Table 7). The sensitivity in predicting squeak or grumble as the second call was less than 34%, even when including all the significant explanatory variables in logistic discriminant functions. The sensitivity was only 55% in predicting spit vocalization as the second call, with the explanatory variables being squeak as the first call (V1SQ), the second ear display (E2), signaller's dominance, and not showing BHET (Table 7).

The difficulty in predicting the call types was also observed in the third call (Table 8). In predicting squeak or grumble as the third call, the sensitivity was less than 20%, even when all the significant explanatory variables were included in the logistic discriminant functions. Previous call types played no significant role in predicting spit vocalization as the third

call; ear displays (not showing BHET and HUTT) could be used to predict it correctly, but with only 50% sensitivity (Table 8).

## DISCUSSION

### Diverse Aggressive Vocalizations

Squeak, grumble and spit vocalizations were 3 aggressive call types in feeding guanacos. Using sonagram structures, we further categorized squeak into 4 subtypes and grumble into 3 subtypes. MARLER (1967) suggested that close-range communication is usually highly graded and species living in social groups should freely exploit the potential advantages of graded signals. Vocalizations could be combined with visual displays to increase the diversity of graded signals. A feeding guanaco would likely call when it had no physical contact or without turning its head toward a receiver (Table 6); this might suggest that the occurrence of calling could replace those behaviours which might interrupt feeding. In this study, although calling was only involved in one third of the aggressive interactions, the occurrence of calling not only could increase the diversity of graded signals but also replaced the signaller's potential for physical contact and turning its head toward the receiver.

We interpreted the individual and contextual variations of aggressive vocalizations in feeding guanacos to be a reflection of social rank, motivational state, and individual identity. Namely, the spit vocalization indicated high intensity of aggression and social rank; grumble vocalization was associated with low to medium intensity of aggression, social rank, and individual identity which can't be explained by social rank or age; and squeak vocalization was related to low intensity of aggression without indications of social rank, age, or other individual identity.

### Spit vocalization

Spit vocalization was the only call type associated with the context in predicting the winning outcome of an aggressive interaction. It was also the most intense and loudest vocalization. Duration of the spit vocalization not only showed significant individual differences but also linearly increased with individual social rank. As such, the duration of spit may be used as a reliable indicator of individual strength much like the roaring rates of rutting male red deer (CLUTTON-BROCK & ALBON, 1979). When guanacos are feeding, spitting not only involves the rapid expelling of air, but also the expulsion of any food or liquid that may be present in the mouth. Occasionally animals eject additional stomach contents, especially in prolonged and intense spitting bouts. This loss of ruminated food from the stomach may make the spit more energetically expensive, and subordinates either may not be able to afford or are incapable of increasing the duration of spitting. It may also be too costly to fake (ZAHAVI, 1975, 1977; WILEY, 1983). Other evidence to suggest the high intensity of aggression and the higher energy demand of spit vocalization, was the significant effect of first access to the food (observation order) on the rate of spit vocalization, especially at the start of feeding (first 8 minutes of observation). The higher spit rate of all age classes at the start of feeding may be related to both higher hunger levels (resulting in higher aggression) and less energy cost of spitting when there was less ruminated food in the stomach.

Spit vocalization was used by all ages classes. In predicting its occurrence, however, neither social status nor the behaviours of signaller and receiver were effective. This may be because every individual could use spit

in association with other behaviours to communicate their high aggressive motivation and to cause the retreat of a receiver.

### Grumble vocalization

Grumble and squeak vocalizations were considered less intense forms of aggression because of their ineffectiveness in thwarting receivers and because they were not as loud as spit vocalization. Call structure analysis revealed that the duration of the call, the width of first and last inter-note of G1 (subtype 1 of grumble) increased with higher social rank. Thus, these 3 properties of G1 may serve as alternative cues for higher rank individuals to communicate their dominance without employing the more costly spit.

Selection should favor dominant individuals which honestly advertise their strength (rank) by the cheapest possible cue (CLUTTON-BROCK & ALBON, 1979). In addition, bluffing with simpler and cheaper cues such as G1 which constituted 75% of all grumbles could possibly be neutralized by repeated encounters with familiar group members, thus adopting the TIT-FOR-TAT strategy within the social group (VAN RHJN & VODEGEL, 1980; WILEY, 1983). In fact, as the social rank of signaller increased (lower value of SRTOTAL), grumbles were more likely to occur in guanacos (Table 6).

For G2-3, we found 5 variables with individual differences but without the significant effects of age or social rank. The subtype G2 was used by more individuals than G3. This suggests that G2 calls may play an important role in individual recognition without age and strength (social rank) being factors.

### Squeak vocalization

Most sonagram measurements of squeaks (87%) showed no significant individual differences. SQ4 (13% of squeaks) was the only subtype with 4 variables having significant individual difference, but social rank and age had no significant effects. Perhaps we did not measure the right variables to show significant individual differences on the sonagrams of squeak except SQ4, or the usage of most squeak vocalizations may simply indicate the low intensity of aggression without individual identity. However, there was no evidence to indicate that the signaller with lower social rank than the receiver would likely use the squeak to hide their identity (Table 6, nonsignificant DOMINANCE on the occurrence of squeak).

Juvenile guanacos didn't use grumble and squeak, the lower intensity of aggressive calls. This could have resulted from developmental limitations, such as neural coordination or learning how to use those subtle calls in the right contexts.

Squeak may have been derived from nonaggressive vocalization-humming (bleating) and lost the characteristics of individual identity except in SQ4. The continua of call structures from squeak (tonal, higher frequency change) to the nonaggressive humming (tonal, less frequency change, personal data) may represent different levels of excitement (KILEY, 1972). That is, squeak represented a higher level of excitement than that of humming. Further analysis comparing the nonaggressive humming and aggressive squeak might clarify this point.

### Motivation-Structural Rules

AUGUST & ANDERSON (1987) found that aggressive sounds among mammals generally followed the predictions of M-S rules, that is, aggressive sound had lower frequencies and wider band widths than nonaggressive sounds. However, most studies have only focused on comparing the two ends of motivation rather than the continuous properties as MORTON (1977) emphasized. In this study, we tried to explore the continuous properties of aggressive vocalizations, and classify the degree of aggressive motivation by discriminating the outcome of interactions. The reasoning is that the signaller with a high level of aggressive motivation will more likely win the interaction than a low level of aggressive motivation. In this study, spit vocalization was the only call type associated with the context of winning outcome; therefore, it could be the most intensely motivated form of aggressive vocalization. Grumble and squeak were the less aggressive vocalizations because neither one of them were associated with the context in predicting the winning outcome; there was no evidence to show that the motivation associated with grumble was more aggressive than that with squeak. As a result of testing the M-S rules, we found that the diverse aggressive vocalizations formed a continuum of call structure from a more tonal, harmonic call (squeak), to a nontonal pulsed call (grumble), to the most harsh (up to 20 kHz) and noisy call, the spit vocalization; however, the degrees of aggressive motivation ranged only from the most intense (spit vocalization) to less intense (grumble and squeak).

Most measurements on squeaks showed nonsignificant differences among individuals. This might indicate greater variations of squeak within

the same individual (especially the frequency range and frequency change of the tonal syllable) resulting from indecisive motivation of aggression in different interactions (MORTON 1977).

### Subsequent Callings in An Interaction

For the first call in a series of calling, guanacos used more grumble and spit vocalizations than squeak. If guanacos spit to indicate their high aggression and grumble to state their high social rank (fighting strength), spitting and grumbling at the start of calling might give a subordinate guanaco the maximum threats. Game theorists have suggested that the use of threats with maximum intensity should be at the early stage of a contest (MAYNARD SMITH, 1974; MAYNARD SMITH & PARKER, 1976).

Only the occurrence of spit in subsequent callings was predictable, while the low intensity, squeak, in the subsequent calls was hardly predictable from the preceding call types and other contextual information. In addition, for the second and third calls, guanacos used more spit vocalizations (the most aggressive call) than squeaks (the less aggressive call). This suggests that animals are more likely to show their high intensity of aggression as the contest prolonged (MAYNARD SMITH, 1982a; DAWKINS & KREBS, 1978; CARYL, 1982); and the intent of increasing aggressiveness is more predictable than that of decreasing aggressiveness (ARCHER, 1988; BOND, 1989).

We treated the aggressive interactions of the same individual as independent in the analysis of contextual variations, and focused on the occurrence of vocalizations instead of individual strategy. In addition, the



aggressive interactions were observed when animals were fed hay, a low valued resource compared to mates in male-male competition. The aggressive strategies and vocalizations in contests over a relatively lower valued resource might be quite different from those in contests over higher valued resource (MAYNARD SMITH, 1982b; MAYNARD SMITH et al., 1988; PARKER & RUBENSTEIN, 1981).

In conclusion, we found that social rank had significant effects on the rates of aggressive call types (squeak, grumble and spit vocalization), and call structures in feeding guanacos. We demonstrated contextual variations of the 3 call types by discriminating the outcome of aggressive interactions, the occurrences of calling and call types, and the sequence of call types. These findings will help behavioural ecologists to understand the causation of subtle vocalizations in wild groups, which are difficult to investigate because of windy environments and long observation distance. They will also provide an insight to the study of the evolutionary function of the diverse aggressive vocalizations in social ungulates.

## SUMMARY

We investigated aggressive vocalizations in a captive group of guanacos, Lama guanicoe, composed of adult females, subadults, yearlings, and juveniles. During aggressive interactions of feeding animals, we categorized 3 aggressive call types, squeak, grumble, and spit vocalization. Sonagrams analysis further classified grumble and squeak into 3 and 4 subtypes respectively. Social rank of individuals had significant effects on the rates of aggression and the rates of the 3 call types. Analysis of sonagram measurements showed that the duration of spit and grumble subtype 1 (G1) were positively correlated with social rank. On sonagrams of squeak and grumble, there were variables which showed significant individual difference but the effects of social rank and age were not significant. Logistic Discriminant Analysis of aggressive interactions revealed that spit vocalization was the only call type associated with the context in predicting the winning outcome. Furthermore, the occurrence of grumble increased with the social rank. From the individual and contextual variations, we propose that the diverse aggressive vocalizations in feeding guanacos reflect the combinations of aggressive intensity, social rank, and individual recognition.

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TABLE 1. Described vocalizations of Lama.

Category	Situations	Source
<b>Intraspecific</b>		
<b>Aggressive calls</b>		
Chasing	Territorial defense	Wood 1981
Screech	Territorial defense, male-male interactions	Pilters 1956, Franklin 1982
Gurgle	Male-male interactions	Pilters 1956
Spit	Territorial defense, feeding, male-female interactions	Pilters 1956
Grumble (Growl)	Feeding	Franklin 1982 (Pilters 1956)
Squeak	Feeding	This study
Click	Pre-copulatory chase, meeting strange animals	Pilters 1956
Snort	Male-male, male-female interactions	Wood 1981
<b>Nonaggressive calls</b>		
Scream	Fear, distress	Franklin 1982
Orgling	Mating	Franklin 1982
<b>Hum (Bleat)</b>		
Normal Hum	Mother-newborn auditory contact	Franklin 1982
Interrogative Hum	Baby supplicating for nursing	Franklin 1982
Separation Hum	Separation, reunion	Franklin 1982
<b>Interspecific (Alarm calling)</b>		
Normal call (Neighing)	Alarm	Wood 1981 (Pilters 1956)
Screech	Alarm	Wood 1981
Intermediate	Alarm	Wood 1981
Chirp	Alarm	Wood 1981



TABLE 2. Behavioural variables (from signaller's perspective) used in an aggressive interaction between feeding guanacos.

Variable	Description
<b>Vocalizations of signaller</b>	
SQ	Squeak vocalization
G	Grumble vocalization
SP	Spit vocalization
V1SQ	The first call is squeak
V1G	The first call is grumble
V1SP	The first call is spit vocalization
V2SQ	The second call is squeak
V2G	The second call is grumble
V2SP	The second call is spit vocalization
V3SQ	The third call is squeak
V3G	The third call is grumble
V3SP	The third call is spit vocalization
VHSQ	The most aggressive call is squeak
VHG	The most aggressive call is grumble
VHSP	The most aggressive call is spit vocalization
CALL	Calling occurred
<b>Displays and behaviours of signaller</b>	
AHET	Above horizontal ear threat
HET	Horizontal ear threat
BHET	Below horizontal ear threat
FET	Flat ear threat
HUTT	Head uptilt threat
E1	The first ear display
E2	The second ear display
E3	The third ear display
EARH	The most aggressive ear display (assuming aggressive intensity: HUTT>FET>BHET>HET>AHET)
VISUAL	Ear threat display occurred
HTT	Head turn toward receiver
HTA	Head turn away from receiver
CLOSE	Moving toward receiver
CONTACT	Physical contact with receiver: bite, kick, and/or body contact

TABLE 2. (continued)

**Age and social rank of signaller**

<b>SCL</b>	Age class of signaller. Adult=4, Subadult=3, Yearling=2, Juvenile=1
<b>SRTOTAL</b>	Social rank of signaller. Higher the number, the lower the social rank
<b>DOMINANCE</b>	Signaller has higher social rank than receiver.

**Age and social rank of receiver**

<b>RCL</b>	Age class of receiver. Adult=4, Subadult=3, Yearling=2, Juvenile=1
<b>RRTOTAL</b>	Social rank of receiver. Higher the number, the lower the social rank

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TABLE 3. Descriptions of variables on sonagrams of aggressive vocalizations in feeding guanacos.

Variable	Description
<b>SPIT</b>	
DUR (sec)	Duration of a call
FREQ (Hz)	The highest frequency of a call
PEAK	The number of frequency peaks in a call
<b>GRUMBLE</b>	
G1 (subtype 1 of grumble with 1 phrase of notes)	
DUR (sec)	Duration of a call
FUP1 (Hz)	The highest frequency of a call
NNOTE	The number of notes in a phrase
DFNOTE (sec)	Duration of the first note
DFIN (sec)	Duration of the first internote
DLNOTE (sec)	Duration of the last note
DLIN (sec)	Duration of the last internote
G2 (subtype 2 of grumble with 2 phrases of notes)	
DUR (sec)	Duration of a call
DPHR1 (sec)	Duration of the first phrase
DPHR2 (sec)	Duration of the second phrase
DIPHR1 (sec)	Duration of the first interphrase
FUP1 (Hz)	The highest frequency of the first phrase
FUP2 (Hz)	The highest frequency of the second phrase
NNOTE1	The number of notes in the first phrase
NNOTE2	The number of notes in the second phrase
DFNOTE1 (sec)	Duration of the first note in the first phrase
DFIN1 (sec)	Duration of the first internote in the first phrase
DLNOTE1 (sec)	Duration of the last note in the first phrase
DLIN1 (sec)	Duration of the last internote in the first phrase
DFNOTE2 (sec)	Duration of the first note in the second phrase

TABLE 3. (continued)

DFIN2 (sec)	Duration of the first internote in the second phrase
DLNOTE2 (sec)	Duration of the last note in the second phrase
DLIN2 (sec)	Duration of the last internote in the second phrase

## G3 (subtype 3 of grumble with 3 phrases of notes)

DUR (sec)	Duration of a call
DPHR1 (sec)	Duration of the first phrase
DPHR2 (sec)	Duration of the second phrase
DPHR3 (sec)	Duration of the third phrase
DIPHR1 (sec)	Duration of the first interphrase
DIPHR2 (sec)	Duration of the second interphrase
FUP1 (Hz)	The highest frequency in the first phrase
FUP2 (Hz)	The highest frequency in the second phrase
FUP3 (Hz)	The highest frequency in the third phrase
NNOTE1	The number of notes in the first phrase
NNOTE2	The number of notes in the second phrase
NNOTE3	The number of notes in the third phrase
DFNOTE1 (sec)	Duration of the first note in the first phrase
DFIN1 (sec)	Duration of the first internote in the first phrase
DLNOTE1 (sec)	Duration of the last note in the first phrase
DLIN1 (sec)	Duration of the last internote in the first phrase
DFNOTE2 (sec)	Duration of the first note in the second phrase
DFIN2 (sec)	Duration of the first internote in the second phrase
DLNOTE2 (sec)	Duration of the last note in the second phrase
DLIN2 (sec)	Duration of the last internote in the second phrase
DFNOTE3 (sec)	Duration of the first note in the third phrase
DFIN3 (sec)	Duration of the first internote in the third phrase
DLNOTE3 (sec)	Duration of the last note in the third phrase
DLIN3 (sec)	Duration of the last internote in the third phrase

## SQUEAK

## SQ1 (subtype 1 of squeak with 1 tonal syllable)

DUR (sec)	Duration of a call
BW (Hz)	Band width of the first harmonic

TABLE 3. (continued)

FUP1 (Hz)	The highest frequency of the first harmonic
FLO1 (Hz)	The lowest frequency of the first harmonic
FRANGE (Hz)	Frequency range of the first harmonic (=FUP1-FLO1)
FFCH (Hz/sec)	Frequency change of the first harmonic (=FRANGE/DUR)
SUP1 (Hz)	The highest frequency of the second harmonic
SLO1 (Hz)	The lowest frequency of the second harmonic
SRANGE (Hz)	Frequency range of the second harmonic (=SUP1-SLO1)
SFCH (Hz/sec)	Frequency change of the second harmonic (=SRANGE/DUR)
HARMON	The number of harmonics in a call
DARKEST	The lowest and darkest harmonic in a call

## SQ2 (subtype 2 of squeak with 2 tonal syllables)

DUR (sec)	Duration of a call
DARKEST	The lowest and darkest harmonic in a call
DSYLL1 (sec)	Duration of the first syllable
DSYLL2 (sec)	Duration of the second syllable
IDSYLL1 (sec)	Duration of the intersyllable
BW1 (Hz)	Band width of the first harmonic in the first syllable
BW2 (Hz)	Band width of the first harmonic in the second syllable
HRAMON1	The number of the harmonics in the first syllable
HARMON2	The number of the harmonics in the second syllable
FUP1 (Hz)	The highest frequency of the first harmonic in the first syllable
FLO1 (Hz)	The lowest frequency of the first harmonic in the first syllable
FUP2 (Hz)	The highest frequency of the first harmonic in the second syllable
FLO2 (Hz)	The lowest frequency of the first harmonic in the second syllable
SUP1 (Hz)	The highest frequency of the second harmonic in the first syllable
SLO1 (Hz)	The lowest frequency of the second harmonic in the first syllable
SUP2 (Hz)	The highest frequency of the second harmonic in the second syllable
SLO2 (Hz)	The lowest frequency of the second harmonic in the second syllable
FRANGE1 (Hz)	Frequency range of the first harmonic in the first syllable (=FUP1-FLO1)
FRANGE2 (Hz)	Frequency range of the first harmonic in the second syllable (=FUP2-FLO2)

TABLE 3. (continued)

SRANGE1 (Hz)	Frequency range of the second harmonic in the first syllable (=SUP1-SLO1)
SRANGE2 (Hz)	Frequency range of the second harmonic in the second syllable (=SUP2-SLO2)
SQ3	(subtype 3 of squeak with 1 noisy syllable)
DUR (sec)	Duration of a call
SQ4	(subtype 4 of squeak with 1 tonal syllable and 1 noisy syllable)
Tonal syllable	
DUR (sec)	Duration of the tonal syllable
BW (Hz)	Band width of the first harmonic
FUP1 (Hz)	The highest frequency of the first harmonic
FLO1 (Hz)	The lowest frequency of the first harmonic
FRANGE (Hz)	Frequency range of the first harmonic (=FUP1-FLO1)
FFCH (Hz/sec)	Frequency change of the first harmonic (=FRANGE/DUR)
SUP1 (Hz)	The highest frequency of the second harmonic
SLO1 (Hz)	The lowest frequency of the second harmonic
SRANGE (Hz)	Frequency range of the second harmonic (=SUP1-SLO1)
SFCH (Hz/sec)	Frequency change of the second harmonic (=SRANGE/DUR)
HARMON	The number of harmonics
Noisy syllable	
DUR (sec)	Duration of the noisy syllable

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TABLE 4. Percentage of major call types and subtypes observed in aggressive interactions of feeding guanacos by age class. Numbers in parenthesis are percentages of subtypes within that major call type.

Call types <sup>a</sup>	Age class <sup>b</sup>				Total
	Juvenile	Yearling	Subadult	Adult	
Spit	100	71	47	37	40
Grumble		19	34	45	42
G1		(75)	(59)	(77)	(75)
G2		(25)	(36)	(19)	(21)
G3			(5)	(4)	(4)
Squeak		10	19	18	18
SQ1		(100)	(69)	(52)	(55)
SQ2			(3)	(9)	(8)
SQ3			(25)	(24)	(24)
SQ4			(3)	(15)	(13)
n	17	21	180	1017	1235

<sup>a</sup>: See Table 3 for descriptions of abbreviations.

<sup>b</sup>: Juvenile (0-5 months old), Yearling (6-12 months old), Subadult (2-4 years old, Adults (>4 years old).

TABLE 5. ANOVA of sonagram variables of aggressive vocalizations in feeding guanacos.

Call type <sup>a</sup>	Variable <sup>a</sup>	Sample size		Sources of variations		
		n1	n2	Individual	Rank	Age
SPIT	LN(DUR)	19	489	***	***	ns
	FREQ	19	467	***	ns	ns
GRUMBLE-G1	LN(DUR)	15	390	***	***	ns
	LN(NNOTE)	15	389	**	ns	ns
	SQRT(DFIN)	15	350	***	***	ns
	SQRT(DLNOTE)	15	350	**	ns	ns
	SQRT(DLIN)	15	344	***	**	ns
GRUMBLE-G2	LN(DIPHR1)	11	108	**	ns	ns
	SQRT(DFIN1)	11	88	ns	ns	ns
	SQRT(DLNOTE1)	11	88	**	ns	ns
	SQRT(DLNOTE2)	10	91	***	ns	ns
	SQRT(DFIN2)	10	92	**	ns	ns
GRUMBLE-G3	DUR	7	24	**	ns	ns
SQUEAK-SQ4 (Tonal syllable)	LN(SRANGE)	7	27	ns	ns	ns
	LN(DUR)	7	29	**	ns	ns
	SUP1	7	27	**	ns	ns
	SQRT(FFCH)	7	29	**	ns	ns
	LN(SFCH)	7	27	**	ns	ns
SQUEAK-SQ1	SQRT(SRANGE)	14	122	ns	ns	ns

\*\*\*:  $p < 0.01$ , \*\*:  $p < 0.05$ , ns:  $p > 0.05$ .

<sup>a</sup>: See Table 2 for descriptions of variables; the first 2 letters before parentheses indicate natural log (LN) or square root (SQRT) transformation. n1= the number of individuals, n2 = the number of calls measured.



**TABLE 6. Results of Logistic Discriminant Analysis on call types, calling occurrence and outcome of aggressive interactions in feeding guanacos.**

Explanatory variable <sup>a</sup>	Dependent variable <sup>a</sup>				
	SQ	G	SP	CALL	WIN
SQ		--	--		
G	--		--		
SP	--	--			+
FET		--			
HUTT				+	
E3					+
HTT				--	+
CONTACT				--	+
CLOSE					+
SRTOTAL		--		--	
SCL				--	+
DOMINANCE				+	+
RRTOTAL					+
Correct % (n)	93 (1095)	90 (1095)	85 (1095)	62 (2949)	82 (2949)
Sensitivity % (n)	65 (216)	87 (605)	64 (455)	51 (1095)	97 (2308)
Specificity % (n)	100 (879)	94 (490)	100 (640)	69 (1854)	26 (641)

<sup>a</sup>: See Table 2 for descriptions of variables.

+: Significantly positive effect in predicting the occurrence of the dependent variable in stepwise logistic regression ( $p < 0.01$ ).

--: Significantly negative effect in predicting the occurrence of the dependent variable in stepwise logistic regression ( $p < 0.01$ ).

Correct % = the rate of correctly classifying observations, Sensitivity % = the rate of correctly classifying the "occurred" or "win" events, Specificity % = the rate of correctly classifying the "not occurred" or "not win" events, n = sample size.

TABLE 7. The predictability of the second call type in a series of aggressive calls of guanacos by Logistic Discriminant Analysis.

Explanatory variable <sup>a</sup>	Dependent variable <sup>a</sup>		
	SQ	G	SP
V1SQ			+
V1G	-		
V1SP		+	
SCL		+	
RCL	-		
E2			+
BHET			-
FET		-	
HUTT	+		
DOMINANCE			+
Correct % (n)	97 (1093)	84 (1093)	60 (1093)
Sensitivity % (n)	0 (34)	34 (56)	55 (158)
Specificity % (n)	100 (1059)	87 (1037)	61 (935)

<sup>a</sup>: See Table 2 for descriptions of variables.

+: Significantly positive effect in predicting the occurrence of the dependent variable in stepwise logistic regression ( $p < 0.01$ ).

--: Significantly negative effect in predicting the occurrence of the dependent variable in stepwise logistic regression ( $p < 0.01$ ).

Correct % = the rate of correctly classifying observations, Sensitivity % = the rate of correctly classifying the "occurred" events, Specificity % = the rate of correctly classifying the "not occurred" events, n = sample size.

TABLE 8. The predictability of the third call type in a series of aggressive calls of guanacos by Logit Discriminant Analysis.

Explanatory variable <sup>a</sup>	Dependent variable <sup>a</sup>		
	SQ	G	SP
V1G	-	+	
RCL	+	+	
E1	-		
E2			+
BHET		+	-
HUTT		+	-
Correct % (n)	86 (248)	95 (248)	71 (248)
Sensitivity % (n)	17 (12)	0 (13)	50 (24)
Specificity % (n)	89 (236)	100 (235)	74 (224)

<sup>a</sup>: See Table 2 for descriptions of variables.

+: Significantly positive effect in predicting the occurrence of the dependent variable in stepwise logistic regression ( $p < 0.01$ ).

--: Significantly negative effect in predicting the occurrence of the dependent variable in stepwise logistic regression ( $p < 0.01$ ).

Correct % = the rate of correctly classifying observations, Sensitivity % = the rate of correctly classifying the "occurred" events, Specificity % = the rate of correctly classifying the "not occurred" events, n = sample size.

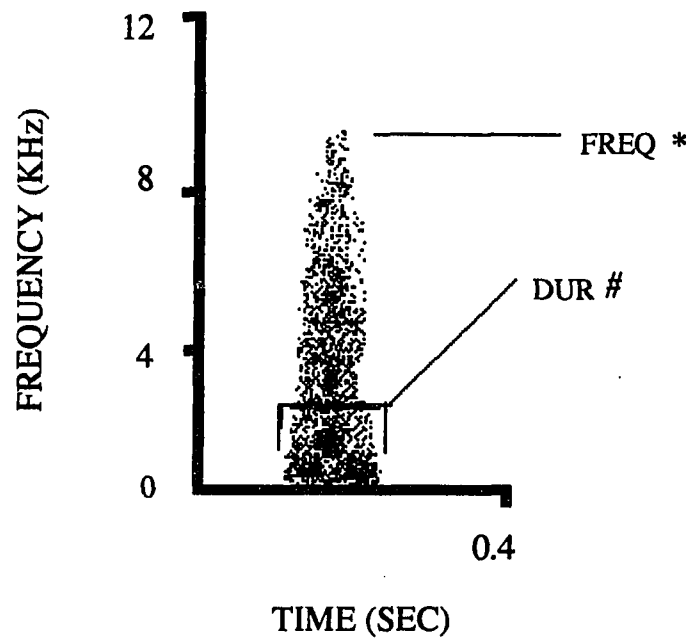


Fig. 1. Diagrammatic sonagrams of a representative spit vocalization in guanacos. See Table 3 for descriptions of variables. \*: significant social rank effect; #: significant individual difference, but without significant effects of social rank or age.

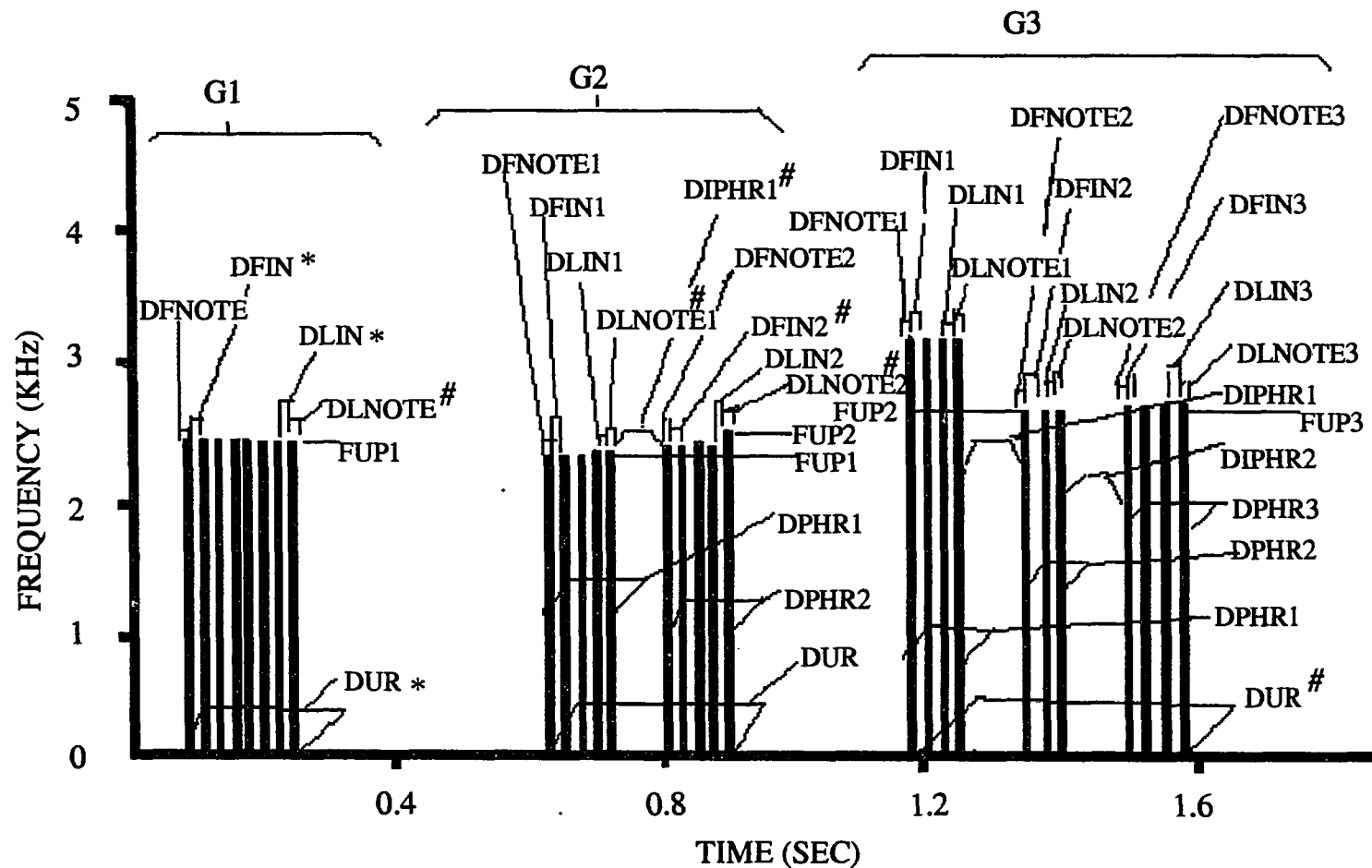


Fig. 2. Diagrammatic sonograms of representative grumbles (subtypes G1-G3) in guanacos. See Table 3 for descriptions of variables. \*: significant rank effect; #: significant individual difference, but without significant social rank or age effect.

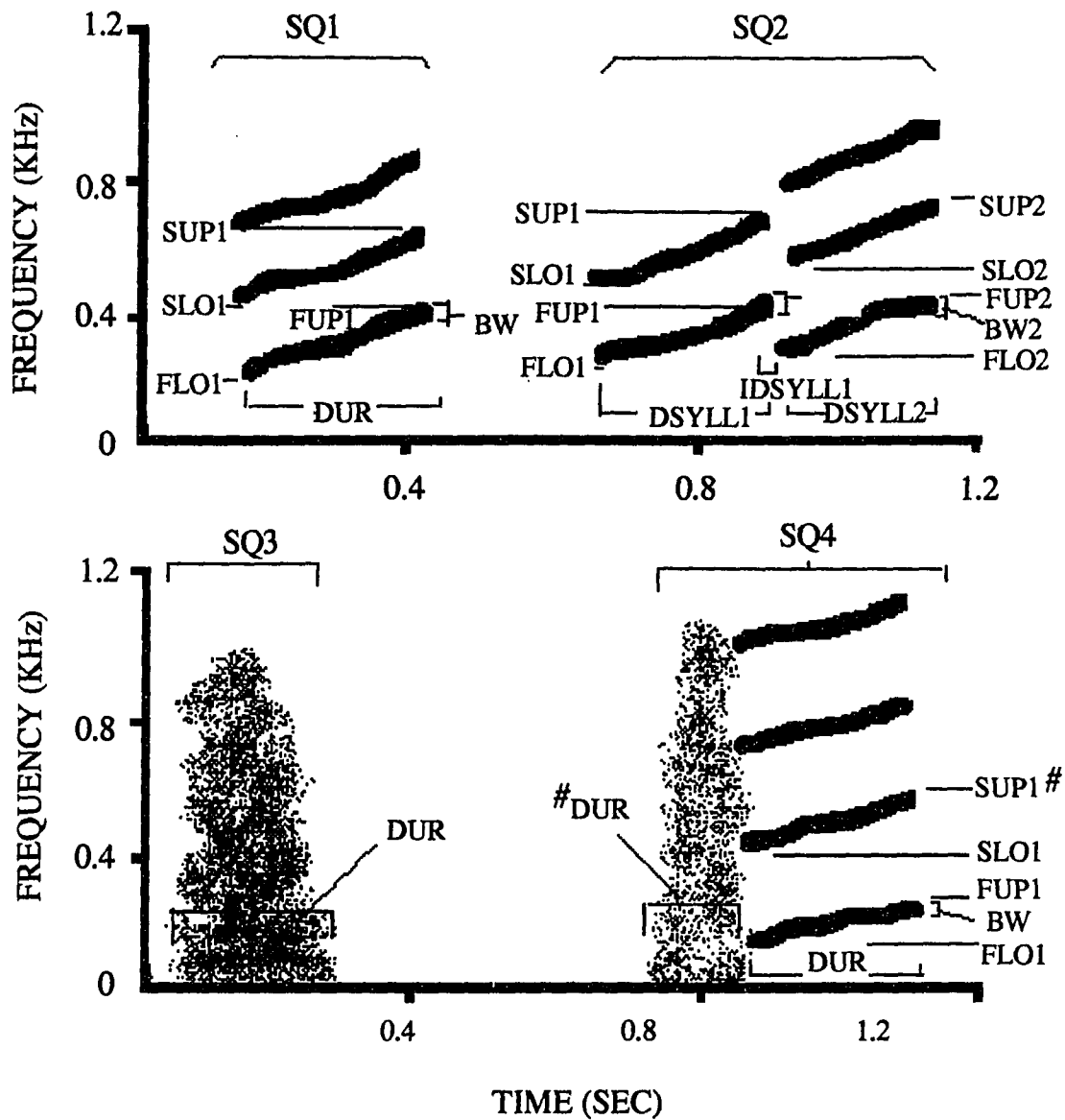


Fig. 3. Diagrammatic sonograms of representative squeak vocalizations (subtypes SQ1-4) in guanacos. See Table 3 for descriptions of variables. #: significant individual difference, but without significant effects of social rank or age.

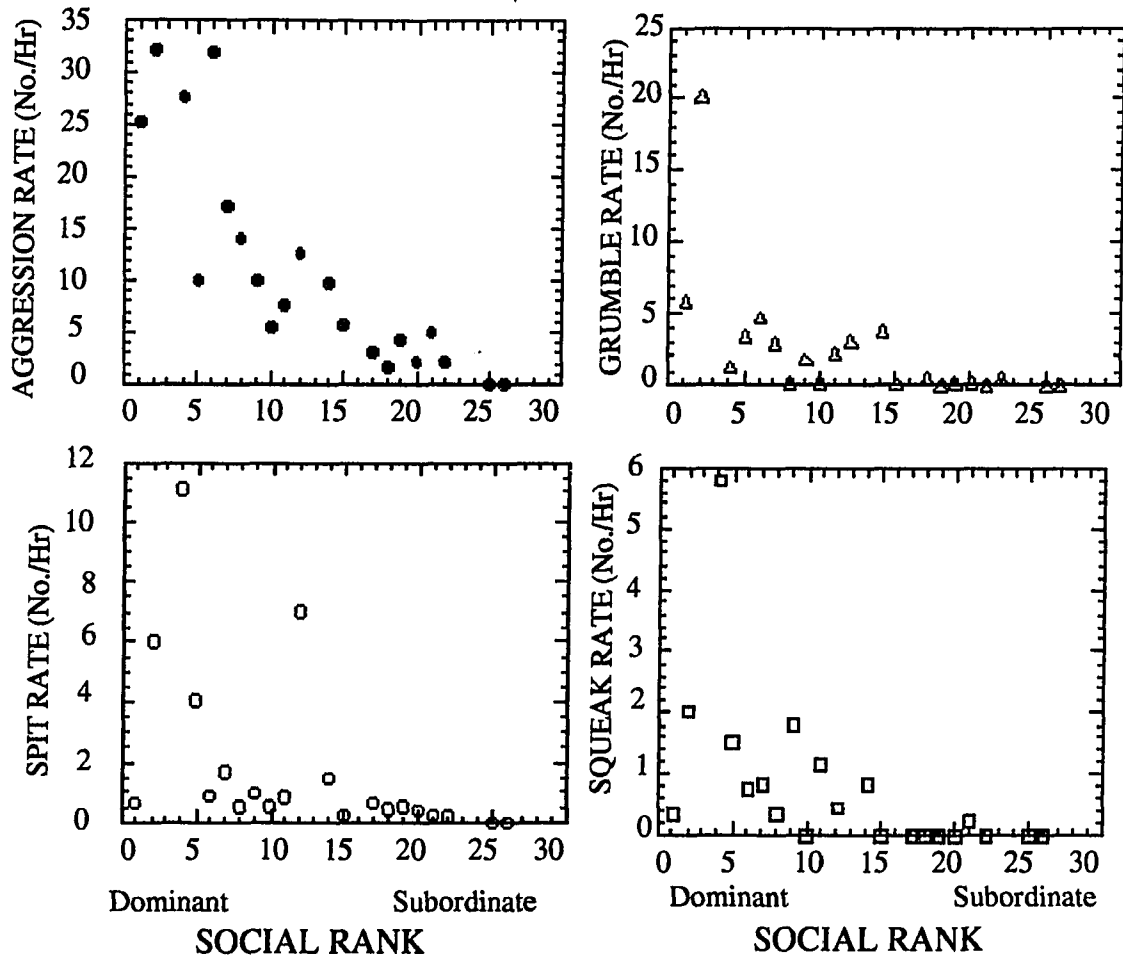


Fig. 4. The rates of aggression, spit, grumble, and squeak compared to social rank of guanacos.

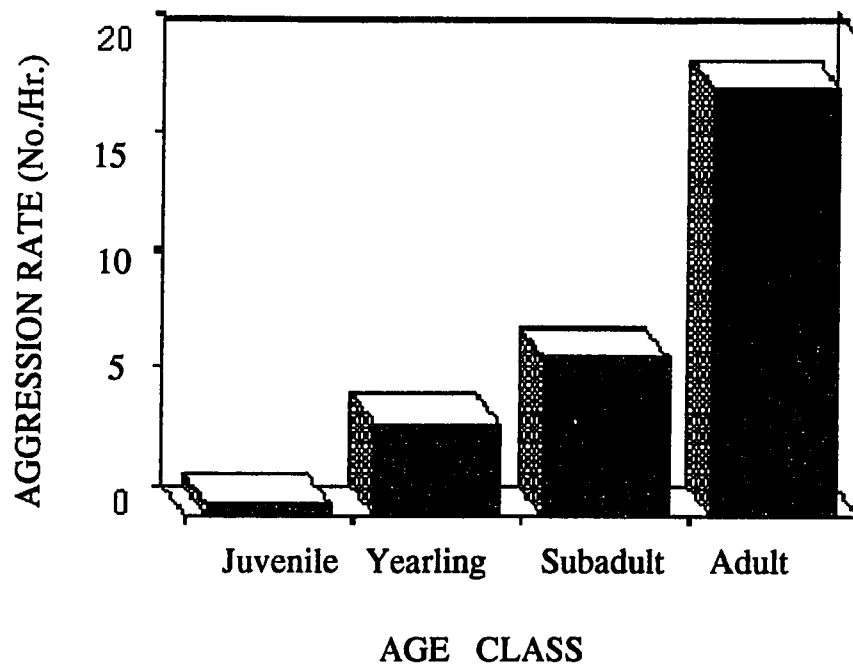


Fig. 5. The aggression rates by 4 age classes of feeding guanacos. Age class: Juvenile (0-5 months old), Yearling (6-12 months old), Subadult (2-4 years old), Adult (>4 years old).



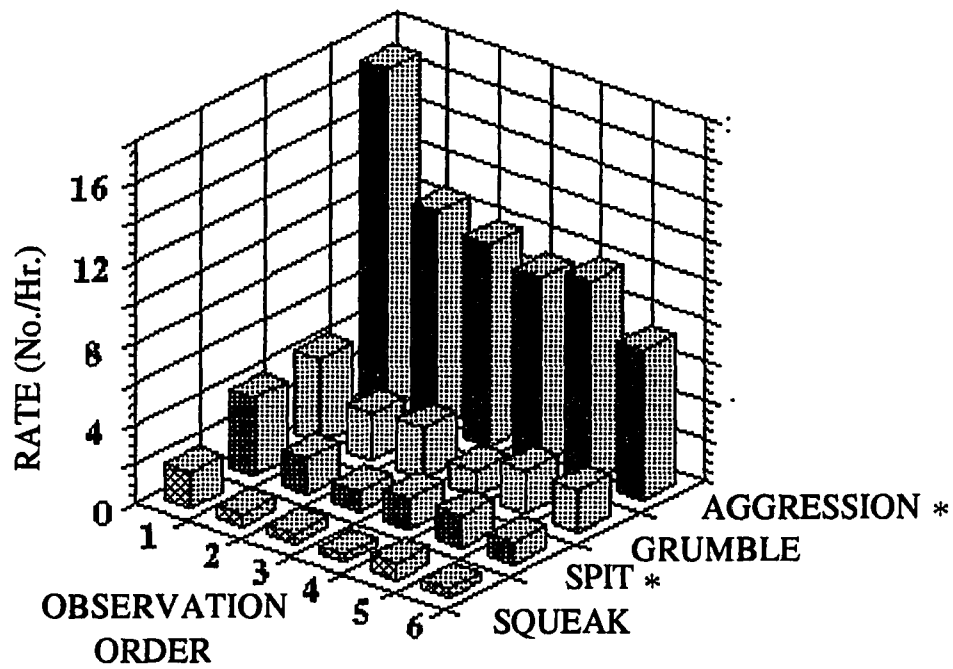


Fig. 6. Rates of aggression and 3 aggressive call types during different observation order (8 minutes per observation order) in feeding guanacos. \*: significant effects of observation order.

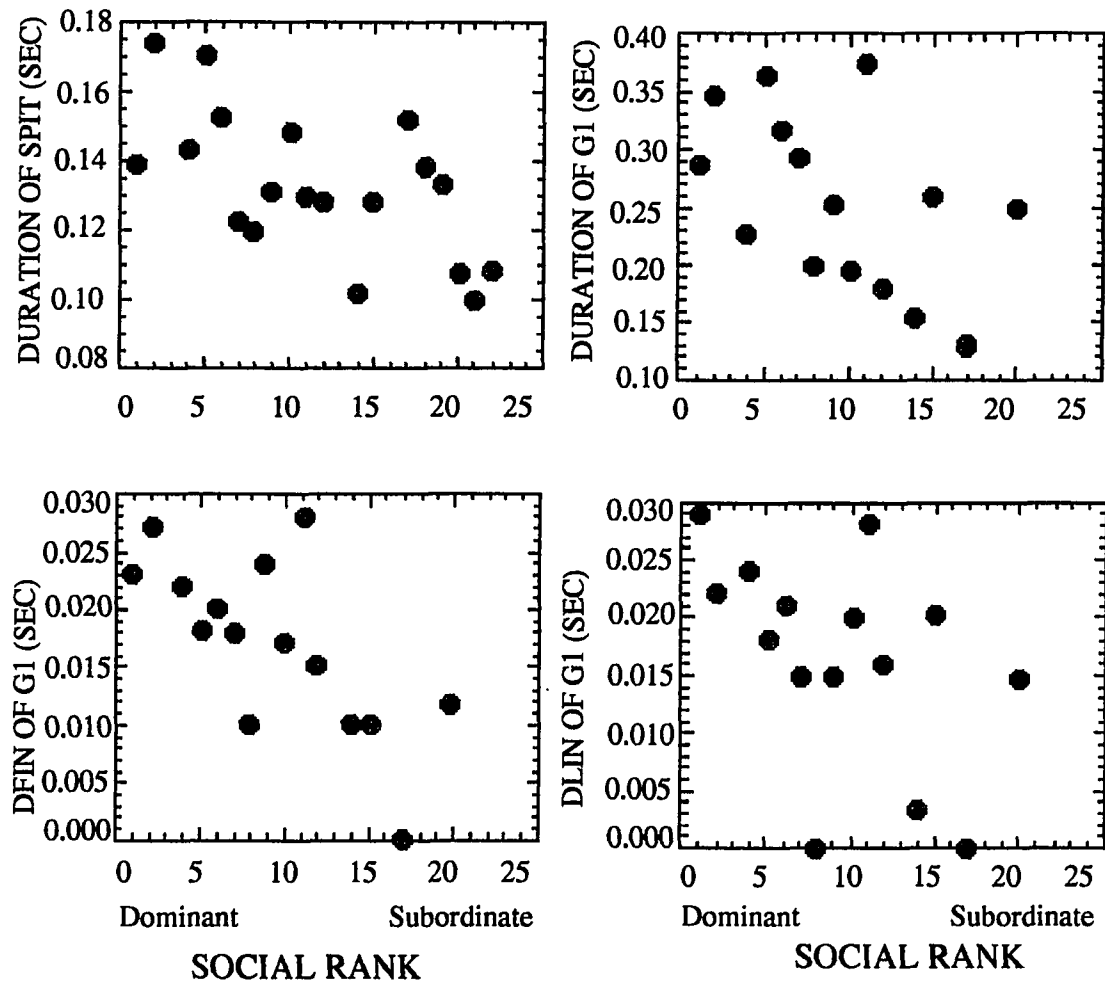


Fig. 7. Sonagram measurements of aggressive vocalizations compared to social rank in guanacos. Each dot represents the average for an individual. See Table 3 for descriptions of abbreviations (G1, DFIN, DLIN).

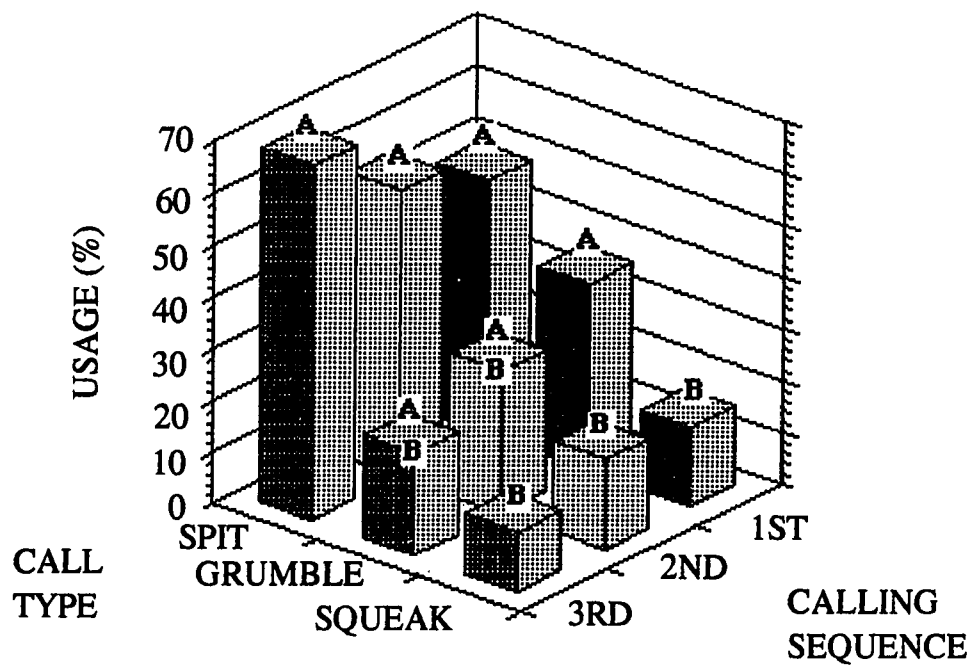


Fig. 8. The percentages of aggressive call types used in a series of calls by guanacos. The usage of call types within the same calling sequence, with the same letters were not significantly different.

**APPENDIX 1A. Sonagram measurements of spit vocalization in feeding guanacos.**

Variable a	n1	n2	Min.	Max.	Mean	SD	CV(%)	H
DUR (sec)	19	489	0.04	0.71	0.15	0.06	39	58.6 ***
FREQ (Hz)	19	467	1520	20320	9855	3742	38	51.2 ***
PEAK (no.)	19	489	1.00	3.00	1.04	0.19	19	11.4

\*:  $p < 0.10$ , \*\*:  $p < 0.05$ , \*\*\*:  $p < 0.01$ .

a: See Table 3 for descriptions of variables.

n1= the number of individuals, n2= the total number of calls measured,

Min.= minimum, Max.= maximum, SD= standard deviation, CV= coefficient of variation, H= Kruskal-Wallis test value.

APPENDIX 1B. Sonagram measurements of grumble vocalization in feeding guanacos.

Variable a	n1	n2	Min.	Max.	Mean	SD	CV(%)	H	
<b>G1</b>									
DUR (sec)	15	390	0.02	1.16	0.32	0.19	60	38.5	***
FUP1 (Hz)	15	367	280	5040	2403	1424	59	14.2	
NNOTE	15	389	1	26	8	4	55	27.0	**
DFNOTE (sec)	15	350	0.01	0.05	0.022	0.007	32	15.6	
DFIN (sec)	15	350	0.00	0.14	0.023	0.016	68	51.5	***
DLNOTE (sec)	15	350	0.01	0.05	0.021	0.007	33	26.8	**
DLIN (sec)	15	344	0.00	0.12	0.021	0.015	72	33.4	***
<b>G2</b>									
DUR (sec)	11	109	0.12	1.6	0.58	0.25	44	12.6	
DPHR1 (sec)	11	108	0.01	0.89	0.22	0.17	80	14.6	
DPHR2 (sec)	11	108	0.01	0.93	0.20	0.15	71	8.9	
DIPHR1 (sec)	11	108	0.04	0.65	0.17	0.12	71	16.6	*
FUP1 (Hz)	11	104	377	5000	2264	1431	63	8.2	
FUP2 (Hz)	11	104	354	5000	2423	1459	60	13.3	
NNOTE1	11	109	1	23	6	4	74	15.1	
NNOTE2	11	109	1	23	5	4	74	7.0	
DFNOTE1 (sec)	11	103	0.01	0.04	0.023	0.008	37	11.6	
DFIN1 (sec)	11	88	0	0.08	0.023	0.013	57	20.3	**
DLNOTE1 (sec)	11	88	0.01	0.04	0.020	0.006	29	17.9	*
DLIN1 (sec)	11	82	0	0.11	0.026	0.018	71	8.8	
DFNOTE2 (sec)	11	103	0.01	0.04	0.021	0.008	36	12.8	
DFIN2 (sec)	10	92	0	0.11	0.024	0.016	69	20.9	**
DLNOTE2 (sec)	11	91	0.01	0.04	0.020	0.007	34	22.4	***
DLIN2 (sec)	10	83	0	0.06	0.021	0.013	61	12.8	
<b>G3</b>									
DUR (sec)	7	24	0.33	1.2	0.77	0.23	29	14.3	**
DPHR1 (sec)	7	24	0.03	0.36	0.17	0.09	56	5.9	
DPHR2 (sec)	7	24	0.02	0.41	0.13	0.10	76	4.9	
DPHR3 (sec)	7	24	0.02	0.52	0.18	0.12	67	4.4	
DIPHR1 (sec)	7	26	0.04	0.44	0.15	0.11	78	9.2	

## APPENDIX 1B. (continued)

DIPHR2 (sec)	7	24	0.05	0.38	0.15	0.10	67	8.9
FUP1 (Hz)	7	24	509	5000	3045	1471	48	2.3
FUP2 (Hz)	7	24	204	5192	2569	1796	70	9.8
FUP3 (Hz)	7	24	827	5000	2776	1525	55	9.7
NNOTE1	7	24	1	13	5	3	65	5.6
NNOTE2	7	24	1	14	4	3	83	4.8
NNOTE3	7	24	1	10	5	3	57	8.7
DFNOTE1 (sec)	7	23	0.01	0.05	0.023	0.009	38	6.7
DFIN1 (sec)	7	21	0	0.06	0.026	0.014	56	5.4
DLNOTE1 (sec)	7	21	0.01	0.04	0.022	0.008	37	5.2
DLIN1 (sec)	7	19	0	0.10	0.022	0.023	108	4.8
DFNOTE2 (sec)	7	22	0.01	0.04	0.021	0.008	36	5.1
DFIN2 (sec)	7	19	0	0.09	0.026	0.027	103	6.3
DLNOTE2 (sec)	7	19	0.01	0.04	0.024	0.010	43	6.2
DLIN2 (sec)	7	17	0	0.04	0.015	0.010	66	7.4
DFNOTE3 (sec)	7	23	0.01	0.04	0.023	0.008	36	5.1
DFIN3 (sec)	7	21	0.01	0.04	0.020	0.010	50	8.9
DLNOTE3 (sec)	7	18	0.01	0.03	0.021	0.006	28	6.2
DLIN3 (sec)	7	18	0	0.04	0.016	0.013	80	4.6

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\*:  $p < 0.10$ , \*\*:  $p < 0.05$ , \*\*\*:  $p < 0.01$ .

a: See Table 3 for descriptions of variables.

n1= the number of individuals, n2= the total number of calls measured,

Min.= minimum, Max.= maximum, SD= standard deviation, CV= coefficient of variation, H = Kruskal-Wallis test value.

APPENDIX 1C. Sonagram measurements of squeak vocalization in feeding guanacos.

Variable a	n1	n2	Min.	Max.	Mean	SD	CV(%)	H
<b>SQ1</b>								
DUR (sec)	14	122	0.06	1.17	0.37	0.22	60	15.5
BW (Hz)	14	119	20	142	40	15	38	14.4
FUP1 (Hz)	14	121	226	1744	408	161	39	9.3
FLO1 (Hz)	14	121	132	1328	258	122	47	11.3
FRANGE (Hz)	14	121	48	528	150	82	54	11.7
FFCH (Hz/sec)	14	121	64	3556	574	527	92	11.7
SUP1 (Hz)	14	106	236	2520	729	262	36	12.3
SLO1 (Hz)	14	104	160	2320	563	241	43	5.6
SRANGE (Hz)	14	104	16	592	164	109	66	20.4 *
SFCH (Hz/sec)	14	104	37	2511	561	437	78	15.3
HARMON	14	120	1.00	16.00	3.45	2.32	67	15.8
DARKEST	14	107	1.00	2.00	1.02	0.13	13	6.7
<b>SQ2</b>								
DUR (sec)	6	17	0.23	1.12	0.52	0.23	44	4.4
DARKEST	6	17	1.00	1.00	1.00	0.00	0	0.0
DSYLL1 (sec)	6	17	0.12	0.51	0.25	0.13	51	3.2
DSYLL2 (sec)	6	17	0.09	0.98	0.27	0.22	84	6.2
IDSYLL1 (sec)	6	17	0.00	0.06	0.01	0.02	284	9.1
BW1 (Hz)	5	16	20	56	38	8	21	5.8
BW2 (Hz)	6	17	28	56	38	7	18	3.4
HARMON1	6	17	1.00	6.00	2.35	1.27	54	7.1
HARMON2	6	17	1.00	13.00	3.65	3.08	84	4.9
FUP1 (Hz)	6	17	128	832	408	179	44	4.2
FLO1 (Hz)	5	17	96	512	258	124	48	3.2
FUP2 (Hz)	5	17	96	736	398	165	42	8.6
FLO2 (Hz)	5	17	64	566	259	142	55	7.2
SUP1 (Hz)	6	13	256	1622	727	360	50	6.4
SLO1 (Hz)	6	13	208	1180	570	300	53	4.4
SUP2 (Hz)	6	13	176	1488	763	375	49	5.0
SLO2 (Hz)	5	13	128	1344	615	346	56	5.5
FRANGE1 (Hz)	5	17	32	320	150	92	62	3.7
FRANGE2 (Hz)	5	17	32	304	138	76	55	7.7
SRANGE1 (Hz)	6	13	38	442	157	133	85	5.3

## APPENDIX 1C. (continued)

SRANGE2 (Hz)	6	13	42	256	147	77	53	5.6	
SQ3									
DUR (sec)	11	54	0.11	1.16	0.37	0.22	58	11.5	
SQ4									
Tonal syllable									
DUR (sec)	7	29	0.07	0.96	0.31	0.19	60	12.2	*
BW (Hz)	7	28	28	56	39	7	18	9.7	
FUP1 (Hz)	7	29	240	560	356	80	22	6.9	
FLO1 (Hz)	7	29	76	400	227	74	33	4.9	
FRANGE (Hz)	7	29	28	278	129	61	47	6.7	
FFCH (Hz/sec)	7	29	50	1231	527	331	63	14.1	**
SUP1 (Hz)	7	27	352	896	620	146	24	11.1	*
SLO1 (Hz)	7	27	226	755	479	133	28	6.4	
SRANGE (Hz)	7	27	32	336	141	88	63	10.7	*
SFCH (Hz/sec)	7	27	66.67	1684	549	399	73	16.9	***
HARMON	7	29	1.00	10.00	4.03	2.20	54	1.7	
Noisy syllable									
DUR (sec)	7	29	0.06	0.58	0.25	0.14	55	8.9	

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\*:  $p < 0.10$ , \*\*:  $p < 0.05$ , \*\*\*:  $p < 0.01$ .

a: See Table 3 for descriptions of variables.

n1= the number of individuals, n2= the total number of calls measured,  
 Min.= minimum, Max.= maximum, SD= standard deviation, CV=  
 coefficient of variation, H= Kruskal-Wallis test value.



**PAPER 2.**

**AGGRESSIVE VOCALIZATIONS IN GUANACO FEEDING GROUPS:  
OPTIMAL LEVEL OF DECEIT OR AGGRESSION?**

**Aggressive vocalizations in guanaco feeding groups:  
optimal level of deceit or aggression?**

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## ABSTRACT

Guanacos, Lama guanicoe, when feeding used 3 types of aggressive calls: squeak, grumble, and spit vocalizations. The functional significance of these diverse calls was investigated by logistic curves (probability of winning against difference of fighting ability rank). According to the fitted curves, the best calling strategies were determined and compared with observed frequencies of call type usage. Logistic curves of grumble and spit vocalizations were the flattest and steepest, respectively. According to the optimal deceit model, the grumble was the most deceitful call and spit the most truthful. However, based on the social living style and measurements of grumble sonagrams in guanacos, an alternative hypothesis, optimal level of aggression, was suggested. The optimal level of aggression is a balance between the effectiveness in thwarting receivers and tolerance by high ranked receivers. When compared with predicted calling strategies, signallers who ranked higher than receivers used the grumble more than the predicted spit vocalization. This may have resulted from contesting the low valued resource (hay) and settling contests with cheaper cues in guanacos. In the most subordinate and youngest guanacos, developmental limitation in learning and a lower risk in provoking challenge might have resulted in using the spit vocalization more than the predicted grumble.

## INTRODUCTION

Information and manipulation are two conflicting viewpoints suggested for the evolutionary adaptations of animal communication. From the information viewpoint, researchers have suggested that signallers transmit information about themselves by aggressive signals, either about their intentions or qualities (i.e. fighting ability, body size) (Van Rhijn 1980; Van Rhijn & Vodegel 1980; Smith 1986; Grafen 1990). Signals are honest when higher quality individuals use costly cues to state their superiority (Barnard & Burk 1979). Costly signals are evolutionarily stable as reliable indicators of signaller quality (Grafen 1990). In contrast, manipulation theorists argue that animals should use signals not to inform, but rather to manipulate (misinform) receivers before a conflict (Dawkins & Krebs 1978; Krebs & Dawkins 1984). Because receivers might settle for cheaper signals to avoid the high costs of fully assessing a signaller (Dawkins & Guilford 1991), dishonest signals remain stable as a result of frequency dependence (Andersson 1980).

Less attention has been directed towards social animals, for which aggressive communication is a complex process and subordinate animals sometimes can win over dominants (Senar et al. 1989). Deception might be an explanation for the winning of subordinates. In a stable social group, dominance rank is the most important asymmetry (Van Rhijn & Vodegel 1980). Bond (1989) constructed the optimal deceit model, the first game theory model incorporating the deception in signalling process and the asymmetry of fighting abilities in contestants. According to Bond (1989), optimal deceit is the best strategy for signallers when the cost of challenge is

low or medium, and it is a balance between the advantages of bluffing and the disadvantages of selecting for skepticism in the receiver. Based upon the optimal deceit model, it should be possible to plot the winning probabilities of signallers against the relative fighting abilities of contestants using different signals, and compare the levels of exaggeration for those signals (Bond 1989).

Guanacos, Lama guanicoe, are highly social ungulates with subtle displays and diverse aggressive calls (Franklin 1982), including squeak, grumble, and spit vocalizations used by individuals in feeding groups. These 3 call types might reflect different motivational levels of aggression, rank, or individual identity (Shieh 1993). Subordinate guanacos occasionally repel dominants when feeding on hay. Only one of the 3 call types, spit vocalization, was associated with the winning contexts (Shieh 1993). However, the functional significance of these diverse forms of aggressive calls in guanacos remains unknown.

The purpose of this study was to examine the applicability of the optimal deceit model to aggressive vocalizations in feeding guanacos. The objectives were (1) to analyze the relationship of winning probabilities and relative fighting abilities by logistic curves for 3 types of aggressive calls, (2) based on these fitted curves, to predict the calling strategies with the highest winning probabilities, and (3) to compare these strategies with frequencies of call type usage observed in the field.

## METHODS

We recorded aggressive interactions in a captive group of guanacos with 10 adult females (>4 years old), 5 subadults (2-4 years old), 3 yearlings (6-12 months old), and 2 juveniles (0-5 months old) from March to November 1989 at Ames, Iowa. Guanacos were fed hay during the observation period and neck tagged for identification. Focal sampling (Altmann 1974) was used in 135 hours of observation (Shieh 1993).

An interaction began at the start of the signaller's aggressive behaviour and ended with a nonaggressive behaviour, such as feeding and head or body turned away. Identities of signaller and receiver, aggressive threat displays (Franklin 1982; Wilson & Franklin 1985), and vocalizations were recorded for each aggressive interaction. We adapted the fighting success index (Clutton-Brock et al. 1979) to represent social rank. Animals were ranked based on their fighting success index with the highest-ranked animal numbered 1. We identified the signaller as winning an encounter only if the receiver displayed a clear 'head turn away' or 'body turn away' response. The fighting success index was calculated from the outcomes of all aggressive interactions during the study period:

Fighting Success Index =  $(W + \Sigma w + 1) / (L + \Sigma l + 1)$ , where

W = the number of guanacos the subject defeated,

$\Sigma w$  = the total number those defeated guanacos (W) defeated,

L = the number of guanacos the subject lost to, and

$\Sigma l$  = the total number those guanacos (L) lost to.

By logistic regression (Ashton 1972; Barlow 1983), we plotted the probability of winning of signallers against the difference of rank (receiver's

rank - signaller's rank) separately for different conflict scenarios: no calling (Nocall), spit vocalizations only (Spit), grumbles only (Grumble), and squeaks only (Squeak). Because the occurrence of a particular call type was strongly influenced by another call type, but not by visual displays (Shieh 1993), we focused on the functions of call types and ignored all visual displays that accompanied calls. Logistic regression was calculated as

$$\text{logit}(p) = \log [p/(1-p)] = a + b * X, \text{ where}$$

$X$  = the difference of rank = receiver's rank - signaller's rank,  
( $X > 0$  if a signaller was dominant over a receiver, and vice versa),

$p$  = the probability of winning of the signaller,

$a$  = the constant, and

$b$  = the logistic coefficient.

The difference of rank when a signaller and a receiver had equal probabilities of winning was indicated as  $X_{0.5} = (-a/b)$ . When a signaller and a receiver had equal rank ( $X = 0$ ), the probability of winning was calculated as  $p = 1/(1 + e^{-a})$  and confidence interval of  $p$  could be derived from the constant  $a$  and the standard error of the constant  $a$ . The constant  $a$  and coefficient  $b$  and their standard error (SE) were estimated by the maximum likelihood method using the CATMOD procedure of SAS software (SAS Institute 1989).  $X_{0.5}$ ,  $a$ , and  $b$  were compared between those logistic curves (Nocall, Spit, Grumble, and Squeak) by the student's  $t$  test at  $\alpha = 0.05$ .

From those fitted curves, we determined the calling strategies with the highest probabilities of winning. If individual guanacos followed those

strategies, we would expect higher frequency (%) of usage. Additionally, in order to better understand how those strategies might change for guanacos of different social rank, we classified guanacos into 4 groups. Group 1 had the 5 most dominant individuals, and group 4 the 5 most subordinate. For each of the 4 groups, we calculated the frequency of Spit, Grumble, and Squeak in calling scenarios individually and plotted the average of individual usage in difference of rank.



## RESULTS

### Comparisons Between Conflict Scenarios

Three of the logistic curves (Nocall, Spit, and Grumble) resulted in a constant 'a' which was significantly greater than 0 (Table 1, Fig. 1). The probability of winning ( $p$ ) when a signaller and a receiver had equal rank ( $X=0$ ) was significantly greater than 0.5 for those 3 logistic curves (Table 1, Fig. 1). The constant 'a' was not significantly different from each other between those 3 logistic curves (Table 1). Only the logistic curve for Squeak was not either significantly greater than 0 in constant 'a' or greater than 0.5 in the probability of winning when a signaller and a receiver had equal rank.

The coefficient 'b' of all logistic curves was significantly different from 0. Only the coefficients of Spit and Grumble curves were significantly different from each other (Table 1).

The Spit curve was the steepest and had the highest  $X_{0.5}$  (-5.33), but did not differ from that of Squeak curve (Table 1, Fig. 1). The Grumble curve was the flattest and had the lowest  $X_{0.5}$  (-8.33), which was significantly different from other  $X_{0.5}$  values (Table 1, Fig. 1). Based on the results, a subordinate signaller with spit vocalization could do equally well ( $p=0.5$ ) as a receiver 5.33 ranks higher, while a subordinate signaller with grumble could do equally well as a receiver 8.33 ranks higher. The Nocall curve was similar to the Grumble curve (Fig. 1); their coefficients did not differ but their  $X_{0.5}$  values were significantly different (Table 1).

### Calling Strategies of Feeding Guanacos

According to the fitted logistic curves (Fig. 1), the best calling strategies would be as follows. Guanacos should spit when signallers have higher rank than receivers (region I in Fig. 1). All scenarios do similarly well when signallers and receivers have similar rank (difference of rank close to 0 (region II in Fig. 1). Guanacos should grumble when signallers are more than 5 ranks lower than receivers because the winning probabilities for both squeak and spit vocalizations at  $X = -5$  began close to 0.5 and decreased to be less than 0.5 (region III in Fig. 1).

Field results which matched the predicted calling strategies were: (1) for individuals in groups 2 and 3, grumble was the most common call type when signallers were 5 or more ranks lower than receivers (Fig. 2), (2) guanacos in group 3 produced only grumble when they were 13-16 ranks lower than receivers (Fig. 2). Generally, the prediction of having more grumbles when signallers were 5 or more ranks lower than receivers was observed, except for the most subordinate group, which instead used more spit vocalizations.

The prediction of having more spit vocalizations when ranked higher than receivers (difference of rank  $>0$ ) was not observed in groups 1, 2 and 3. Specifically, in group 1, the most dominant group, guanacos produced more grumbles than spit vocalizations when ranked higher than receivers. However, when the differences in rank were extreme, spit and grumble had the same percentages of usage (Fig. 2). In group 2, grumbles were used more than spit vocalizations when signallers were 9-12 ranks higher than receivers, and squeak vocalizations occurred the most when signallers were

13-16 ranks higher than receivers. In group 3, signallers grumbled more when they were 1-4 ranks higher than the receivers (Fig. 2).

## DISCUSSION

### Optimal Level of Deceit or Aggression?

In the optimal deceit model, Bond (1989) hypothesized that if aggressive displays are noninformative, the probability of winning should be independent of relative fighting ability (a straight line parallel to relative fighting ability). The greater the logistic coefficient, the aggressive display should be more truthful. According to his predictions, spit vocalization in guanacos would be the most truthful call because it is the steepest logistic curve with the highest coefficient, and the grumble would be the most deceitful call because it is the flattest curve with the lowest coefficient. However, the sonagram measurements (duration and the widths of the first and last internotes) of grumbles were highly correlated with social rank (Shieh 1993). This could mean that guanacos use the grumble to inform others of their fighting abilities.

Bond's (1989) optimal deceit model assumed that players had no prior experience with one another, and that they were evenly matched in apparent physical capabilities. However, in highly social ungulates like guanacos, it is very probable they are familiar with each other's fighting ability based upon physical appearance and prior experience. Under such circumstances, changing the internal state of aggression is easier than faking one's fighting ability. Therefore, we propose that the winning probability curves of different call types indicate optimal level of aggression, rather than optimal level of deceit.

The optimal level of aggression is a balance between the advantages of causing receivers to retreat and the disadvantages of selecting for

tolerance in receivers. High levels of aggression should be effective in thwarting receivers, but would result in less tolerant receivers. On the contrary, low levels of aggression should be ineffective in thwarting receivers, but would result in more tolerant receivers.

We propose the following explanation of the functional significance of the guanaco's diverse vocalizations according to the hypothesis of optimal level of aggression. Spit and grumble vocalizations were both truthful to transmit the information about the signaller's fighting ability. However, spit vocalization indicated a high level of aggression and was the least tolerated by higher ranked receivers. Therefore, the probability of winning ( $p$ ) should greatly depend upon the relative fighting abilities of contestants ( $X$ : difference of rank in this study). The grumble indicated a medium level of aggression and was tolerated more by higher ranked receivers. When signallers ranked lower than receivers, they had a higher probability of winning with grumble than with spit vocalization (as seen in Fig. 1). This occurred because a medium level of aggression would be tolerated more by higher ranked receivers. When signallers ranked higher than receivers, their probability of winning was higher with spit vocalization than with grumble, because a high level of aggression would be more effective in thwarting lower ranked receivers. The winning probability of grumble was less dependent on the relative fighting abilities than spit vocalization.

The squeak was the most tolerated aggressive call, but it was the least effective in thwarting receivers by its lowest level of aggression. The winning probability of squeak is more dependent on relative fighting abilities than on its low level of aggression. Therefore, the winning

probability curve for squeaks should be steeper than the curve for grumbles. In addition, the squeak curve should be flatter than that of spit vocalization because of the tolerance. In this study, the coefficient of the squeak curve was not significantly different from that of the grumble curve or the spit curve. This may be due to small samples of squeak scenarios.

There are several explanations for the discrepancies between predictions and observations (see Figs 1 & 2). First, the most subordinate group did not grumble as much as predicted. This may be because they were usually the youngest members of the group (less than 1 year old), had developmental limitations (either physical or learning), or offered a lower risk in provoking dominant receivers which had close rank to them (Fig. 2). In addition, the youngest and subordinate group might not have learned how to use medium aggressive calls in appropriate contexts; therefore, they called only with maximum aggression, i.e. spitting. Secondly, when signallers ranked higher than their receivers, they did not spit as much as predicted. This might be the result of settling contests for cheaper cues (Dawkins & Guilford 1991), such as grumble, rather than spit vocalizations, which require higher energy costs and could provoke greater intolerance (Shieh 1993).

### Tolerance by Dominants

As the exaggeration of signallers is the rational form of deception in the game of optimal deceit (Bond 1989), the tolerance of receivers is the driving force in the hypothesis for the optimal level of aggression. Animals use aggressive displays to communicate tolerance (Senar 1990). Senar et al.

(1989) found that subordinate siskins (Carduelis spinus) repelled more dominant intruders simply by using aggressive displays. They suggested that dominants were able to reduce a subordinate's probability of leaving the flock and gain benefits from the long term advantage of being in a stable flock. That is, dominant animals may tolerate rather than be deceived by subordinates if temporary competition is over a low valued resource and the advantages of long term group living are high. In this study, guanacos used grumbles more often than spit and squeak vocalizations when competing for food (hay). This observation could be explained by the low resource value of hay allowing more tolerance in selecting for the medium level of aggressive call, the grumble. If guanacos compete for high valued resources, such as mates or high caloric grains, we would expect them to use more spit vocalization, the highest level of aggressive call, than squeak or grumble. Qualitative observations support this prediction (unpublished data).

Communication of social animals is a complex social process, and participating individuals are interdependent in sharing both short and long term consequences (Smith 1986). Noncooperative communication in the short term may be confounded with cooperative communication in the long term. Animals temporarily competing for food may be cooperative within a social group over the long term. To further model optimal aggression, it would be necessary to consider the present and future values which affect the degree of tolerance in a social group.

### Why Call?

We have discussed the calling strategies of guanacos when they choose to call. There is a basic question which has yet to be considered: Why call at all? In this study, Nocall represented the conflict scenario with visual displays and behaviours but without calling. The winning probability curve of Nocall, was very close to the curve of grumble, the medium level of aggressive call. This might suggest that visual displays and behaviour without calling indicate a medium level of aggression. Guanacos may use spit vocalizations to state a higher level of aggression easily without biting or other physical contacts (Shieh 1993). They also could use squeak to indicate a lower level of aggression and grumble to reinforce their medium level of aggression. We conclude that the diverse forms of aggressive calls in guanacos function to signal different levels of aggression, which are selected by effectiveness to thwart receivers and tolerance in receivers.



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Table 1. Statistics of logistic curves estimated from different conflict scenarios in feeding guanacos.

Scenario	$a \pm SE$	$b \pm SE$	$X_{0.5} \pm SE$	S	N
Nocall	$0.75 \pm 0.07$ c	$0.101 \pm 0.009$ cd	$-7.44 \pm 0.12$ c	38	1722
Spit	$0.91 \pm 0.23$ c	$0.171 \pm 0.039$ c	$-5.33 \pm 0.37$ d	30	182
Grumble	$0.68 \pm 0.18$ c	$0.081 \pm 0.020$ d	$-8.33 \pm 0.32$ e	32	378
Squeak	$0.59 \pm 0.31$ c	$0.110 \pm 0.045$ cd	$-5.42 \pm 0.49$ d	22	94

a = the constant, b = the coefficient,  $X_{0.5}$  = the difference of rank at which both signaller and receiver have equal win probabilities, S = the number of pairs, N = the number of interactions. cde: different letters in the same column indicate significant difference.

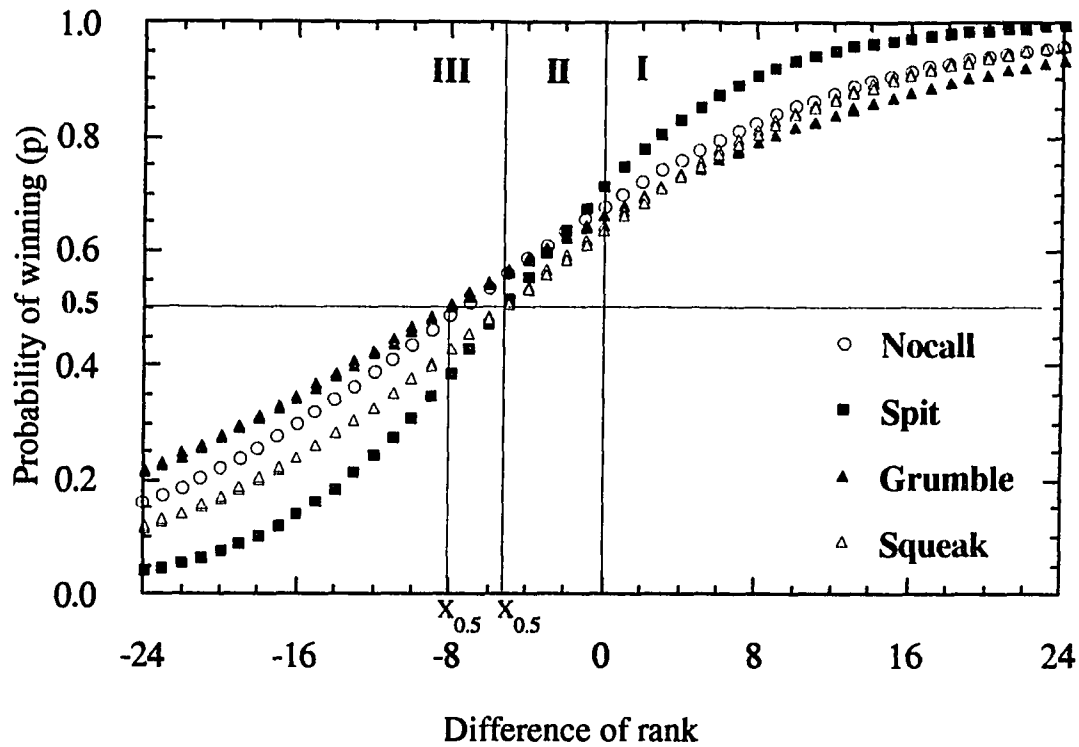


Figure 1. Fitted logistic curves of different conflict scenarios in feeding guanacos.  $\text{Logit}(p) = a + b * X$ , where  $p$  = probability of winning,  $a$  = the constant,  $b$  = the coefficient, and  $X$  = the difference of rank at which a signaller and a receiver have equal probability of winning. The constant determines the probability of winning when  $X = 0$ ; that is,  $p = 1/(1+e^{-a})$ . The coefficient determines how fast the probability of winning increases as the difference of rank increases. I, II, and III are regions of predicted calling strategies: grumble in region III, spit vocalization in region I, and all vocalizations equal in region II.

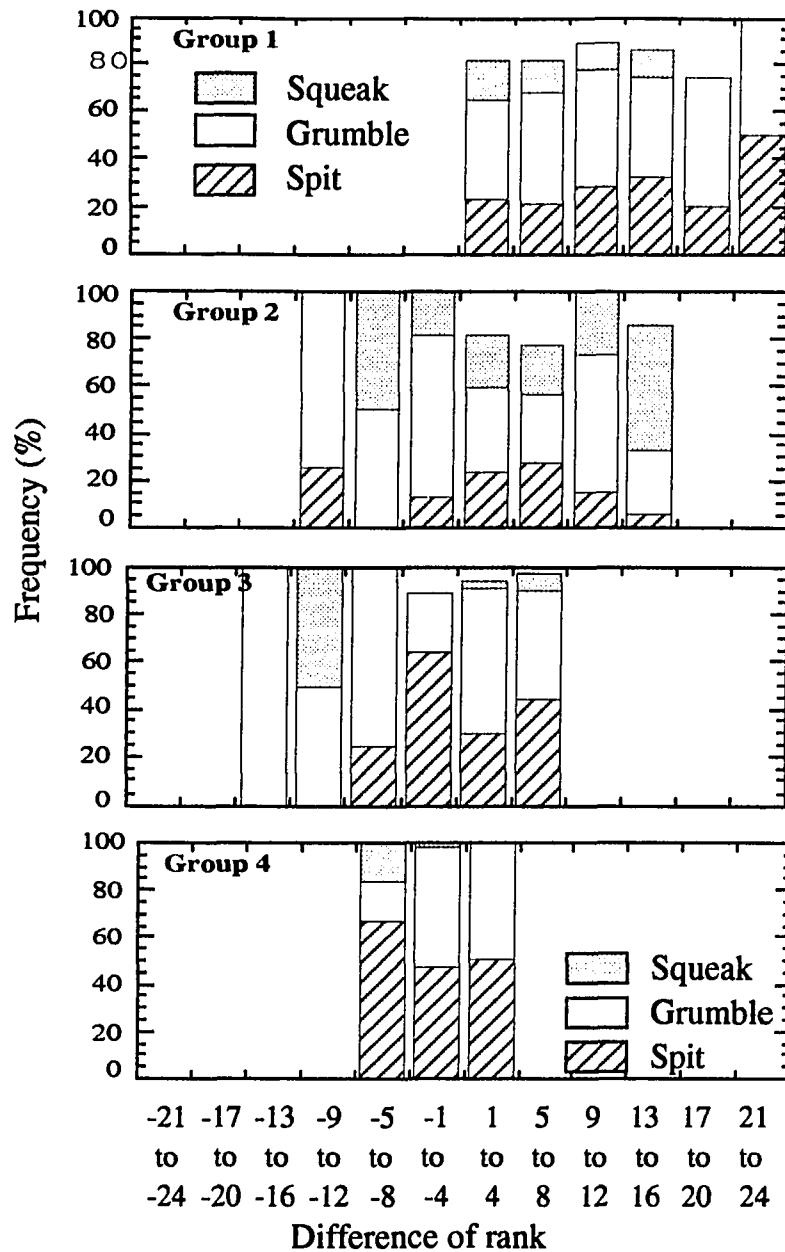


Figure 2. The frequency (%) of call types by difference of rank among 4 groups of feeding guanacos in calling interactions. Group 1 included the 5 most dominant guanacos, and group 4 the 5 most subordinate.

## GENERAL SUMMARY

Aggressive interactions were investigated in a captive group of feeding guanacos, Lama guanicoe, composed of adult females, subadults, yearlings, and juveniles. Three call types, squeak, grumble and spit vocalizations were recorded during aggressive interactions. Grumbles and squeaks were further classified into 3 and 4 subtypes respectively according to sonagrams. Social rank had a significant effect on the rates of aggression and the rates of the 3 call types. Analysis on sonagram measurements showed that the duration of spit and grumble subtype 1 (G1) were positively correlated with the social rank. Four variables of grumble subtype 2 (G2) showed significant individual difference but age and social rank had no significant effects. Sonagrams measurements of most squeaks (except subtype SQ4) showed nonsignificant individual differences.

Logit Discriminant Analysis on contextual variations revealed that spit vocalization was the only call type associated with the context of winning outcomes. Therefore, spit vocalization, the harshest and noisiest call, represented the most aggressive call type. Grumbles and squeaks indicated a lower level of aggression than spit vocalization. For the first call during an aggressive interaction, guanacos produced more grumbles and spit vocalizations than squeaks. For the second and the third calls, they produced more spit vocalizations than squeaks; furthermore, spit vocalization, the most aggressive vocalization, was more predictable than squeaks and grumbles. From the individual and contextual variations, we propose that the diverse aggressive vocalizations in feeding guanacos reflect the combinations of aggressive intensity, social rank, and individual recognition.



The functional significance of these diverse calls was investigated by logistic regressions (probability of winning against difference of social rank). Logistic curves of grumble and spit vocalizations were the flattest and steepest, respectively. According to the optimal deceit model, the grumble was the most deceitful call and the spit vocalization was the most truthful. However, based on social living style and sonagram measurements of grumble in guanacos, we suggested an alternative hypothesis, optimal level of aggression, which is a balance between effectiveness in thwarting receivers and tolerance by high ranked receivers. Based on the optimal level of aggression, the spit vocalization is the most aggressive call, the grumble is the medium, and the squeak is the least. When compared with predicted calling strategies, signallers who ranked higher than receivers used grumble more than the predicted spit vocalization. This may have resulted from contesting the relatively low valued resource (hay) and settling contests with cheaper cues in guanacos. In the most subordinate and youngest guanacos, developmental limitation in learning and a lower risk in provoking challenge might have resulted in using spit vocalizations more than the predicted grumbles.

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