Using Information Theory to Assess the Diversity, Complexity, and Development of Communicative Repertoires

Brenda McCowan
University of California, Davis

Laurance R. Doyle
SETI Institute

Sean F. Hanser
University of California, Davis

The application of quantitative and comparative measures from information theory on animal communication can provide novel insights into the ecological, environmental, social, and contextual properties that shape the structure, organization, and function of signal repertoires. Using 2 phylogenetically different mammalian species that share similar ecological and social constraints as examples, the authors quantitatively examined the internal structure and development of a subsystem of these species' vocal repertoires in comparison with that of human language and illustrated that these species exhibit convergent developmental processes. The authors also discussed how predictions on the structure and organization of animal communication systems can be made from this new application of information theoretic measures with respect to behavioral ecology.

Information theory, developed by Shannon (Shannon & Weaver, 1949) in the early 1950s, revolutionized the field of communication by providing an elegant methodology for encoding telephone signals that can effectively and efficiently transmit information across a variety of noisy communication channels. The same criteria for efficient and effective communication apply, within an ecological and evolutionary context, to the transmission of information within the natural communication systems of both humans and nonhuman animals (McCowan, Hanser, & Doyle, 1999; Pierce, 1980). On the basis of the idea that all communication occurs in a noisy channel, information theory both predicts and quantitatively measures the *degrees of freedom*, or amount of choice, a communication system contains under the physical, biological, and social environment in which it evolved and currently functions. Noisier communication channels require communication systems to exhibit more stereotypy and redundancy, or fewer degrees of freedom or choices, which result in a lesser amount of transmitted information at each level of organization (i.e., signal structure, repertoire structure, sequential structure), such that perceivers accurately receive signals from senders.

All communication channels are subject to the constraints of some type and degree of noise. *Noise* has traditionally been defined by ecological constraints across habitats (e.g., aquatic, terrestrial, arboreal) and by environmental constraints within habitats (e.g., climatic, anthropogenic, heterospecific, and conspecific interference). However, all communication also occurs within social and contextual conditions. Researchers, therefore, include social and contextual constraints (i.e., the value of information, Bradbury & Vehrencamp, 1998; or the pragmatic and semantic properties of signals, Smith, 1977) as equally important sources of noise (also see King, West, & White, 2002). By defining social and contextual constraints as degrees of noise in the communication channel, researchers can use information theory to not only examine the effects of ecological and environmental properties (Endler, 1992, 1993), but also the effects that social and contextual properties (Endler, 1992, 1993; Owings & Morton, 1998; i.e., pragmatic and semantic features) have on signal design and use (i.e., syntactic features), and thus, the amount of information exchanged between signalers and perceivers.

Although the importance of measuring information has received considerable attention by investigators of animal communication (for review, see Bradbury & Vehrencamp, 1998; also see McCowan et al., 1999), most past investigators have limited their application of information theory to dyadic signal exchanges between interacting individuals under very specific and restricted behavioral conditions (for review, see Bradbury & Vehrencamp, 1998; Dingle, 1969; Hazlett & Bossert, 1965; Preston, 1978; Steinberg & Conant, 1974). Few studies have examined the amount of information contained in the structure and use of signals and signal repertoires at the individual, population, or species level (Chatfield & Lemon, 1970; Ficken, Hailman, & Hailman, 1994; Hailman, 1994; Hailman & Ficken, 1986; Hailman, Ficken, & Ficken, 1985, 1987; Haldane & Spurway, 1954; Wilson, 1962). No studies to date have quantitatively examined the amount of infor-

mation in signal, repertoire, or sequential structure in relationship to the social or ecological strategies of different populations or species. This lack of comparative study on the structure and organization of signal repertoires across populations and species has hindered the understanding of the behavioral ecology and evolution of animal communication. Yet because of its mathematical nature, measures from information theory provide a common currency for examining and comparing the potential amount of information contained in different signals and signal repertoires within and across individuals, populations, and species (Bradbury & Vehrencamp, 1998; McCowan et al., 1999). This application of information theory can range from the structure of signals to the complexity of their sequential use and therefore spans multiple levels of communication. In addition, although information theory cannot directly measure the type of information transmitted, it can indirectly give insight into signal meaning because the amount of information is often linked to the type of information being transmitted (for review, see Bradbury & Vehrencamp, 1998).

The importance of vocal communication, indeed of any modality, is a consequence of the ecological and environmental conditions in which a species evolved and lives. For example, as a result of constraints on the visual modality of communication (e.g., amount of light, interfering substrates), most nocturnal, arboreal, and aquatic species have evolved sophisticated vocal systems that serve as the primary modality of communication. The degree to which a vocal system or any other modality can exhibit complexity is related to a species' social dynamics and, specifically, to the number, type, and complexity of social interactions a communication system mediates. In a previous publication, McCowan et al. (1999) reported that information theory models could predict and measure the amount of diversity and redundancy expected in the structure and sequential organization of developing and adult vocal repertoires in species for which vocal communication plays an important role in complex social interactions. In this article, we present data on three phylogenetically unrelated species—humans, bottlenose dolphins, and squirrel monkeys—which demonstrate the efficacy of these predictions and the utility of information theory for analyzing and comparing the structure of human and nonhuman communication systems and their development in relationship with behavioral ecology.

Method and Materials

Vocalizations were collected from 22 preadult and 22 adult subjects from two phylogenetically distinct species that exhibit similar dependence on vocalizations as a primary mode of communication because of ecological constraints: the aquatic bottlenose dolphin (*Tursiops truncatus*) and the arboreal squirrel monkey (*Saimiri sciureus*). The subsystems of vocal repertoires used in this analysis, which included bottlenose dolphin whistle repertoires (McCowan & Reiss, 1995a, 1995b) and squirrel monkey chuck call repertoires (Newman, Smith, & Talmage-Riggs, 1983), were chosen because of their importance in mediating social relationships within each species' social system and, thus, because they are generally analogous to human languages in this social function. For the total 44 subjects across both species and their different age classes, we recorded vocalizations from individuals during normal social interactions within captive social groups. We analyzed the individually identified calls using a modified version of the contour similarity technique (McCowan, 1995; McCowan & Reiss, 2001; in which 60 instead of 20 frequency and time points were extracted across the duration of each signal) to categorize the vocalizations (adult whistles and their precursors for infants in dolphins; adult and subadult chuck calls and their precursors for infants in squirrel monkeys) into types

for each individual on the basis of their similarity in relative frequency contour. The data from the adult and infant dolphins were summarized in McCowan and Reiss (1995a, 1995b) and McCowan et al. (1999), with the exception of the new sequential vocal data from infant dolphins as described below. The data for the adult, preadult, and infant squirrel monkeys were collected as a part of a long-term study on the vocal development of chuck calls in squirrel monkeys (McCowan & Newman, 2000) and analyzed using the same criteria as described in McCowan (1995) and in McCowan and Reiss (1995a, 1995b). As with the dolphin whistle analyses, the categories of chuck calls and infant chuck precursors were quantitatively determined by the maximum number of statistically discrete clusters based on their relative frequency contour structure (McCowan, 1995).

Information theory analyses were conducted on the resulting categories: 4 adults, 12 chuck call categories using $n = 529$ calls; 4 subadults, 11 of the 12 adult chuck call categories using $n = 112$ calls; and 4 infants, three chuck precursor categories using $n = 941$ calls. Cross-validation of categories using discriminant function analysis (see McCowan, 1995; McCowan & Reiss, 1995a, 1995b) revealed that the chuck and infant chuck precursor categories exhibited 89%–100% correct classification to their original categories.

Once calls were categorized into statistically independent structural types, several subsequent calculations were conducted to generate the final results for each age class as follows (which is described in detail in McCowan et al., 1999). First, we tallied the frequency of occurrence for each categorized type and ordered them according to their rank. We then regressed the $\log_{10}$ of the frequency of occurrence of the call types against the $\log_{10}$ of their ranks to generate the Zipf slope or coefficient (McCowan et al., 1999; Zipf, 1949) for the intra- and interspecies comparisons of repertoire structure for each age class. Additionally, we used the sequences of these vocalizations (for data on adult dolphins, see McCowan et al., 1999; for infant dolphins, 47 sequences with 212 whistles; for adult squirrel monkeys, 197 sequences with 394 chuck calls; for subadult squirrel monkeys, 48 sequences with 96 chuck calls; and for infant squirrel monkeys, 177 sequences with 941 chuck precursors), positively identified from each individual for both species within their respective age classes, to calculate Shannon's zero- through third-order entropic values (see McCowan et al., 1999; Yaglom & Yaglom, 1983, for the entropic equations) using an Excel macro program developed by Brenda McCowan. We then regressed these entropic values against their entropic orders to obtain an entropic slope, as described in McCowan et al. (1999), for intra- and interspecies comparisons of sequential organization for each age class. The slope measures and their standard errors from both the Zipf's measure and Shannon's entropic measures were the final outcomes for our subjects of different age classes for each species. Data are also shown in Table 1 and Figure 1 for human languages, where available, from Zipf (1949) and Yaglom and Yaglom (1983) for comparison with our nonhuman subjects.

Results and Discussion

To comparatively examine the diversity and redundancy in the structure of vocal repertoires across development (McCowan et al., 1999), we regressed the logarithm of the frequency of use of each component in the vocal repertoire against the logarithm of its rank as described above, known as the Zipf statistic or coefficient (McCowan et al., 1999; Zipf, 1949), for three phylogenetically distinct mammalian species. Figure 1 presents the Zipf coefficients and their standard errors for developing and adult humans (Figure 1A), bottlenose dolphins (Figure 1B), and squirrel monkeys (Figure 1C). As indicated by Figure 1, each species exhibits a similar pattern across development from more diversity (a less negative Zipf slope) to more redundancy (a more negative Zipf slope) to more diversity again in the relative frequency of use of call types in their respective repertoires. Data for human juveniles and young adults were unavailable for comparison, but studies of human
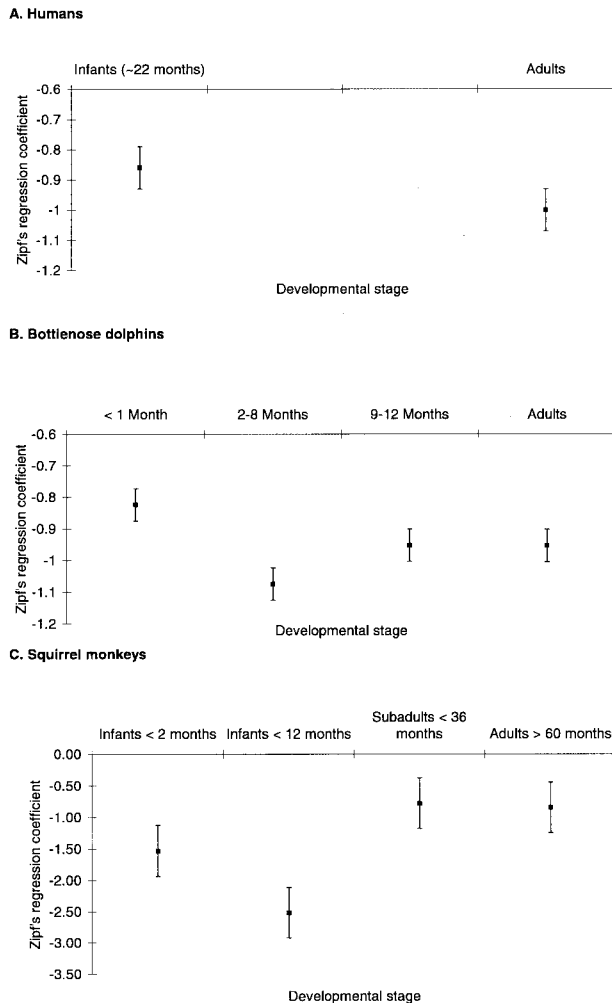
A. Humans

B. Bottlenose dolphins

C. Squirrel monkeys

Figure 1. Zipf coefficients (a measure of repertoire complexity) and their standard errors for developing infant and adult (A) human English words, (B) bottlenose dolphin whistle repertoires, and (C) squirrel monkey chuck call repertoires. Data on juveniles and subadults for humans and dolphins were unavailable.

language acquisition have shown that developing humans go through stages of echolalia (continuous repetition) at both the phonemic and the word levels that correspond to the redundancy observed at analogous stages in dolphin and squirrel monkey vocal development (for review, see Locke, 1993). This pattern was predicted in McCowan et al. (1999) for these and other species in which learning plays an important role in vocal development (for review, see King et al., 2002; Locke, 1993; McCowan & Newman, 2000; McCowan & Reiss, 1995b; Reiss & McCowan, 1993; Snowdon & de la Torre, 2002; Snowdon & Hausberger, 1997).

Thus, early in development, dolphin and human infants appear to exhibit vocal repertoires that possess a higher degree of freedom than their respective adult repertoires. Younger dolphin and squirrel monkey infants exhibit more structurally diverse repertoires than older dolphin and squirrel monkey infants do. Perhaps this higher degree of freedom in infant vocal production is due to differences in channel noise at early stages of development. Young infant dolphins and squirrel monkeys tend to interact socially with

highly familiar individuals in relatively restricted social contexts and thus in quieter communication channels, effectively reducing the constraints on repertoire structure found in the noisier channel of older individuals. In fact, the noisiness of the communication channel may explain why the acoustic structure of some calls is vocally learned (e.g., social calls) whereas that of others is generally not (e.g., alarm calls, isolation calls). For example, the behavioral contexts of alarm and isolation calls place these calls in such relatively extreme, noisy communication channels (e.g., separation from group, predatory threat) that their contexts may require these signals to be fully formed at birth. However, quieter channels do not dictate that communication systems must necessarily exhibit more structural diversity, only that they have the potential to do so (McCowan et al., 1999). So although the constraints on acoustic structure and use may be less severe for the social signal repertoires, these constraints do not explain why certain species actually do exhibit more diversity in these vocal repertoires early in development. Rather, this developmental flexibility is likely because learning is required to achieve communicative competence for these calls and thus reflects the mechanisms underlying the learning process (Hauser & Marler, 1992). This pattern may also have a more functional basis that requires developmentally adaptive strategies for different age groups (Hersek & Owings, 1994; Owings & Loughry, 1985). Further research is needed to determine whether young infant dolphins or squirrel monkeys obtain specific benefits from perceivers by producing more diversely structured repertoires than older infants and adults (see Locke, 1993, for evidence in the babbling of humans; see Snowdon & de la Torre, 2002, for evidence in the babbling of marmosets).

In addition, it is important to note that Zipf coefficients can only be understood at the repertoire level and not at the sequential or linguistic level. Because this measure is an internal look at Shannon's first-order entropy (Pierce, 1980; see McCowan et al., 1999, for a detailed description), Zipf coefficients cannot provide any information about the importance of signal sequences or dependencies and thus should not be considered a linguistic tool. However, the value of the Zipf coefficient and its approximation to a balanced system of diversity and redundancy (i.e., the −1.00 slope found for a diversity of human languages; Zipf, 1949) likely indicates that further information can be stored within signal sequences and thus in higher entropic orders. Therefore, this quantitative measure of repertoire complexity, and its changes over development, provides a comparative tool for examining repertoire structure in relationship to behavioral ecological parameters. Such parameters include habitat structure, social organization and complexity, and life history parameters, each of which in part define the type and extent of noise (e.g., ambient noise and topography, social familiarity, and behavioral context) in the communication channel.

Because Zipf coefficients can provide no information about linguistic structure or signal sequences, researchers must turn to Shannon's (Shannon & Weaver, 1949) higher entropic measures to examine the importance of interdependencies of signals in sequences. Shannon's lower entropic orders measure repertoire structure: Zero-order entropy measures repertoire diversity, and first-order entropy measures repertoire complexity (McCowan et al., 1999). Shannon's higher entropic orders measure the importance of dependencies between signals in sequences. For example, second-order entropy measures the dependency among signals in sequences of two signals, third-order entropy measures the depen-

dency among signals in sequences of three signals, and so forth. The more dependency between signals at each sequential level in a communication system results in a communication system that has less entropy or fewer degrees of freedom in signal choice given that certain signals have already occurred (see McCowan et al., 1999). Therefore, as the importance of signal sequential dependencies increases, the entropic values for each subsequent entropic order progressively drop. We can regress these entropic values against their entropic orders to obtain a slope that represents the degree to which signals in sequences are dependent on one another (McCowan et al., 1999). A more negative slope indicates a higher degree of dependency and, thus, fewer degrees of freedom or lower entropy.

Table 1 presents the values of Shannon's (Shannon & Weaver, 1949) zero-, first-, second-, and third-order entropies for various human languages, the whistles of developing and adult bottlenose dolphins, and the chuck calls of developing and adult squirrel monkeys as well as the slopes of the linear fit of the entropic values against their entropic order (see Figure 2). As indicated by Table 1 and Figure 2, bottlenose dolphins and squirrel monkeys exhibit a similar developmental pattern from less signal interdependency (a less negative entropic slope) to more intersignal dependency (a more negative entropic slope) among signals in sequences (also see McCowan et al., 1999). Human data were unavailable for the developmental comparison, but studies of human language acquisition have provided clear evidence that human infants exhibit an analogous pattern from less-to-more signal sequential dependency (such as in syntactical structure) at both phonemic and word levels (for review, see Locke, 1993). Accurate values for the entropic slopes for dolphins and squirrel monkeys require additional data because we are currently undersampled for entropic orders greater than two (see McCowan et al., 1999, for a discussion of this issue). However, despite the equivalent undersampling of data sets, each species exhibits a similar developmental pattern, which is comparable with human language acquisition.

Therefore, these data suggest that in addition to repertoire structural diversity as shown by the Zipf coefficients, developing infants of different species that vocally learn exhibit organizational diversity in their vocal repertoires (a less negative entropic slope) eventually become more constrained or redundant (a more negative entropic slope) by adulthood. This increase in organizational constraint or internal sequential structure (e.g., from babbling to syntax) suggests that infants achieve communicative competence by decreasing the amount of diversity in the sequential structure of their repertoires. These developmental changes likely occur for the same reasons as proposed for the Zipf coefficients. In addition, increased constraint on dependencies in signal sequences over development provides the necessary redundancy for effective and efficient transfer of information in the more socially complex and thus noisier communication channel of the adult environment.

Thus, similar to the Zipf analysis, this quantitative measure of entropic slope can be used (once sufficient and representative or ergodic samples are collected and analyzed; Pierce, 1980) as a comparative tool to examine the organizational complexity and its development of call repertoires both within and across species. In general, a less negative entropic slope indicates less organizational complexity, whereas a more negative entropic slope indicates more organizational complexity. However, it is important to recognize that an extremely negative entropic slope would indicate that signals in sequences are completely interdependent (with almost all degrees of freedom or choices in selecting signals lost). An extremely negative entropic slope would actually indicate a lack rather than a high degree of organizational complexity, exemplified in some forms of music and perhaps even in crystallized bird- and whale song. With no degrees of freedom, very little information can be transmitted. Thus, the entropic slope, like Zipf's statistic, must exhibit some balance between extreme diversity and extreme redundancy for a repertoire or communication system to contain organizational complexity.

General Discussion

Taken together, these results demonstrate that phylogenetically different species, showing similar life history characteristics (such as the importance and duration of the mother–infant bond in social development) and an importance of vocal communication in mediating complex social interactions, also exhibit convergence in the process of vocal development. For the species in this study, vocal communication evolved as a primary modality in mediating complex social interactions for different reasons. In dolphins, vocal communication is important because of their morphological adaptations to and the turbidity of their aquatic environment. In squirrel

Table 1

Entropic Values and Slopes for Human and Nonhuman Animal Signaling Systems and for Their Developmental Trajectories

| Signaling system	Slope	R^2	Sampling	Zero-order	First-order	Second-order	Third-order
Letters							
Russian	−0.50	.93	Adequate	5.00	4.35	3.52	3.01
English	−0.57	.96	Adequate	4.75	4.03	3.32	3.10
Arabic	−0.80	.96	Adequate	5.00	4.21	3.77	2.49
Dolphin whistles							
Adults (> 96 months)	−1.33	.86	Under	4.75	1.92	1.15	0.56
Infants (< 12 months)	−1.03	.91	Under	4.32	2.38	1.68	1.11
Squirrel monkey chucks							
Adults (> 60 months)	−0.79	.98	Under	2.81	2.21	1.23	
Subadults (< 36 months)	−0.84	.98	Under	2.58	1.92	0.91	
Infants (< 12 months)	−0.54	.91	Under	1.58	0.76	0.50	

A. Bottlenose dolphins
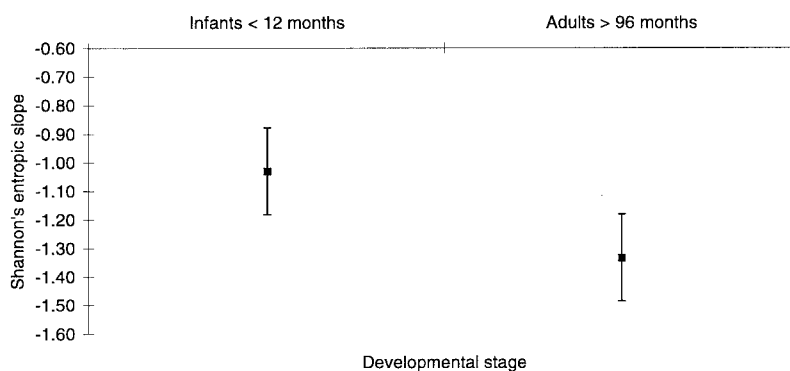
B. Squirrel monkeys

Figure 2. Entropic slopes (a measure of organization complexity) and their standard errors for developing infant and adult (A) bottlenose dolphin whistle repertoires and (B) squirrel monkey chuck call repertoires. Data on humans and subadult dolphins were unavailable.

monkeys, vocal communication is adaptive because of their use and the visual obscurity of an arboreal environment. In humans, vocal communication is adaptive possibly because of constraints in our evolutionary past on the usefulness of other communicative modalities due to our history of tool use. More generally, vocal communication is an efficient and effective means of communication when the transmission of information needs to be rapid under biological, ecological, environmental, and/or social conditions that effectively hinder the use of other modalities of communication.

In addition, information theory measures can be applied to examine cross-species comparisons and developmental patterns in other communicative modalities (e.g., gestural, olfactory, tactile) if the signals can be sufficiently sampled, well quantified, and appropriately classified into discrete categories (McCowan, 1995; McCowan et al., 1999; Pierce, 1980). The application of Zipf's statistic and Shannon's entropies can reveal differences in communication structure in any modality, or combination of modalities, as a function of noise in different communication channels, which is defined by the environmental, ecological, and social conditions particular to a species, population, sex, or age group.

Furthermore, information theory can predict and measure the redundancy or diversity of a communication system at each level

of communication with respect to a species' social system, in general, as well as the particular behavioral contexts in which a species' communication system is used and develops. For example, researchers can test the hypothesis that social organization in the context of its physical environment predicts both the types of communication modalities used by different species and the diversity and complexity of each communication modality within each species. Researchers can predict within a given species that sets of signals or signal repertoires may differ in their degrees of freedom or diversity at the parameter, component, repertoire, and sequential levels in both adults and developing infants because of the differences in channel noise or constraints imposed by their respective contexts of use. For example, intragroup social and play repertoires are predicted to have more degrees of freedom (less stereotypical, less redundant, more diverse), whereas alarm, isolation, and intergroup repertoires are predicted to have less degrees of freedom (more stereotypical, more redundant, less diverse) at each level of communication (signal structure, repertoire structure, sequential structure) in a given species. Thus, information theory may provide insight into aspects of signals or signal repertoire's meaning or intent, especially when meaning and intent are unknown by the very nature of the signals or signal repertoire's structure. For other examples, researchers might predict that hu-

mans speak more stereotypically and redundantly using their own language or dialect when conversing with speakers of another language or dialect than with speakers of their own language or dialect. Researchers might also expect human speakers of a similar language or dialect to communicate using more diversity at each level of organization with perceivers who are familiar rather than with those who are strangers to a language or dialect. Finally, researchers might predict speakers to communicate more stereotypically and redundantly when deceptive, manipulative, or persuasive than when honest with familiar or unfamiliar individuals. Noisier channels between signalers and perceivers require more stereotypy and redundancy in communication structure at each level of organization. Quieter channels allow communication structure to exhibit more diversity at each level of organization.

In summary, information theory provides a powerful and efficacious approach because it links the physical, biological, and social properties of the environment to the structure of communication systems on multiple conceptual and analytical levels. Information theory provides an important predictive framework that can be used to compare the structure and development of communication systems (both within specific modalities and across multimodal systems) across a diversity of species. It can be used to evaluate the balance between degrees of freedom and constraint (a measure of complexity) of different communicative modalities and their development within a given species in relationship to particular aspects of its physical and social environment. Information theory can also examine the complexity of the components and their development within each communicative modality in relationship to their behavioral contexts. Therefore, information theory can be used to assess (a) the relative importance of different modalities within a species inhabiting a specific environment, (b) the general complexity of repertoires (or subrepertoires) of one or more modalities and their comparison across the types of social systems exhibited by different species, (c) the general complexity of subrepertoires within or across modalities in relationship to their context of production within a species, and (d) the specific complexity of subrepertoires within or across modalities in a species with respect to variations in social and ecological strategies across populations, gender, individuals, or over development. Each of these applications can be conducted at each level of communication (i.e., acoustic [element], call [signal], repertoire, sequential), which can be used to examine and mathematically compare systematic patterns among the communication systems of humans and nonhuman animal species. With broad use, this new application of information theory has the potential to significantly advance the understanding of the behavioral ecology of animal communication and its complexity.

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- Reviewing a manuscript takes time (1–4 hours per manuscript reviewed). If you are selected to review a manuscript, be prepared to invest the necessary time to evaluate the manuscript thoroughly.

Write to Demarie Jackson, Journals Office, American Psychological Association, 750 First Street, NE, Washington, DC 20002-4242.