

ON THE OCCURRENCE AND SIGNIFICANCE OF
MOTIVATION-STRUCTURAL RULES IN SOME BIRD
AND MAMMAL SOUNDS

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This paper describes a concept, not altogether new but largely neglected, that should lead to a greater understanding of the information contained in certain classes of vocal communication signals of birds and mammals. The concept is based on empirical data, first pointed out by Collias (1960, p. 382), showing that natural selection has resulted in the structural convergence of many animal sounds used in "hostile" and "friendly" contexts. Simply stated, birds and mammals use harsh, relatively low-frequency sounds when hostile and higher-frequency, more pure tonelike sounds when frightened, appeasing, or approaching in a friendly manner. Thus, there appears to be a general relationship between the physical structures of sounds and the motivation underlying their use.

I hope to develop the idea that this relationship has had a far greater influence on the evolution of animal communication systems than has hitherto been discussed. I will discuss the idea that there exist motivation-structural rules (MS) governing the physical structure of close contact sounds in animal communication systems. The greatest value of the MS concept is that it provides the opportunity to compare the evolution of vocal communication in any species against an abstract concept. The adaptive nature of communication systems against varying backgrounds of environment, social system, and competition will appear in clear relief.

OCCURRENCE OF MOTIVATION-STRUCTURAL RULES

I will discuss the occurrence of MS on two levels. The first level is intraspecific and shows where MS affect sound signal structure within a species' repertoire. The second is interspecific and shows that the empirical evidence mentioned by Collias (1960) indeed justifies the term "rule" and that discussion of its biological significance is warranted.

Intraspecific Occurrence

MS rules affect primarily, but not exclusively, sounds used by animals when they are close to one another. In animals that are "face to face," the possibility and consequences of attack, escape, or association are immediate, and selection

will favor sound signals that express current and rapidly changing motivational states. Proximity lessens the difficulties of communicating but the consequences are more immediate.

Signals used by animals in close proximity may consist of high frequencies that attenuate rapidly, or they may have amplitude and sound-quality changes (e.g., harmonic emphasis or modulation rate changes) that may be quickly masked over distance. Close proximity thus permits the MS rules to exist, but it is the immediate consequence of close proximity that produces selective pressures favoring their existence.

In contrast, sounds used in long-distance signalling are molded to a lesser extent by some selection pressures affecting short-range signals. For example, selection favors specific distinctiveness in long-distance sound signals because other communication modes are not possible simultaneously (Marler 1967). Because these signals are broadcast through the environment, the environment may produce selection pressures favoring certain physical properties that increase their propagation (Morton 1975).

Interspecific Occurrence

Tables 1 and 2 list some bird and mammal species whose close contact hostile and friendly vocal signals have been described. The list is not an exhaustive survey; it is meant to show signals from animals varying greatly in size, taxonomic affinity, evolutionary age, demography, ecology, and social system. The vocalizations are either paraphrased onomatopoeically or described verbally, whichever the respective authors used.

If one quickly scans the sounds listed under "aggressive," and imagines them occurring simultaneously, an aural picture of vocal convergence is formed. Low, harsh sounds are consistently associated with hostile motivation. The same relationship between higher, pure-toned sounds and friendly or appeasing motivation is true, if the sounds listed in the nonaggressive column are scanned. We are also able to perceive the convergence in underlying motivation, because humans use vocal intonations expressing hostility or appeasement in the same general way.

The convergent evolution exhibited in these sound structures has been suggested to reflect Darwin's principle of antithesis (Collias 1963). There have been no other attempts to identify sources of selection behind the convergence. Darwin (1873) explained only the divergence in signal structure.

Convergence in sound structures correlated with motivational state is badly in need of theoretical explanation. I have made such an attempt, first by discussing the MS rules and then by providing hypotheses on the sources of selection operating. I will incorporate examples of the MS rule operation into the arguments to illustrate how the concept may provide insight into the evolution of sound signal structure in other than obvious ways.

THE MOTIVATION-STRUCTURAL RULE THEORY

Harsh (covering a wide-frequency band), low-frequency sounds used in hostile contexts and more pure tonelike, relatively high-frequency sounds in friendly

TABLE 1
 AVIAN SOUNDS USED IN HOSTILE OR "FRIENDLY," APPEASING CONTEXTS

Species (family)	Aggressive	Nonaggressive	Source
White pelican, <i>Pelicanus erythrorhynchus</i> (Pelicanidae)	Harsh nasal growls*	Not given	Schaller (1964)
Mallard, <i>Anas platyrhynchos</i> (Anatidae)	Loud harsh <i>gaeck</i> (♀)	Soft whimpers: <i>kn</i> and <i>quais</i> (♀)	Abraham (1974)
Sparrow hawk, <i>Falco sparverius</i> (Falconidae)	Harsh <i>chitter</i>	Whine	Mueller (1971)
Bobwhite, <i>Colinus virginianus</i> (Phasianidae)	Loud, rasping "caterwauling"	<i>Tseep</i> ; <i>squee</i>	Stokes (1967)
Ring-necked pheasant, <i>Phasianus colchicus</i> (Phasianidae)	Hoarse <i>krrrrah</i>	Squeak (♀)	Heinz and Gysel (1970)
Solitary sandpiper, <i>Tringa solitaria</i> (Scolopacidae)	Harsh, metallic sound	Rising shrill whistle	Oring (1968)
Stilt sandpiper, <i>Micropalama himantopus</i> (Scolopacidae)	<i>Trrrr</i>	<i>Toi, weet</i>	Jehl (1973)
Cassin auklet, <i>Ptychoramphus aleutica</i> (Alcidae)	Growled <i>krrr krrr</i>	Kreek	Thoresen (1964)
Orange-chinned parakeet, <i>Brotogeris jugularis</i> (Psittacidae)	<i>rrrrr</i>	Low intensity "chirp"	Power (1966)
Burrowing owl, <i>Speotyto cunicularia</i> (Strigidae)	<i>esp</i>	<i>eep</i>	Martin (1973)
Red-headed woodpecker, <i>Melanerpes erythrocephalus</i> (Picidae)	Chatter, rasp	Not given	Bock et al. (1971)
Harlequin antbird, <i>Rhegmatorhina berlepschi</i> (Formicariidae)	Growling <i>chauh</i>	<i>chee</i>	Willis (1969)
Chestnut-backed antbird, <i>Myrmeciza exsul</i> (Formicariidae)	Snarling nasal <i>chiangh</i>	Musical chirps: <i>cheup</i>	Willis and Oniki (1972)
Eastern kingbird, <i>Tyrannus tyrannus</i> (Tyrannidae)	Harsh <i>zeer</i>	High-pitched <i>tee</i>	Smith, W. J. (1966)
Barn swallow, <i>Hirundo rustica</i> (Hirundinidae)	Deep harsh stutter	White call	Samuel (1971)
Purple martin, <i>Progne subis</i> (Hirundinidae)	<i>zwrack</i>	<i>sweet</i>	Johnston and Hardy (1962)
Mexican jay, <i>Aphelocoma ultramarina</i> (Corvidae)	Not given	Variable <i>weet</i>	Brown (1963)
Scrub jay, <i>A. coerulescens</i> (Corvidae)	Harsh rattle	<i>whew, scree</i>	Brown (1963)
Dwarf jay, <i>A. nana</i> (Corvidae)	Harsh rasp	<i>shreeup</i>	Hardy (1971)
Common crow, <i>Corvus brachyrhynchos</i> (Corvidae)	Growl	Soft and plaintive	Chamberlain and Cornwell (1971)
Carolina chickadee, <i>Parus carolinensis</i> (Paridae)	Click-rasp	Lisping <i>tee</i> , soft <i>dee</i> , high <i>see</i>	Smith, S. T. (1972)
Blue-gray gnatcatcher, <i>Poliophtila caerulea</i> (Sylviidae)	<i>peew</i>	<i>spee</i>	Root (1969)
American redstart, <i>Setophaga ruticilla</i> (Parulidae)	Snarl	<i>zeeep</i> , high-pitched <i>titi</i>	Ficken (1962)
Yellow-headed blackbird, <i>Xanthocephalus xanthocephalus</i> (Icteridae)	Harsh, nasal <i>rahh-rahh</i>	<i>pree pree pree</i>	Nero (1963)
Crimson-backed tanager, <i>Rhamphocelus dimidiatus</i> (Thraupidae)	Rasping harsh hoarse notes	<i>Sseeeeeeeet</i>	Moynihan (1962)
Brown towhee, <i>Pipilo fuscus</i> (Fringillidae)	Snarling throaty notes	<i>Seeep</i> , squeal duet	Marshall (1964)
Common redpoll, <i>Acanthis flammea</i> (Fringillidae)	Harsh <i>cheh cheh cheh</i>	<i>sweeeee</i>	Dilger (1960)
African village weaverbird, <i>Ploceus cucullatus</i> (Ploceidae)	Harsh growl	look! see!; high squeal	Collias (1963)

* Verbal or onomatopoeic (italics) renditions of sounds quoted from source author's descriptions.

TABLE 2
MAMMALIAN SOUNDS USED IN HOSTILE OR "FRIENDLY," APPEASING CONTEXTS

Species (family)	Aggressive	Nonaggressive	Source
Virginia opossum, <i>Didelphis marsupialis</i> (Didelphidae)	Growl	Screech	Eisenberg et al. (1975)
Tasmanian devil, <i>Sarcophilus harrisii</i> (Dasyuridae)	Growl	Whine	Eisenberg et al. (1975)
Wombat, <i>Vombatus lasiorhinus</i> (Phascolomidae)	Deep growl	quer-quer-quer	Eisenberg et al. (1975)
Guinea pig, <i>Cavia porcellus</i> (Caviidae)	Grunt, snort	Squeak, <i>wheet</i>	Eisenberg (1974)
Mara, <i>Dolichotis patagonum</i> (Caviidae)	Low grunts	Inflected <i>wheet</i>	Eisenberg (1974)
Curo curo, <i>Spalacopus cyanus</i> (Octodontidae)	Growl	Short squeaks	Eisenberg (1974)
Degu, <i>Octodon degus</i> (Octodontidae)	Growl	Inflected squeak	Eisenberg (1974)
Spiny rat, <i>Proechimys semispinosus</i> (Echimyidae)	Growl	Twitter, whimper	Eisenberg (1974)
Agouti, <i>Dasyprocta punctata</i> (Dasyproctidae)	Growl, grunt	Squeak, <i>creak-squeak</i>	Smythe (1970)
Pocket mouse, <i>Heteromys</i> (2 sp.) (Heteromyidae)	Low scratchy growl	Whining squeal	Eisenberg (1963)
Pocket mouse, <i>Liomys pictus</i> (Heteromyidae)	Low scratchy growl	Whining squeal	Eisenberg (1963)
Desert pocket mouse, <i>Perognathus</i> (4 sp.) (Heteromyidae)	Low scratchy growl	Whining squeal	Eisenberg (1963)
Kangaroo rat, <i>Microdipodops pallidus</i> (Heteromyidae)	Low scratchy growl	Whining squeal	Eisenberg (1963)
Kangaroo rat, <i>Dipodomys</i> (6 sp.) (Heteromyidae)	Low scratchy growl	Whining squeal	Eisenberg (1963)
Lemming, <i>Dicrostonyx groenlandicus</i> (Cricetidae)	Snarl, grind	Whine, peeps, squeals	Brooks and Banks (1973)
Uinta ground squirrel, <i>Citellus armatus</i> (Sciuridae)	Growl	Squeal	Balph and Balph (1966)
Maned wolf, <i>Chrysocyon brachyurus</i> (Canidae)	Growl	Whine	Kleiman (1972)
Bush dog, <i>Speothos venaticus</i> (Canidae)	Buzzing growl	Squeal	Kleiman (1972)
Coati, <i>Nasua narica</i> (Procyonidae)	Growl	Squeal	Kaufmann (1962)
Large spotted genet, <i>Genetta tigrina</i> (Viverridae)	Growl-hiss	Whine or groan	Wemmer (1976)
African elephant, <i>Loxodonta africana</i> (Elephantidae)	Roaring, rumbling sounds	High-frequency sounds	Tembrock (1968)
Indian rhinoceros, <i>Rhinoceros unicornis</i> (Rhinocerotidae)	Roaring, rumbling	Whistling	Tembrock (1968)
Pig, <i>Sus scrofa</i> (Suidae)	Growl	Squeal	Tembrock (1968)
Llama, <i>Lama guanacoe</i> (Camelidae)	Growl	Bleat (long distance only?)	Tembrock (1968)
Muntjac, <i>Muntiacus muntjac</i> (Cervidae)	Not given	Squeak	Barrette (1975)
Squirrel monkey, <i>Saimiri sciureus</i> (Cebidae)	Shriek calls, err	Peep calls, trills	Schott (1975)
Spider monkey, <i>Ateles geoffroyi</i> (Cebidae)	Growl, roar, cough	Tee tee, chirps, twitter squeak	Eisenberg and Kuehn (1966)
Rhesus monkey, <i>Macaca mulatta</i> (Cercopithecidae)	Roar, growl	Screech, clear calls, squeak, nasal grunting whine, long growl	Rowell and Hinde (1962)

or appeasing contexts represent endpoints of a behavioral spectrum. Generally, animals do not commit themselves immediately to act out either of these endpoints when they encounter or join another conspecific unless, perhaps, when they have had previous experience with one another (i.e., they “know” each other). This is true even in situations where the encounter usually results in fighting or chasing as, for example, when a male songbird enters the breeding territory of another conspecific male (e.g., Emlen 1972, p. 135). An animal’s commitment to one of the diverse array of possible behaviors when near a conspecific is under extremely strong selection pressures. To give a well-worn example: If the species’ food is found in a certain degree of abundance and with a patchy distribution, selection may favor responses that promote group cohesiveness because of the antipredator and/or food locating value of being in a group. In this situation, an individual whose genome (and/or previous experience) results in a highly aggressive phenotype and does not join others has a lower survival potential, all else being equal. However, food availability and distribution change, and so do the relative merits of an individual’s increasing or decreasing the distance between it and conspecifics. The point is that selection can never mold an animal’s overt reactions on even so simple or easily measured a parameter as distance relations between individuals to an optimum point; it is always a dynamic equilibrium. What selection does favor is the ability of the individuals in a population to respond to one another in a way that maximizes fitness. Communication is the means by which the animals in a population ultimately adjust their social relationships to various environmental and physiological fluctuations. The *endpoints* in the sound structures used in this communication are rarely adaptive for an individual to employ consistently. Rather, various grades between sounds used in fighting and appeasement are favored by selection.

I contend that we may better understand evolution in signal structure if we assume that the endpoint sound structures permeate the communication signals to indicate various degrees of hostility or friendly appeasing behavior, even if no overt reactions can be observed (since often neither sender nor receiver commits itself while uttering sounds that reflect indecision).

There are innumerable examples to show that this view has merit. Marler (1956) in his study of chaffinch (*Fringilla coelebs*) sounds lists a “social call” used to bring separated birds together (and thus not governed strictly by the close contact MS rules) and several other variants used in close contact situations. These latter variants range from a “shrill form” used in escape and appeasement contexts to a lower frequency, harsh form used when fighting. Thus, even though the “social call(s)” can be distinguished from other calls, its variants reflect sound qualities approaching those in the chaffinches’ *seeee* high-intensity-alarm and sexual-excitement call, on the one hand, and the low, buzzing *zzzzz* fighting call, on the other.

Susan T. Smith (1972) describes communicative behavior in the Carolina chickadee (*Parus carolinensis*), a species that is never solitary but has periods of aggressive rivalry as well as social flocking. Its complex social interactions are finely tuned by variable calls. The MS rules are evident throughout the

close contact calls of this species. For example, Smith lists three "displays" associated with an attack probability, rendered phonetically as *T-slink*, *slink-rasp*, and *click-rasp*. They are all variable in structure, particularly the *click-rasp* forms. Smith found that a bird giving *T-slink* was less apt to attack than one giving *slink-rasp*, a *slink-rasping* bird less apt to attack than a *click-rasping* one. The MS rule predicts this motivational sequence because we find that high-frequency pure tonelike sounds are reduced and harsh low-frequency sounds are increased as the calls change from *T-slink* to *click-rasp*. But an important point to note is that the chickadee employs sounds that are *composites* of hostile and friendly motivation. That is, there are two signal structural endpoints (harsh and pure tonelike) that are varying, perhaps independently, to produce composite structures communicating extremely subtle motivational changes in the signaler. (I suspect that the syntactical order of these sounds is also important.) Both the *T-* to *click-* and *-slink* to *-rasp* portions of the sounds vary greatly, but the variations were not described in depth because of the categorization procedure used (i.e., the display concept).

In his excellent analysis of kingbird (*Tyrannus* sp.) sounds, W. John Smith (1966) discusses variations to the extent that we may easily identify the operation of MS rule. Smith categorizes eastern kingbird (*T. tyrannus*) sounds into seven displays but recognizes that each grades considerably: "The LHV forms intermediates with nearly every other vocalization of the species" (p. 13). Each vocalization changed into a "harsher" form whenever the calling bird became aggressive. A kingbird being attacked by another gives high-pitched *tee* sounds (Smith's AeV sound). "A Kingbird that attacks a larger bird (like a Robin) and loses the initiative will usually switch from the harsh RV to the high AeV . . ." (p. 23).

An unusually high level of intra- and interspecific aggressiveness during the breeding season has been selected for in eastern kingbirds. The evolution of their sound signals, which are nearly all harsh, probably reflects the kingbird's aggressive nature. In migration and on their tropical wintering grounds, kingbirds aggregate in monospecific flocks and search for fruit (Morton 1971). Even though they are in flocks, almost no vocal or hostile interactions take place. Vocal communication is adapted to breeding season behavior which favors aggressive sound structure.

Gradation in kingbird sounds serves to communicate rather subtle variations in motivation. The evolutionary need for such variation may be related to pair bond formation and maintenance which occur against a background of sexual monomorphism and high aggression, attributes which detract from the easy recognition of potential breeding partners.

These examples illustrate ways that the MS rules are incorporated into the physical structure of sounds. It is significant that painstaking effort was involved in inferring the underlying motivation of the sounds because the conclusions were based on overt responses, some of which were quite subtle. Even so, much information in the sounds, particularly information contained in small changes of physical structure, probably escaped notice because no overt responses occurred. MS influences the physical structure of close contact

sounds in other ways that, for the sake of brevity, I will list. The list includes all of the known or probable ways that MS influences signal structure.

1. Harsh, low-frequency sounds indicate that the sender is likely to attack if the receiver comes closer to the sender or remains at the same distance. In some species, the harsh endpoint is given only during the attack, in others when attack is imminent as well.

2. Relatively tonal, high-frequency sounds indicate that the sender is submissive, will not be hostile if approached or if approaching, or is fearful.

3. Harsh sound quality, tonal quality, and sound frequency (pitch) interact such that: (a) the higher the frequency, the more fearful or friendly the sender; the lower the frequency, the more hostile; (b) the greater the sound's harshness, the greater the aggressive motivation; the more pure tonelike, the more fearful or friendly, no matter what frequency range is used.

4. Sounds rising in frequency (no matter what the sound's quality) indicate a lower hostility or increasing appeasement or fear, but a motivational endpoint is not indicated. Sounds decreasing in frequency indicate an increasing hostile motivation.

5. A sound whose frequency rises and falls more or less equally or is frequency constant but midrange in the overall frequency range reflects a conflict of motivation to approach or withdraw from a stimulus. It indicates that a stimulus of "interest" has been received by the sender.

6. A species that is generally more aggressive to conspecifics will tend to have a harsher close contact vocal repertoire as opposed to a species that often joins or is joined in flocks, especially mixed species groups. The latter will have a prevalence of high-frequency pure tonal sounds in its repertoire.

7. A species with greater complexity of social interactions will evolve sound signals containing a more complete range of sound qualities indicating more points along motivational gradients and rapid changes in motivation (as in paragraphs 1-5 above) than will a species with less complex social interactions.

8. An individual uttering "alarm" sounds will be more likely to withdraw from the alarming stimulus, the higher pitched its sounds, if the alarm system is graded. The alarm system will tend to be graded if kin are predictably (to the sender) near or if coordination of an escape attempt as a group will reduce the chances of predation on the sender.

Figure 1 depicts diagrammatically the sound structures associated with varying degrees of hostile and appeasing contexts according to the MS rules. Height above the baseline reflects frequency; arrows indicate that the sound structure may be positioned higher on the frequency scale if the sender is more appeasing, friendly, or fearful and lower in more hostile animals. The slope of the calls with ascending or descending frequencies may vary, as indicated by dotted lines. Thus there is potential grading from the signals in each box to an adjacent signal. Presumably, a sound indicating ambivalence, such as occurs in mobbing behavior (e.g., Andrew 1961), may acquire a steep slope so as to become nearly a pulse if selection pressure derived from the sound's function favors qualities that enhance the sender's location by the receiver (Marler 1956).

This type of sound structure, in the center of figure 1, is predicted by MS to

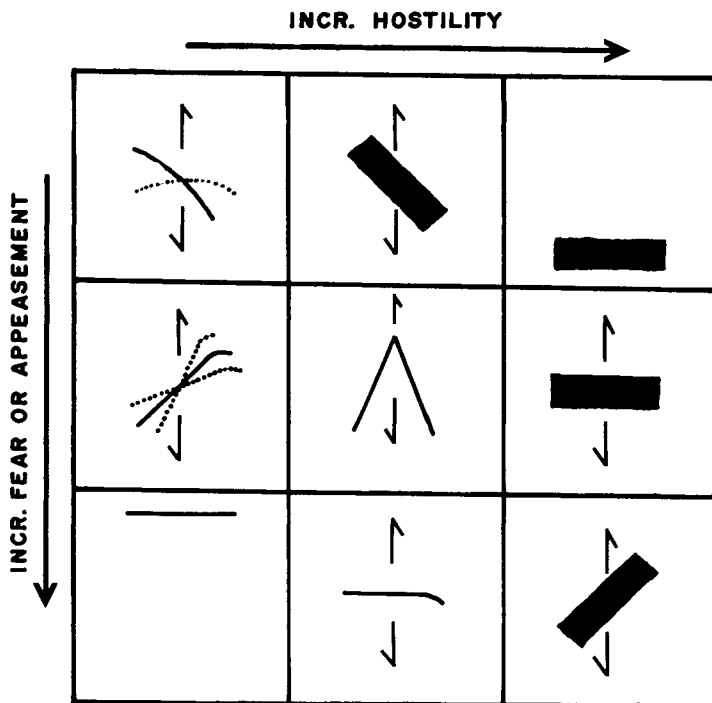


FIG. 1.—Sound structures associated with varying degrees and combinations of hostile and fearful or appeasing motivational states. In each block, the frequency is indicated by the figure's height above the baseline. A harsh sound is indicated by a wide black line, a tonal sound by a thin line. Arrows indicate the potential for frequency change within each "motivation square," and the dotted lines indicate that the figure's slope may change (see text).

have a chevron shape because it is intermediate to the two structural and motivational endpoint sounds (fig. 1, lower left and upper right boxes; paragraph 5 on the list). The chevron shape is, in fact, extremely common in avian vocal repertoires, usually rendered phonetically as *chip*. In mammals, the intermediate structure tends to be frequency constant but still short or abrupt, and the sounds are termed *barks* or *grunts*. For both birds and mammals, this sound type indicates the sender is indecisive (i.e., it may either go toward or away from or become more or less aggressive or appeasing toward the stimulus), usually because the stimulus is too far from the sender for it to make an adaptive response. Or the stimulus itself may produce the indecision, such as when small birds give *chips* while mobbing a potential predator.

To understand the prevalent use of intermediate sound structures in the MS range, we find that it is not possible to separate function from communication. That is, an indecisive sound structure will be adaptive when the sender perceives a stimulus too far away for its sensory system to adequately produce an adaptive response. In mobbing, however, the stimulus is known but the response is indecisive because function has produced selection favoring indecisiveness. Selection favors the sender remaining indecisive for a time period because, in

this example, to other small birds the sender communicates that something "of interest" is perceived. (How something becomes of interest is another story, but it may be genetically determined, e.g., S. M. Smith 1975, or learned.) Others are attracted to "mob" and thereby increase the foraging time (this seems the most likely benefit) of the sender by causing the stimulus to move away or by reducing the chances of the predator catching something and thereby reducing the sender's foraging time by keeping its "interest up" (e.g., if a snake catches a bird, the long time it takes to swallow a bird keeps it, as a stimulus for mobbing, more stimulating of mobbing because of its continuous movement and other stimulus changes [see Shalter 1975] that inhibit habituation [personal observation]). On the other hand, because *chips* are also given when the sender-stimulus distance may be great, selection may also add specifically distinctive qualities if they function, e.g., in mate attraction or territorial defense as well.

I have thus far restricted the discussion of MS rules to close-contact sounds for reasons outlined above. However, there appear to be many cases in which they may affect signal structure in broadcast calls and many cases in which a sound is used for both close-contact and distance communication. The MS rules are especially likely to operate on the long distance or broadcast calls of species living in groups. In these species, intragroup hostile communication involves low, harsh sounds and it is reasonable to expect that intergroup communication over distance will evolve from the same sounds used in close-contact (intragroup) situations. For example, the low-frequency roar (energy is concentrated at about 360 Hz) of the howler monkey (*Alouatta* sp.) is often cited as an example of selection favoring low frequencies for distance sound propagation in forests (Altmann 1967, p. 329). However, data for sound propagation suggest that the howler could do just as well by calling at 1500 Hz (Morton 1975). I suggest that the low-frequency roar of the howler resulted from selection favoring the use of what was originally a close-contact hostile sound as a long-distance hostile sound. The difficulty involved in turning a close-contact sound into a broadcast signal is attested to by the development of the howler's laryngeal sacs and enlarged hyoid bone resonating system. The result is the ability to broadcast a low, harsh hostile sound over great distance.

An avian example of MS rules affecting long-distance sounds is found in the stripe-backed wren (*Campylorhynchus nuchalis*) which defends permanent group territories by using harsh, low frequency duets and uses shorter, softer versions of the same sound during intragroup aggression (personal observation). However, most bird songs, because they are long-distance signals, do not incorporate MS characteristics. Perhaps as a consequence many species have several to many song types to avoid habituation by receivers to the aggressive message in bird song (Petrinovich and Peeke 1973; Falls and Krebs 1975).

EVOLUTIONARY SIGNIFICANCE

Why should the close-contact vocal signals of animals converge to such a great extent that we may postulate a motivation-structural rule? Why do some

animals not "growl" when they are appeasing and "whine" when they are aggressive or do something entirely different?

I believe some insight into these questions may be gained by viewing the two motivational endpoints separately, as if they were under completely different sorts of selective pressures, which indeed they may be.

Low, Harsh Sounds

I hypothesize that low-frequency sounds will be favored in hostile encounters because there is a direct relationship between low frequency and the size of the animal producing the sound: The larger the animal, the lower the sound frequency it *can* produce. This is presumably a law of physics. So is harshness: A vibrating membrane will produce harmonics as the result of increasing nonlinearity as the frequency (membrane tension) falls (Greenewalt 1968). So if there is selection favoring the use of low-frequency sounds by hostile animals, these sounds will automatically be accompanied by increased harshness due to harmonic production and other off tonal sounds produced by a vibrating flaccid membrane.

Interestingly, Greenewalt (1968, p. 154) illustrated this phenomenon using black-capped chickadee (*Parus atricapillus*) "scold" notes. This ca. 9 g species produced a fundamental frequency of 415 Hz (nearly as low as a howler monkey roar) in this hostile sound. But the bird's small size brought about the amplitude emphasis of higher harmonics due to resonance. Harshness derived from its physically inevitable association with low-frequency sound production has been ritualized as a component of hostile communication even when it occurs apart from the hostile endpoint sound during a sender's more ambivalent motivational states.

The use of low-frequency sound represents the size of the sender to the receiver. This communicative relationship between sound frequency and body size is undoubtedly an ancient coupling. It probably first arose in animals having indeterminant growth such as reptiles and functioned simply to intimidate a smaller animal or formed part of the basis by which animals judged each other's size before committing themselves to an action.

Body size bears a strong relation to the concept of MS rules in communication and its evolution. An appreciation of this relationship necessitates an understanding and appreciation of the two edged sword that body size represents in evolution. A larger animal will generally win in a fight against a smaller one; this relationship has had an enormous selective effect on organisms. Interspecific social dominance (the ability of a larger species to exclude a smaller from some resource) is an important source of selection molding ecological relationships between species (Morse 1974). Morse (p. 826) points out that species of birds and mammals are prone to dominance-mediated niche partitioning because they are characteristically aggressive intraspecifically and use the same aggressive patterns interspecifically. Fighting with conspecifics generates selection pressure favoring increasing size (e.g., Johnston et al., 1972). However, body size must ultimately be kept within *energetic* boundaries. Realizing that

body size may increase due to intraspecific sources of selection arising from aggressive behavior, it is likely that, during evolutionary time, species that tend to fight for resources may be rather prone to extinction. These are farther from an energetically optimum size in terms of their ability to survive environmental fluctuations (Van Valen 1973). We can now envision a dynamic relation between body size and social behavior that, if the intricacy of social behavior is related to brain size, may explain both the extensive use of MS rules in communication and the enlargement of brains over time (Jerison 1973).

The argument is that genes that promote fighting, where larger body size is favored, will tend to be replaced by genes involved in the communication of motivation if the communication genes are as effective as fighting in acquiring the resources in question. Genes promoting communication will be as effective as those promoting fighting if the communication system replaces size as the main determinant of which gene carrier obtains the resources. This seems to lead inevitably to low harsh sounds as the adaptive sound structure in hostile contexts, since lower sounds represent larger size. But the neural processing of vocal communication signals and the ability to recall past experiences in aggressive encounters, to enable an adaptive response to close contact with a conspecific and thus be able to use vocal communication effectively, probably requires and favors a larger brain. The result and selective value of using communication over fighting is that size will be more in balance with energetic requirements (i.e., the communicating population will be more likely to survive environmental changes than the fighting population). The fact that the visual communication channel is also size indicative adds considerable weight to this hypothesis (e.g., piloerection to increase apparent size in aggressive encounters and vice-versa).

High, Pure Tonelike Sounds

The same discussion, in reverse, could apply to the MS rule of high tonal sounds in fearful or appeasing contexts, namely, that a well-stretched vibrating membrane produces more pure tonelike sounds as well as higher frequencies. This in itself does not explain why the use of this sound is adaptive for the sender, because it does not tell us why it might change the receiver's behavior in a manner beneficial to the sender.

Two related attributes of parent-young relationships in birds and mammals seem most likely to provide the answer. It is well known that many morphological features of infant animals are adapted for releasing parental responses in the adult parent(s) (e.g., Lorenz 1943). Vocal sounds are probably adapted for the same function in infant animals; nearly all infant vocalizations are high frequency and pure tonelike sounds that would tend to attract the adult rather than repel it, according to MS rules. In altricial birds, young in nests are both competing for food with siblings and attempting to attract the adult. One wonders why they should vocalize at all in this predator-vulnerable stage, but apparently selection favors vocalizations to elicit parental care and to direct food toward the calling nestling. In nestlings old enough to see, these calls are

sometimes graded such that, when the parent approaches closely with food, the calls rise in pitch and rate of utterance. The young bird is sending an increasingly appeasing and therefore attracting message to the adult, attracting the adult to put food into a gaping mouth which might be intimidating without the sound. We find, then, selection arising from sibling food competition that favors nestling vocal communication following the MS rules.

Selection also favors adults to respond appropriately to stimuli designed to elicit parental care. Because young animals are smaller than adults, it seems axiomatic that vocalizations of infants would be rather high in the species' frequency range. Thus an adult vocalization designed to reduce aggression by eliciting a parental care-hostile behavior conflict in the receiver and/or by a vocal indication of small size (thereby reducing a fear response in the receiver), should be high frequency and tonal. The probability of a signal system evolving that contains high-frequency sound structures in hostile contexts, the reverse of the MS rules, seems remote on these grounds.

SIGNIFICANCE TO COMMUNICATION RESEARCH

I have refrained from using a great number of examples of the use of MS rules so that the concept itself would stand clear as an abstraction. The utility of the concept as a means to tie signal structure to motivation may be tested by studying communication in particular species. It is hoped that by doing so we will demonstrate that communication systems are adaptive on more general levels than current literature indicates. We will be able to describe aggressiveness at the species level, for example, as indicated in paragraph 6 in the above list.

On an individual level, we may be able to characterize "personality" in species in which individuals in social groups differ in aggressiveness according to their use of graded sound signals following MS rules and then ask how differences in "personality" may be adaptive from a population genetics standpoint. The link between sound structure and motivation will bring other sources of selection on signal structure into clear relief. The effect of differing social systems and their underlying ecological bases on communication will be more obvious. We should be able to explain, e.g., that nocturnal monkeys use stereotyped sounds not only because they cannot afford "misunderstandings" (e.g., Moynihan 1964, p. 45; Schott 1975, p. 245) but because the use of long-distance calls is more prevalent, and thus the use of the sound structure-motivation relationship is not selected for.

It is probably correct to point out the analogy between the universal rules of grammar found in human speech (e.g., Chomsky 1975) and MS rules of animal communication—both operate during close-contact vocal communication. Perhaps a major difference in the evolution of human speech and animal vocal communication is that more signals function, in general, for long-distance communication in animals than for man. The "display" concept of ethology, when applied to vocal communication, emphasizes stereotypy and species distinctiveness in vocal signals. It is largely derived from studies of long-

distance vocal signals and is most useful for describing only those. Close contact permits "greater exploitation of signals that are highly graded in structure rather than stereotyped" (Marler 1967, p. 771).

The concept of MS rules in animal communication should permit studies with a greater interpretation of the significance of variations in vocal signals than was provided by the display concept, which neglected the dynamic nature of communication for the ease of descriptive categorization of signals.

SUMMARY

The convergent use of harsh, low-frequency sounds by hostile animals and more pure tonelike, high frequency sounds by fearful or appeasing animals is discussed in an evolutionary context. It is proposed that many sounds in species' repertoires are evolved from motivation-structural rules derived from selection pressures favoring the use of communication instead of, or in conjunction with, fighting to attain resources. The use of this concept should further the appreciation of the relationship between sound structure and function.

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