THE EVOLUTIONARY SOCIOECOLOGY OF COMMUNICATION

This paper begins with a brief introduction to multi-process selection theory, to what explains the existing array of alternatives in evolving populations, and to some basic principles of evolutionary ecology. Evolutionary ecology asks, and seeks to answer, the question of under what ecological conditions selection favours what kinds of characteristics including the behavioural, characteristics oriented towards the physical environment and other species. While communication is sometimes involved in interactions among species, it is most prevalent among members of the *same* population or species. Evolutionary *socio*ecology then asks and seeks to answer the same question about ecologically versus socially oriented characteristics as well as about the purely social. In discussing some general principles of the evolutionary socioecology of communication, this paper pays particular attention to the sometimes cooperative, sometimes antagonistic, and often mixed nature of social communication. It concludes with a discussion of what determines the 'loudness' of signals and what 'rituals' are communicating.

1. Multiprocess Selection Theory.

By way of background, the approach to evolutionary theory I find most congenial could be called "multiprocess" selection theory. This may be more familiar to this audience as Donald Campbell's "evolutionary epistemology", but I prefer the more scientific over the more philosophical terminology. In any case, the basic principle is that all knowledge acquiring and utilizing processes are selection processes. These include biological (gene-based) evolution in biological populations, sociocultural (social learning or meme-based) evolution in cultural communities, as well as certain physiological process which take place within, rather than between individuals - such as learning by reinforcement and punishment and the adaptive immune response (Hull, Langman & Glenn 2001). This is not to imply that what spreads successfully socioculturally or what is reinforcing psychologically are always biologically adaptive - far from it. Rather it is only to imply, as David Hull has frequently emphasized, that they are all instances of the same general class of selection processes. I mention this at the outset because while most of the principles and examples mentioned in this paper are drawn from biological theory, from time to time for convenience, I utilize psychological or sociocultural examples because I don't think the fundamental principles involved differ.

2. What Explains the Existing Array of Alternatives in Evolving Populations?

The existing array of alternatives in any evolving population is explained by constraints, chance, history and necessity in the form of selection (Blute, 1997). There are constraints on what can evolve, most obviously the laws of physics and chemistry. It might be adaptive for a bird or a plane to fly at the speed of light but none ever will. Other kinds of possible biases are

more controversial. Some would have it that transmission rules (e.g. in biology, the laws of genetics) constrain what evolves. However, others argue that the rules themselves (e.g. genetical systems) evolved, and therefore are to be explained rather than being explanatory. Similarly, every entity that evolves also develops and some would argue that there are developmental principles that constrain what evolves. However, others argue that development itself evolved, and hence it too is to be explained rather than being explanatory. When we get into the relationship among various selection processes concretely things become even more complex. Does biological evolution constrain what can be acquired culturally or do genes and culture coevolve? Are biologists and social scientists (on the same side for a change) right that biological and sociocultural evolution "programme" what individuals find reinforcing, or do unique individual learning experiences alter circumstances sufficiently that they become a causal factor in what evolves biologically or socioculturally? I do not intend to pursue these kinds of issues further here except to note that at least everyone agrees that there are *some* constraints on all selection processes, particularly the laws of physics and chemistry.

Chance also plays an explanatory role in all selection processes. As the synthetic theorists always emphasized, evolution is an "opportunistic" process. Something has to arise in the first place before it can be selected. Wheels are a very efficient mechanism of transportation yet did not evolve biologically. We can well imagine that many herbivores grazing on grasslands in east Africa or western North America might well have benefitted from having wheels for hind feet - perhaps pushing themselves along with their front legs used in a fashion similar to the way poles are used by rafters. (According to a student of mine, the wheel principle, powered by wind, is in fact used by tumbleweed but you get the idea). Chance in the

more technical sense plays a role in the form of sampling error or "drift" as it is called. In populations that are divided up spatially into a large number of small, but still somewhat connected local populations, or in populations that have temporally undergone a "bottleneck", sampling error can take place. Rare variants that would otherwise be adaptive can sometimes be lost or rare variants that would otherwise not be adaptive can sometimes be maintained in such circumstances. While all evolutionists pay at least lip service to the importance of constraints and chance, the majority emphasize the next two factors - history and necessity. The study of these constitute the two largest research programmes in evolutionary sciences.

The first law of any evolutionary process is that the relative frequency of alternatives in an evolving population will remain constant unless some force like selection acts to change them. This is an inertial principle not unlike Newton's first law of motion. Social scientists sometimes refer to the weight of history as 'path dependence'. What takes place at any one time is, in part, dependent on what happened previously. One of the great achievements of the social sciences has been the demonstration by historical linguists that languages within each of some 200 language families around the world are descended with modification from a common ancestral language, that some of these families in turn are historically related in superfamilies, and that more controversially, all human languages on earth may have descended with modification from a common ancestral language, sometimes called "the mother tongue" or "protoworld". According to George Basalla (1988), the history of human technology first and foremost displays "continuity". In case after case, he shows how technological artifacts can be shown to have been derived with modification from previously existing artifacts. Nothing comes from nothing; everything comes from something, . He goes so far as to hypothesize that all the

material culture that surrounds us today has descended with modification from the first few stone tools used by human beings. And even before that there were antecedents, in nature. Barbed wire, invented in the American west to enclose livestock, was inspired by the thorn bushes originally used for the same purpose. Because the weight of history can frustrate adaptation, George Williams (1997) calls it a "burden" which is demonstrable on many scales. Most of us are familiar with the lowered larynx which permits us to make a variety of sounds but also makes us more vulnerable to choking, or the retina with its blind spot where the optic nerve exits, or the way in which a relatively few body plans were laid out early in the history of multicellular evolution, and how, probably after some pruning, subsequent evolution has taken place largely within the framework of those body plans. While this inertia, weight, or burden of history may sound like the "constraints" previously discussed, it is different in that the kind of internal "channeling" now under discussion is a result of the past history of evolution itself. The research programme of those who emphasize the role of history in evolution is that of "tree building" which, without getting technical, uncovers the historical affinities among groups. There are a variety of algorithms employed in this endeavour which have various strengths and weaknesses (for recent compendiums see Hall 2004, Felsenstein 2004).

The other large research programme emphasizes the power of selection rather than the weight of history. Evolutionary ecology seeks to complete Darwin's mission by providing not just a theory that evolution happens and that selection is important, perhaps even most important in the process, but a theory *of* selection in the sense of a theory of the conditions under which selection favours various alternative kinds of characteristics. By comparison with the "tree-building" programme, evolutionary ecology is about similarity which is analogous (due to

similar selection pressures) rather than homologous (due to a common history). It seeks potential universal laws governing classes (e.g. small things, species) over descriptions of historically unique lineages (e.g. mammals) and their affinities. In a sense, it emphasizes the "modification" over the "descent" aspect of Darwin's description of evolution as "descent with modification". One of the great tasks for the future of evolutionary studies is a more complete integration of these two research programmes - controlling for historical causes of similarity in testing ecological principles and controlling for ecological causes in historical tree building. While the former is well underway, the latter has been hindered by the fact that general principles of evolutionary ecology are only now beginning to emerge

3. Some Basic Principles of Evolutionary Ecology.

As a consequence of assuming that basic physical features of the ecological environment (energy content, time and space - both literal and metaphorical i.e. niche space) are the properties things are most likely to evolve adaptations to, the most important variables in evolutionary ecology are density, scale, heterogeneity and frequency. This section summarizes some of these basic principles (for more detail and references see Blute 2003) which in turn, are applied to socioecology, including of communication, in the next section.

Low densities relative to resources (uncrowded circumstances) favour growth while high densities favour maintenance in a renewable environment, motility in a colonizable one, and mutability in an environment with capacity unutilized for historical reasons. Business people understand these principles well. When times are too tough to 'grow' a business, what are the alternatives? Depending upon other conditions, you may be able to perhaps downsize, holding

out while waiting for good times to return; expand elsewhere e.g. overseas; or innovate, altering the product or service you provide and/or the market you compete in. (With densities measured relative to enemies rather than resources, the strategies favoured are reversed. High densities relative to predators are circumstances you can cope with by defending yourself, whereas low densities are circumstances you are wise to flee whether in time, space or niche.) If instead of assuming spatio-temporal boundaries are fixed while the amount of resources vary, we assume the opposite - that the amount of resources are fixed while boundaries vary - the result is scale-dependence. Small scale environments with spatiotemporally or otherwise concentrated resources favour fast specialists while large scale environments with spatiotemporally or otherwise dispersed resources favour longer, slower generalists - fleas and elephants, mice and men. Environments are not always homogeneous - low versus high density, small versus large scale - instead they may vary and change. Assuming reliable signals are available, this favours investment in flexibility, the ability to vary and change according to circumstances. Strategies favoured can also depend not just on the ecological environment strictly speaking, but on what other members of the population are doing - game playing over optimizing in the narrow sense. For example, it is commonly advantageous to avoid competition by doing the opposite of what the majority are doing (negative frequency-dependence). Finally, these principles are not mutually exclusive but can be applied reiteratively or in concert. Motility can be scale dependent e.g. be rapid but short or take place more slowly but for longer - ambush predators are sprinters, pursuit predators are distance runners. The combination of density and frequency-dependence can yield equilibria different from those resulting from either operating independently.

4. The Evolutionary Socioecology of Communication.

These principles can be applied not only to ecological strategies, but to the ecological versus the social, as well as to the purely social. Moreover, since communication is an aspect of social relationships and interaction, they are relevant to explaining communication. Consider density-dependence of the ecological versus the social for example. Low densities relative to resources favour competing ecologically, but what if at high densities, either the environment is neither renewable, colonizable, nor contains capacity unutilized for historical reasons, or if it is, strategies appropriate to these conditions are not available in the population? Is there any alternative to dispersing in time, space or niche? The most obvious alternative is social conflict which comes in many forms. If other members of the population have already acquired food from the environment thus depleting it, you can steal yours from them (kleptoparasitism), if they have not only acquired but also ate it, you can eat them (cannibalism), if they have not only acquired and ate it but also turned it into offspring you can produce offspring to parasitize their offspring (intraspecific nest parasitism). Similarly with the purely social. Hence with a male biased sex allocation (e.g. with males at high densities relative to their resource, females), whatever the reason for their ecological success, they may engage in contests with each other whether somatic (fighting), reproductive (sperm competition) or both and whether by means of force (fighting), fraud (sneaker males who appear small and sexually immature), or breach of trust (so-called 'transvestite' males who disguise themselves as females). Just as among people where poverty is one factor in crime and war, and conflicts are commonly accompanied by threats (we shout, shake fists, nations send notes, call in ambassadors, go on alert etc.), animal

"contests" as their overt conflicts are called are commonly associated with communication - threat displays, badges of status etc. This is because, while the participants interests conflict, they also commonly have a mutual interest in avoiding escalated fights.

If individuals working together can achieve more per capita (economies of scale) than they can working separately, social cooperation can be an alternative to social conflict - acquiring partners rather than dispersing or acquiring victims. Among animals, maintenance in the form of heat conservation for example can often best be achieved by crowding together, motility is often more efficient in flocks and schools because of reduced per-capita resistance, and innovation is often achieved more readily if living in groups because innovations discovered by individuals can be learned socially from each other. Pack hunting can be an alternative to food theft, intergroup warfare and cannibalism an alternative to the intragroup, and communal nesting an alternative to nest parasitism. Similarly, males sometimes attract females and females choose male mates collectively (as in leks). In general, social cooperation tends to be more common in defense than it is in acquisition for the basic physical reason that perimeter or surface area increases less than linearly with area or volume. As a consequence, close contact with others decreases contact with the external environment (generally desirable in defense) while separation from others increases it (generally desirable in resource acquisition). Social cooperation as well as conflict is associated with communication. Groups of animals resting or moving together commonly engage in "contact calling" - a kind of affiliative chatter that assists them in making contact and staying together.

Of course in few populations or species are social relationships purely antagonistic or cooperative and hence in few is communication likely used exclusively to express aggression or

affiliation. A flock of birds or a social group of primates may move around feeding and chattering affiliatively, but when individuals actually acquire some bit of food, the message may switch from "I'm here. Where are you? Let's keep together" to "Keep away, this is mine" - conflict within a cooperative context. Similarly, when conflicts break out in a troop of primates, individuals have been observed (by de Waal 1998 among chimpanzees for example) to take sides forming cliques which threaten each other, a phenomenon he called chimpanzee "politics" - cooperation within an antagonistic context. Of course ecological competition, social conflict and social cooperation have different consequences. Maintenance, motility and mutability commonly carry organisms to a time, place or niche in which growth may resume. Conflict, because of its associated morbidity and mortality, reduces densities in situ permitting growth to resume. Social cooperation, while commonly thought of as benign, causes the carrying capacity of the environment to be approached under acceleration rather than deceleration as with social conflict, making the decline, if and when it comes, catastrophic rather than gradual.

Principles other than density-dependence also apply to the socioecology of communication. Factors like scale, heterogeneity, and frequency may be relevant. Communicative action may be rapid and intense or take place more slowly for longer. In heterogeneous circumstances it may pay to communicate flexibly - varying and changing according to circumstances. If some individuals compete ecologically, it may pay others to communicate to socially exploit (acquire victims) or to socially cooperate (acquire partners) and vice versa. If some acquire victims it may pay others to acquire partners and vice versa.

In summary social communication is expected in the same circumstances that other social behavior is - in circumstances in which social conflict or social cooperation rather than pure

competition is favoured. The unique character of communication as a form of social interaction is first that it achieves its effect indirectly, through its effect on the phenotype of others (extended phenotypes), and secondly it does so by means of action at a distance whether the mode is visual, auditory, chemical, electrical etc.

5. What Determines The "Loudness" of Signals?

From an evolutionary perspective, communication has been defined as an action by one organism that alters the behaviour of another in a fashion that is adaptive to either one or both of the participants (Wilson 1975; Krebs & Davies 1993). As such, communication is not so much about what is *conveyed* as about what is *accomplished* (Owings & Morton, 1998:231). Hence evolutionists are as likely to talk about influencing and detecting, about management and assessment, or even manipulating and mind-reading or salesmanship and sales resistance as they are about sending and receiving. This perspective is not entirely foreign to non-biologists. It is obvious for example that, except possibly for academics, most people more often use language to say things like "pass the salt" than they do to say things like "all swans are white".

It has often been thought that all other things being equal (specifically the degree of difficulty of communication in a particular medium in a particular environment), if the interests of the parties involved conflict, signals will be "loud" whereas if they coincide, signals will be "quiet" (e.g. Krebs and Davies, 1993 & references) but I have reservations for two reasons.

To be sure, if a sender has an interest in influencing a receiver but the "receiver" has an interest in *not* being influenced (their interests conflict), loud signals should be the case. The potential for significant gains imply a willingness to pay a significant price, and senders in such

circumstances should be willing to make the effort to "shout". According to some, extreme sexual signals may fall into this category. Sexual ornaments, usually in males, can be both qualitatively bizarre (lime green heads say) and quantitatively extreme (not just big tails, but huge ones say). In some cases it has been shown that the females of related species whose males do not employ the signal, are nevertheless receptive to it when exposed. The implication is that the female "preference" for the display existed in the common ancestor of the two species, prior to the evolution of the male signal! Such a "passive" female preference might better termed a 'vulnerability' or even a 'weakness' rather than a preference. All complex systems including nervous systems have operating characteristics that can be managed, even exploited, a fact that all computer users know. In such species males may have discovered an operating property of female nervous systems, buttons they can press (accounting for the often qualitatively bizarre nature of the signals), while females have been evolving to *resist* having their buttons pressed (accounting for the quantitatively extreme nature of the signals). The whole phenomena has been termed "chase away" sexual selection (Holland and Rice 1998) with males and females coevolving in an antagonistic arms race with males evolving to send (shout), and females evolving to resist receiving (becoming deaf), whereupon males shout more loudly still, and so on (until such a point as the whole enterprise is checked by natural as opposed to sexual selection). While bizarre, loud signals are suggestive of a conflict of interest between signaler and receiver, at the same time, it does not necessarily follow that for signals to be such, interests must necessarily *conflict*. It is only necessary that they *diverge* e.g. with the signaler having a greater interest in influencing than the receiver has in being influenced i.e. with the benefits to the sender being greater than those to the receiver ($Bs - Br > 0$). The loudest signals of course are

apt to obtain when Br is negative, i.e. when interests do conflict.

Secondly, just because loud signals follow from conflicting or divergent interests, it does not follow that quiet signals follow from a mutuality of interest. The latter assumption does not take into sufficient account the energetic costs of receiving. Instead, it seems logical that quiet signals should follow from conflicting or divergent interests as well, but with the *roles reversed* ($Bs - Br < 0$). If a receiver has an interest in finding out something about another who has an interest in it *not* being known, or a lesser interest in its being known, quiet signals should be the case. Again, the potential for significant gains implies a willingness to pay a significant price, and in this case *receivers* should be willing to work hard at detecting, what should (in the conflict case), evolve to be quieter and quieter "signals" (evidence of whatever). One might be inclined to protest that such indications are not "signals" nor their makers "senders" in the ordinary language sense. However, one could equally well argue in the case of loud signals serving the interests of senders only, that we should not claim that "receivers" are receiving "signals" either. For that reason even some biologists would prefer to restrict terms like "communication" and "signals" to the mutually (although not necessarily equally) beneficial case (e.g. Maynard Smith and Harper 2003:3 although even they are not always consistent in this e.g. pp. 74-89). This all goes to underscore the point that I began this discussion with. From an evolutionary perspective communication is about what is accomplished not what is conveyed, about management and assessment (Owings and Morton, 1998). It should not be surprising then that in contrast to extreme male displays, the basis of female choice in many other species is so subtle as to be undetectable to date by even careful human observers.

If loud signals betray the strong interests of the signaler in cases in which interests

diverge and even conflict i.e. (Bs - Br > 0), and quiet signals those of the receiver in cases in which interests also diverge and even conflict but with (Bs - Br < 0), what should indicate an equivalent mutual interest? Equivalent mutual interest (Bs - Br = 0) should result in signals of intermediate intensity. This is because both have an interest in facilitating the communication and both would also prefer that the costs be born by the other. Crudely doing the sums, because of the former senders will work to send (increasing volume) and receivers will work to receive (decreasing volume), but because of the latter senders will foist costs onto receivers (decreasing volume) and receivers will foist costs onto senders (increasing volume) - all averaging out to some intermediate level. Of course all of this assumes managing and assessing are equally costly. If either is intrinsically more expensive than the other, then that would alter the absolute values of "loud", "quiet" and "intermediate", but not the general principles involved.

6. What are "rituals" (mutual displays) communicating?

Students of animal behaviour use the term "ritual" and words derived from it in two ways. One is applied to virtually all animal communication. Since Tinbergen, behavioral ecologists generally believe that animal signals originate in behavior which functions in some related or even wholly different context but which has become "ritualized" to serve a socially communicative function, to serve as a signal. "Ritualization" involves the gesture becoming conspicuous, stereotyped, redundant, and with alerting components added. This conforms somewhat to our usage with respect to humans. For example, the Christian ritual of consecrating bread and wine obviously has a commonplace origin in eating and drinking but has been ritualized in many of the ways animal behaviors become ritualized to communicate, in this case a

belief in the resurrection of Christ. As with the human, animal signals may be indexical, iconic or symbolic. The pitch of an male amphibian's call is an index of its body size. "Intention movements" e.g. teeth bareing are icons of aggression. The different alarm calls given by Vervet monkeys for different kinds of predators are symbols.

There is another phenomenon however which appears to more deserve the term "ritual" in which groups or mated pairs of individuals display together. Groups of storks march up and down, of wolves howl, of some birds chorus, of swallows make short trial flights and so on. Often such groups displays precede some important collective activity like group hunting or migration. In their recent book on animals signals, Maynard Smith and Harper (2003:126-30) drew attention to this rather mysterious phenomenon dubbing it the "Haka phenomenon" after New Zealand football teams who line up before a match and perform a Maori dance which includes jumping up and down, shouting and making aggressive gestures.

"Since, in these displays, the participants simultaneously perform the same acts, it is hard to see what information is being exchanged, or why so much energy is expended." (128)

"They appear to have the effect, not of exchanging information, but of inducing a common emotional state in the participants." (125)

Perhaps however such group displays are communicating exactly what they appear to be communicating, the similarity of their behaviour to each other. At least since Durkheim (1891), in the human social sciences rituals, such as various kinds of religious bowing and scraping, political flag saluting and singing, military marching, shows of school spirit etc. are said to "create and sustain group identity". Like animal rituals, they have also been thought to arouse emotions which somehow meld individuals into a collective, in essence to create and maintain cooperation. Perhaps in both the human and the animal cases however, rather than *creating*

conformity, rituals *test* it i.e. test one's propensity (however acquired) to conform - to each other, to the group average, or sometimes to a leader or leaders. In effect, if one is disposed to conform in this otherwise functionally useless, often even silly in the sense of time and energy wasting way, it might be revealing of a general disposition to conform which will be of adaptive significance when the group engages in some functionally important collective activity like group defense, hunting or migration. Maynard Smith and Harper suggest seeking evidence of punishment e.g. exclusion of non-conformers. It would also be useful to seek evidence of individuals and subgroups excluding themselves because the ritual cost of being part of the larger group is just not worth it. Not all college students are willing to undergo the hazing that joining a fraternity or sorority entails.

What of the other kind of group display - between members of mated pairs? In most sexual displays, members of one gender (usually males) display to, and are chosen among, by members of the other gender (usually females). In some, usually socially monogamous species in which males contribute to parental care however, both members of a pair display to each other. A similar kind of phenomenon takes place vocally in pairs of some bird species which "duet". I suspect that by means of such rituals, individuals are also testing one another's propensity to conform, not conform in the sense of behaving identically, but in the sense of *complementing* one another. After all, dancers dancing face-to-face are commonly not behaving identically, but are mirror-imaging one another. And complementing each other's behaviour is typically what pairs engaged in joint parental care need to do. The message between members of pairs of birds with shared parental care who ritually display to each other in effect may be: "See how disposed I am to complement you". For example: "If/when you brood I'll provision;

if/when you provision, I'll brood."

FURTHER READING AND REFERENCES

Overview of animal sociality

Krause, J. And Ruxton, G.D. 2002. *Living in Groups*. Oxford University Press, Oxford.

Introduction to animal communication

Krebs, J.R. and Davies, N.B. 1993. Chpt. 14, "The Design of Signals: Ecology and Evolution" in *An Introduction to Behavioural Ecology*. Third Edition. Blackwell Scientific Publications, Oxford.

Johnstone, Rufus A. 1997. "The Evolution of Animal Signals" In J.R. Krebs & N.B. Davies, eds. *Behavioural Ecology: An Evolutionary Approach*. Fourth Edition. Blackwell Science Ltd., Oxford.

Rogers, Lesley J. and Kaplan, Gisela. 2000. *Songs, Roars, and Rituals: Communication in Birds, Mammals and Other Animals*. Harvard University Press, Cambridge, Mass.

Other references

Basalla, George. 1988. *The Evolution of Technology*. Cambridge University Press

Blute, Marion. 1997. "History Versus Science: The Evolutionary Solution". *The Canadian Journal of Sociology*. 22(3), Summer.

Blute, Marion. 2003. "The Evolutionary Ecology of Science."*Journal of Memetics* 7(1) <http://jom-emit.cfpm.org/2003/vol7/blute_m.html>

de Waal, Frans. 1998. *Chimpanzee Politics: Power & Sex Among the Apes*. John Hopkins University Press.

Durkheim, Emile. 1891, 1964. *The Elementary Forms of the Religious Life*. Allen & Unwin.

Felsenstein, Joseph. 2004. *Inferring Phylogenies*. Sinauer Associates.

Hall, Barry G. 2004. *Phylogenetic Trees Made Easy: A How-To Manual*. 2nd ed. Sinauer Associates.

Holland, B. and Rice, Wm. R. 1998. "Chase-Away Sexual Selection: Antagonistic Seduction Versus Resistance." *Evolution* 52: 1-7.

Hull, David L., Langman, R.E. and Glenn, S.S. 2001. "A General Account of Selection: Biology, Immunology and Behavior." *Behavioral and Brain Sciences* 24:511-573.

Maynard Smith, J. and Harper, D. 2003. *Animal Signals*. Oxford University Press.

Owings, D. H. and Morton, E. S. 1998. *Animal Vocal Communication: A New Approach*. Cambridge University Press, Cambridge.

Williams, George. 1997. *The Pony Fish's Glow and Other Clues to Plan and Purpose in Nature*. Basic Books.

Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, Mass.