Structural Complexity in a Lizard Communication System: The *Sceloporus graciosus* "Push-Up" Display

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Several measures from information theory are used to describe the structural complexity of the *Sceloporus graciosus* push-up display signal system and to compare this complexity to that of other animal communication systems. Data from focal animal observations of both male and female animals in the field are used to describe the push-up display as a simultaneous combination of three components: display body postures (e.g., lateral flattening, arched back), the number of legs extended during the display (0, 2, or 4), and the number, type, and sequence of head-bobs. Various grammatical rules are described that govern the combination of these components into push-up displays. Body postures are shown to be discrete signals, whereas the number of legs extended and the pattern of head-bobs serve as graded signals. The three structural components are related to each other such that more head-bobs are combined with more legs being extended and a greater likelihood that display body postures are used. Males use more head-bobs, extend more legs, and use display body postures more often than do females; and sexual dimorphism is greater during the mating season than after mating has ended. Finally, the push-up display is "open" or "generative" such that new forms of the signal system will be encountered with an increasing number of displays observed. Overall, the push-up display system is shown to contain most of the types of complexity observed in the communicative displays of birds and mammals.

Although reptiles exhibit substantial complexity in social behavior, behavioral ontogeny, and learning abilities, it is still commonly believed that a qualitative difference exists between the behavior of reptiles and that of birds or mammals in that reptile behavior is somehow more primitive, simple, or stereotyped. This assertion has gone largely untested because of difficulties involved in finding homologies among the very different behavior patterns exhibited by different groups of vertebrates (but see Burghardt, 1988). Information theory provides a useful tool for describing levels of complexity in different behavioral systems and for comparing the behavior of very different animals on a similar scale. Measures from information theory have been used previously to describe the coding efficiency and information content of animal communication signals (e.g., Haldane and Spurway, 1954; Rand and Williams, 1970; Hailman et al., 1985) and in ecological contexts as measures of species diversity (e.g., Pielou, 1975, 1977). They have been particularly important in the debate concerning whether animals have "language" (e.g., Snowdon, 1990; Hailman et al., 1985; Hailman, 1987). The present study uses some of these techniques to describe the structure of the push-up display signal system of the sagebrush lizard, *Sceloporus graciosus*, and to compare the complexity of this signal system with that of other animal communication systems.

The push-up display is one of several visual display systems used by lizards in the Iguania group. During these displays, the head and trunk of the lizard are raised and lowered in a series of "push-ups" or "head-bobs" while the feet remain still on the substrate (Carpenter and Ferguson, 1977). The type, sequence, and timing of head-bobs in push-up displays often contains information regarding the individual and species identity of the displaying animal (e.g., Rothblum and Jenssen, 1978; Bels, 1986; see Carpenter, 1986, for a detailed bibliography of work on lizard push-up displays). Some lizard species exhibit more than one pattern of up-and-down motions, whereas a few do not exhibit a unique pattern at all. The species-specificity of the *S. graciosus* pattern was documented by Ferguson (1971, 1973; see also Carpenter, 1978), whereas Martins (1991) described individual and sex differences in the number of head-bobs, the number of legs extended, and the use of display body postures by this species.

The use of display components also varies across social and behavior contexts. Push-up displays are used in agonistic territorial interactions (e.g., Carpenter, 1965), immediately after moving to a new perch site (Rothblum and Jenssen, 1978; Dugan, 1982) and during court-

ship (Ferguson, 1971, Crews, 1975; Bels, 1986). As do many species, *S. graciosus* uses display body postures ("modifiers," Jenssen, 1977; e.g., lateral flattening, arching of the back) during agonistic interactions (e.g., in "Challenge" displays) but only rarely after moving to a new perch (in Broadcast or "Assertion" displays) and never during courtship interactions (Martins, 1993). Similarly, in those displays that are preceded by locomotion, the number of legs extended and the number of head-bobs produced are positively related to the distance traversed immediately before the push-up display is produced (Martins, 1993).

The complexity of any communicative signal system depends both on the number and type of components available in that system and in the ways in which those components might be combined. There are at least three structural components of the *S. graciosus* push-up display signal system: (1) the number and type of head-bobs in the head-bob pattern, (2) the number of legs flexed and extended to produce the up-and-down motion of the push-up displays, and (3) the use of display body postures. These components are combined simultaneously to produce push-up displays. If all forms of the components are combined at random, several thousand types of push-up display would be possible (depending on how the components are subdivided), suggesting a potentially complex system of communication.

In many signal systems, however, not all theoretically possible forms of a signal occur, and sets of rules or a structural "grammar" governs the combination of components into useful signals (e.g., Snowdon, 1990). Although these rules reduce the total number of display types that are produced, they also add a level of complexity to the signal system. For example, the song system of a mockingbird is more complex than that of a chickadee both because of the larger number of note types and phrases available to the former species but also because of the greater number of ways in which songs are combined into signals. Similarly, certain rules (a grammar or syntax) may govern the combination of body postures, leg extension, and head-bobs into push-up displays; and the frequency of their occurrence may depend on the sex, season, or individual identities of the displaying animals.

The current study provides a detailed analysis of the structure of the *S. graciosus* push-up display. Using data recorded during observations of both male and female lizards in the field, I examine the frequency of use of various combinations of the push-up display structural components and use information theory to describe

grammatical rules or structural constraints that might govern the combination of push-up display components in that species. Male and female *S. graciosus* use push-up displays in different contexts and show seasonal variation in display function (Martins, 1993). Thus, I then examine sex and seasonal differences in the hypothesized grammatical rules while taking differences among individual animals into account. Finally, I use information theory to obtain some overall measures of push-up displays and use these to compare the push-up display system to the signal systems of other animals in terms of communicative complexity.

METHODS

Study animal and site.—*Sceloporus graciosus* is a small phrynosomatid lizard commonly found in sagebrush and in pine woodlands of the western United States (Stebbins, 1944, 1985). The present study was conducted on Table Mountain (elevation 2230 m) in the San Gabriel Mountains of southern California where *S. graciosus* live on and among fallen logs in clearings of the forest. Both sexes defend territories from same-sex individuals throughout the active season, with male territories often overlapping the territories of more than one female (Rose, 1976). *Sceloporus graciosus* is sympatric with its congener, *S. occidentalis*, on this study site.

To begin the study, I chose a 0.5-ha area with a relatively dense population of *S. graciosus* and captured all of the adult lizards living within this area (> 47 mm snout–vent length). Animals were permanently marked with colored beads strung on thin surgical wire through the base of their tails (Fischer and Muth, 1989). Thirty-two adult *S. graciosus* were marked and observed in 1989 (16 males, 16 females). Of these, 25 were rediscovered and observed in 1990, and an additional three adult animals (one male, two females) were marked and observed during that year.

Data collection.—Data for this study were collected in focal animal samples during late June and July of 1989 (after the mating season) and during April and May of 1990 (during the mating season). Data collected during 1989 were also used to examine individual and sex differences in various measures of the push-up display in Martins (1991), whereas data from both years were used to examine the social and behavioral correlates of display production in Martins (1993). In 1989, each animal was observed whenever possible for at least two 0.5-h sessions (once in the morning, once in the afternoon,

not necessarily on the same day) during each of five weeks. Order of observation was randomized each week (from the complete set of 32 adults found that year; separately for the morning and for the afternoon) and then divided in half for the two observers. In 1990, observation sessions began as the lizards were emerging from winter dormancy, and the order of observation was randomized from the set of lizards that had been seen during the previous week. Because males emerged approximately two weeks earlier than females, more data were collected from males than from females.

Animals were not easily disturbed, and observations were made from a distance of less than 5 m, often using binoculars. In this population of *S. graciosus*, body temperatures are known to vary within a rather narrow range (X ± SE = 34.8 ± 0.15 C) during hours of peak activity (Adolph, 1990). Focal animal samples were taken only during those times of day when the lizards were most active (as determined by Adolph, 1990; 0900–1200 h and 1330–1700 h, Pacific Daylight Time), in an attempt to limit any potential effects of temperature on measures of the push-up display.

Whenever a push-up display occurred during a focal animal sample, several aspects of the display were recorded on a data sheet. These included number and type of body postures used (scored as presence or absence of four types of body postures); number of legs extended (zero, two, or four); and number, type, and sequence of head-bobs used in the display. (These components are defined and described in detail below under *Push-up display components*.) Data were also obtained on several push-up displays that occurred outside of focal animal samples (usually while searching for the next subject lizard). Fortunately, displays were usually separated from one another by several minutes, allowing ample time to transcribe the relevant information. (*Sceloporus graciosus* does not produce the long interactive encounters exhibited by many *Anolis*.)

Approximately 10 h of focal animal observations were recorded on videotape in 1989 to create the descriptions of display components given below. Results of a frame-by-frame analysis of the videotape were also compared to information recorded by an observer watching the videotapes at regular speed. No disagreement with the results of the frame-by-frame analysis of the videotape was ever found in the number of legs extended, the use of body postures, or the number of head-bobs as recorded by one of the observers. Because data collected on the head-bob pattern by the second observer

occasionally differed from the videotape analysis, only measures of this variable recorded by the first observer were used in this paper.

Although 35 adult lizards were marked and observed during the two years, recorded displays were produced by only 28 of these individuals (13 females and 15 males; three males and four females were never seen displaying). Twenty-five of the subject animals were observed during both years. A total of 1590 push-up displays was observed during 1989 and 1990 (845 in 1989, 745 in 1990) during approximately 150 h of observation (100 h in 1989, 50 h in 1990). Because I analyzed only the data on the head-bob patterns collected by one of the observers (as described above), only 1151 of the 1590 recorded push-up displays were used in analyses of the head-bob pattern alone or of the relationships among display components.

Push-up display components.—Body postures: The up-and-down motions of the *S. graciosus* push-up display are accompanied by the use of four body postures, used alone, in combination, or not at all. All four of these postures are static and usually remain constant throughout the pattern of head-bobs and leg extension. In some rare cases, the postures were relaxed (and thereby eliminated) during the course of a single display. Because postures were never added during a display, lizards were scored as having used the body postures observed at the beginning of each display. Lateral flattening (LF)—The torso is compressed along the dorsal–ventral axis, thereby increasing the extent of the vertical surface along the side of the animal (in the parasagittal plane) and exposing the colored belly patches of the lizard (blue in most males and some females). Gular extension (GE)—A small patch of colored skin at the throat of the animal (also blue in most males and some females) is lowered, thus also increasing the size of the lizard in a sagittal plane. Arched back (AB)—The spine is bent upward from a straight line parallel to the substrate to a curve arching above the substrate, with the highest point of the curve at the middle of the torso. Tail raise (TR)—The distal quarter of the tail is lifted and held pointing upward. Leg extension: Throughout the series of up-and-down motions the head/trunk/tail axis is held in a stiff line, with the angle of motion determined by the number of legs being extended and retracted during the display. Four legs extended—The head/trunk/tail axis remains parallel to the substrate, with a perpendicular up-and-down motion being produced through the extension and retraction of all four of the limbs. Two legs extended—

Only the two anterior limbs are bent and straightened to produce the up-and-down motion. Thus, the head/trunk/tail axis is moved at an angle to the substrate. Although it is theoretically possible that the two posterior limbs might be used alone to produce the up-and-down motion of the push-up display, this was never observed in *S. graciosus*. Zero legs extended—No discernible motion of any of the four legs is observed. The up-and-down motion is produced through use of the muscles in the chest, shoulder, and back.

In some cases, four-legged displays changed into two-legged displays, or two-legged displays became zero-legged displays during the course of a single push-up display. Because displays never increased in the number of legs extended, lizards were scored as having extended the number of legs observed at the beginning of each display.

Head-bob pattern—The motions produced through the extension and retraction of the legs or shoulder muscles are combined into a continuous series of single and double head-bobs. These single and double head-bobs are combined to form the three-part head-bob pattern of *S. graciosus* (Fig. 1). Both single and double head-bobs usually take less than 2 sec to complete and are separated from each other by intervals of less than 1 sec in duration (Fig. 1). Because entire push-up displays were always separated from each other by at least 1 min (usually several minutes), individual displays were easily distinguished from each other. Single head-bob—The head/trunk/tail axis is raised (until the tip of the nose is about 1 cm above the initial position), held at an elevated position for about 1 sec, and then lowered again. Double head-bob—The head/trunk/tail axis is raised and then lowered in a cycle which is completed twice in quick succession. In the first cycle, the head is raised only slightly (until the tip of the nose is about 0.5 cm above the initial position) and then quickly lowered. This is followed almost immediately by a second cycle of greater amplitude (the tip of the nose is raised about 1.0 cm above the initial position), in which the head is held at an elevated position for approximately one second before lowering. Overall sequence—The overall head-bob pattern consists of a series of double head-bobs (type A), followed by a series of single head-bobs (type B), followed by a series of double head-bobs (type C; Fig. 1). The actual number of single or double head-bobs in each segment of this three-part sequence varied among individual displays. Although any of the three segments might be
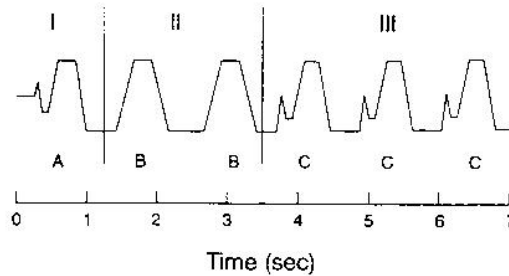

Fig. 1. Visual depiction of the head-bob pattern of *Sceloporus graciosus*. X-axis represents time, in seconds, whereas the y-axis is a schematic depiction of the height the lizard's head is raised or lowered. The head-bob pattern can be divided into three segments: (I) 0–2 initial double head-bobs (Type A), (II) 0–5 single head-bobs (Type B), (III) 0–7 terminal double head-bobs.

omitted entirely from any single display, the sequence of double, single, double head-bobs seems to be invariant. When the entire display consisted only of double head-bobs, these were arbitrarily scored as being part of the initial segment (Type A).—

Statistical analyses.—Data from focal animal samples were easily summarized as frequency distributions for each component and combination of components of the push-up display. Two statistics derived from information theory (Entropy and Evenness, as defined below) were used to describe the magnitude of the deviation of frequency distributions from equiprobability, which suggests the existence of grammatical rules governing the use and combination of components, and chi-squared tests were used to obtain hypothesis tests for these statistics. These estimates of magnitude were also used to compare the push-up display to the signal systems of other species and to test for sex and seasonal differences in frequency distributions. Finally, a form of Zipf's Law was used to determine whether the push-up display signal system is open or generative.

Shannon and Weaver's (1949) index, H or the "Entropy" of a signal system is a measure of the amount of information that is contained in the system or, more specifically, how "equiprobable" different signal categories are. The Maximum Entropy of a signal system is calculated as $H_{max} = \log_2 n$ where n refers to the total number of signals or signal forms that occur in the system. When information is available concerning the use of that signal in naturally occurring situations, the Actual Entropy of the signal system may be estimated as $H_1 = -\Sigma p_i (\log_2$

p_i) where $i = 1, 2, \ldots, n$, and p_i refers to the estimated probability at which the ith form of the signal occurs. Because both the Actual and Maximum Entropies depend on the number of possible signal types, a relative measure of Entropy is necessary for comparisons among signals or signal systems with different numbers of forms. The "Evenness" of a signal system is estimated as $V = H_1 / H_{max}$, and thus provides a relative measure of the equiprobability of signal components when the maximum number of signal types is known (see Pielou, 1975, 1977). (Evenness is similar to "redundancy," $D = H_{max} - H_1$; Gatlin, 1972.)

The Actual Entropy of a signal system is highest when all forms of the signal system are used with equal probabilities and thus has an upper limit at the Maximum Entropy. Evenness ranges from zero to one. An Evenness of one implies that all components occur with equal probabilities, whereas a small value of Evenness implies that one or a few components are used with far greater frequency than are others. When studying theoretically constructed display categories, a low level of Evenness suggests that many of the categories provide little information and might be more useful if combined (although any particular signal category may contain a great deal of information, the system as a whole contains little information). High levels of Evenness may suggest variables (i.e., categorization schemes) that carry a great deal of information and that might be used by the animals as meaningful signals. Thus, these categories may prove fruitful in future studies of information content.

In the present study, both Entropy and Evenness were calculated for each of the three components of the push-up display, as well as for all combinations of these three components. To test for sex and year differences in Entropy and Evenness while taking differences among individual lizards into account, these statistics were calculated independently for each animal and then used as the units of analysis in standard two-way ANOVAs. (Because Evenness is a linear combination of the Entropy, two-way ANOVAs of the two variables are identical. In all cases, standard residual analysis techniques were used to determine whether transformations of the data were necessary to meet the assumptions of ANOVA.) Differences in display structure in these data resulting from differences in social and behavioral context have been addressed at length in Martins (1992). Because Martins (1992) found that about 90% of the push-up displays in this set of data consist of Broadcast or "Assertion" displays (produced in the absence of

any obvious social audience, immediately following a bout of locomotion), it is not surprising that social and behavioral context had little impact on the statistical analyses presented in this study. Analyses in the current study were conducted both for the entire set of data (regardless of context) and for Broadcast displays alone (the small sample size of non-Broadcast displays prohibited detailed analysis of this subset alone). Because no substantial differences were found between these two forms of analysis, results are presented only for the entire set of displays combined. All tests of significance were conducted at the $\alpha = 0.05$ level.

Finally, to estimate the overall complexity of the push-up display signal system, I followed Hailman et al., (1985) in calculating the Total and Actual Entropies of the push-up display system as a whole and by testing the system for openness or generative qualities. Openness was tested by examining a graph of probability of use by frequency-rank for the push-up display. This graph was originally suggested by Zipf (1935) as a means of describing human language and can be used to determine whether a language is an open system of communication. Zipf's Law, as it is commonly called, claims that the relationship between the frequency at which a particular word is used and the rank of this frequency will be a decreasing, monotonic function (when the axes are plotted logarithmically) that asymptotically approaches a line with slope of -1 ($P = ir^{-1}$, where i is the y-intercept; see Fig. 2). In biological terms, new forms of the signal system are constantly being created, and more and more of them are found as the number of observations increases.

Zipf's Law was an empirical result based on Zipf's observations of human written language. In 1953, Mandelbrot attempted to modify this law such that it would provide a better fit to most human languages and to justify it based on mathematical and linguistic arguments. His result was to propose that human languages are both theoretically and empirically better described by the equation $P = i (r+k)^{-s}$, where P is the probability of occurrence of the rth-ranked word, and i, k, and s are allowed to vary. In essence, i (intercept) affects the y-intercept of the curve, s (slope) makes the curve steeper, and k depresses the left side to produce a rounded curve from Zipf's line. This modified equation describes a large family of curves, and reduces to Zipf's Law when $s = 1$ and $k = 0$. Unfortunately, the parameters of Mandelbrot's curve are difficult to estimate statistically, and standard hypothesis tests are not appropriate for use with intrinsically nonindependent data of

this sort. Nevertheless, even a rough fit of Zipf's and Mandelbrot's models can be used as a heuristic tool for describing language.

Whether or not Zipf's line or Mandelbrot's curve actually describe human language well, the relationship between probability of use and frequency-rank can be used to determine whether a communicative system has generative properties. A curve describing data for a given signal system in this way will reach an asymptote at zero probability of use (i.e., a vertical line at the far right side of the graph) when all forms (i.e., words or display types) of the system have been encountered (Fig. 2). If the curve never approaches a vertical line, then the signal system is generative or open, such that increasingly rarer patterns will be encountered as larger samples of displays are examined. Data that are well described by either Zipf's or Mandelbrot's models will have this quality of being open or generative (see Hailman et al., 1985, for a thorough description of Zipf's laws and their use in determining whether nonhuman signal systems share some of the properties of human language).

RESULTS

Frequency of use.—Only 215 of the 1590 push-up displays recorded (118 in 1989, 97 in 1990) included the use of any of the four body postures described above. Because these four postures might be used alone, not at all, or in combination with each other, 16 ($= 2^4$) combinations of body postures are possible. Tail raise was only observed alone or with all three of the other postures together, so that only 10 of these combinations were actually observed during displays. The most frequently occurring combination was the absence of all display body postures (1375/1590 = 86% of all displays). The second most common combination of body postures was a simultaneous combination of three components: LF, GE, and AB (103/1590 or 6.5%). Although some of the other display combinations did occur, these two combinations seem to be almost entirely responsible for the significant difference among combinations in frequency of use ($\chi^2 = 17564.8$; df = 15; $P << 0.01$). The magnitude of these differences among categories can also be seen clearly in the measures from information theory. The Actual Entropy for body posture categories was $H_1 = - \Sigma P \log_2 P = 0.89$ bits/display (Table 1). Because 16 categories were possible, the Maximum Entropy was $H_{max} = \log_2 16 = 4.00$ bits/display, and the Evenness was rather small ($V = H_1 / H_{max} = 0.89/4.00 = 0.22$). Because Evenness
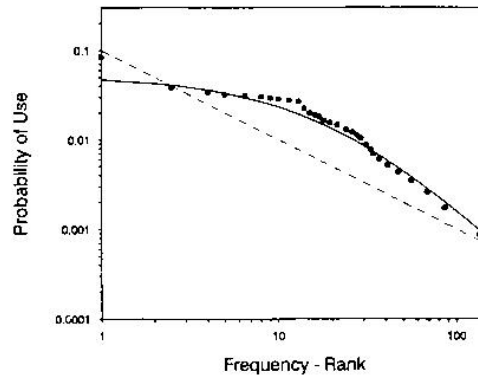

Fig. 2. Scatterplot of probability of use with frequency-rank of displays. Dots mark the results obtained for the *Sceloporus graciosus* push-up display in this study. The push-up display system is shown to be open or generative because a curve fit to these data would never reach an asymptote at zero probability of use (i.e., a vertical line at the right side of the graph). Although these data are also not well described by Zipf's original law (the dashed line), they are reasonably well described by curves in the family of curves proposed by Mandelbrot (1953). More surprisingly, the push-up display data are well described by the exact Mandelbrot curve proposed by Hailman et al. (1985) for the chick-a-dee call of *Parus atricapillus* ($P = 14 (r + 19)^{-1.9}$, where P = the probability of use and r is the frequency rank: the solid line).

was approximately doubled ($V = 0.57$) simply by considering body posture combinations as a variable with only two categories (presence or absence of body postures), many of the future analyses consider use of body postures in this reduced form.

Displays also varied in the number of legs extended and in the number and type of head-bobs used. All three categories of leg extension were exhibited frequently, and the measures of Evenness were, therefore, substantially higher ($V = 0.99$; Table 1; χ^2 value was still significantly different from equiprobability because of the huge sample size; $\chi^2 = 20.65$; df = 2; $P < 0.05$). Between zero and two double head-bobs were observed in the initial segment of the head-bob pattern. About 84% (969/1151) of displays included the use of at least one initial double head-bob (only one individual used two initial double head-bobs). As many as five single head-bobs were observed, but only four of the 1151 displays used more than three single head-bobs. As many as seven double head-bobs were used in the third segment, but only one individual produced more than six terminal double head-

TABLE 1. ENTROPY, EVENNESS, AND TWO-WAY ANOVA RESULTS FOR EACH OF THE THREE MAIN ELEMENTS OF THE PUSH-UP DISPLAY SYSTEM. Overall estimates of Entropy and Evenness were obtained by using all 1590 push-up displays (or 1151 for measures of the head-bob pattern). Evenness was also calculated for each individual lizard during each year and used as the unit of analysis in standard two-way ANOVAs. P-values refer to the results from these ANOVAs (* $P < 0.05$, ** $P < 0.01$).

	Entropy H_t	Evenness V	P-value		
			Sex	Year	Interaction
Body postures	0.89	0.22	0.01**	0.63	0.63
Leg extension	1.58	0.99	<0.01**	0.14	0.05*
Initial double head-bob	0.63	0.63	0.60	<0.01**	0.76
Single head-bob	1.69	0.65	<0.01**	0.04*	0.03*
Terminal double head-bob	2.54	0.85	<0.01**	0.37	<0.01**
Total number of head-bobs	2.91	0.92	<0.01**	0.35	<0.01**

bobs. Overall, up to nine head-bobs (both single and double, summed) were observed in push-up displays, and the number of displays occurring with each total number of head-bobs was not equiprobable ($\chi^2 = 351.2$; df = 8; $P \ll 0.01$). Only 5% (60/1151) of all displays included more than a total of seven head-bobs. If each head-bob in each of the three segments of the push-up display is designated by a single letter (i.e., A, B, or C), a total of 43 combinations of head-bob sequences was observed. The most commonly occurring head-bob patterns were one double head-bob alone (A: 125/1151 = 10.9%) and one double head-bob followed by two single head-bobs followed by three double head-bobs (ABBCCC: 121/1151 = 10.5%). Two shorter versions of this latter case (ABCC and ABBCC) also occurred frequently (109/1151 = 9.5% and 100/1151 = 8.7%, respectively). These last three categories combined account for 330/1151 or 28.7% of the push-up displays.

Use of each of the three components of the display was related to use of the other two (Table 2). Body postures occurred only when at least two and usually four legs were extended, and fewer head-bobs were produced in displays in which fewer legs were extended. When zero legs were extended, displays were more likely to consist of only one or two head-bobs (usually one double head-bob, A). When two legs were extended, most displays contained four or five head-bobs; and when four legs were extended, most displays contained five or six head-bobs (ABBCCC, ABBCC or ABBCCCC). When body postures were used, displays were likely to include at least four head-bobs (usually ABBCCC or ABBCCCC). When body postures were not used, displays were more evenly distributed across categories of head-bob number ($P < 0.01$

for all comparisons using χ^2 tests, results not shown).

There are a maximum of 16 combinations of body postures (four postures used in any combination or not at all), three forms of leg extension (zero, two, or four legs extended), and 143 levels of head-bobs (0–2 initial head-bobs, 0–5 single head-bobs, 0–7 double head-bobs combined—1 for the structurally impossible category of zero head-bobs in each segment). Thus, if all forms are combined at random, there are a total of $16 \times 3 \times 143 = 6864$ types of push-up displays. This yields a Maximum Entropy of 12.74 bits/display. Only 172 of these 6864 push-up displays were actually observed; and, using the observed frequencies, we obtain an Actual Entropy, H_t, of 6.15 bits/display. Thus, the Evenness of the *S. graciosus* push-up display is $V = 6.15/12.74 = 0.48$.

Sex and year differences.—Almost all of the displays in which body postures were used were performed by males (89% or 105/118 in 1989; 99% or 96/97 in 1990), yielding a statistically significant difference in Evenness between the sexes ($V = 0.25$ for males vs $V = 0.10$ for females; Table 1). Differences in the use of body postures between the two years and the interaction between sex and year were not statistically significant. Thus, the use of display body postures depends mostly on sex, with females giving significantly fewer displays with body postures than did males.

The number of legs extended during displays varied both between the years and between the sexes (Table 1). As described in Martins (1991), males used significantly more four-legged push-up displays than did females, but the magnitude of this difference depended on the year in which

data were collected. Males produced more four-legged push-ups than any other category in 1990 (during the mating season) and more two-legged push-ups in 1989 (after the mating season had ended). Females produced mostly zero-legged push-ups in 1990 and approximately equal numbers of zero and two-legged push-ups in 1989. Thus, males and females reacted differently during the two years in terms of leg extension (i.e., the sex-year interaction term was significant, Table 1).

Similar results were obtained for the total number of head-bobs used in displays. Year differences were more critical than sex differences in determining the number of head-bobs in the first segment of the display, whereas year and sex interacted with each other to determine the distributions of number of head-bobs in the second and third segments of the display (Table 1). Although males used the initial double head-bob (Type A) slightly more often than did females (87% or 796/913 for males, 72% or 171/236 for females), the difference between the years was substantially more dramatic. Both males and females used the initial head-bob (Type A) about half of the time during 1989 (after the mating season), leading to very high levels of Evenness during this time ($V > 0.9$). Extremely low levels of Evenness were obtained in 1990 (during the mating season), when very few displays omitted the initial head-bob ($V < 0.1$; Table 1).

As shown by Martins (1991), males also produced more head-bobs than did females in both the middle and final segments of the head-bob pattern (Types B and C). Furthermore, both males and females produced fewer single head-bobs (Type B) in 1990 (during the mating season) than in 1989 (after mating had ended). This shift in behavior between seasons was more pronounced in females than in males. Females produced almost no head-bobs at all in the final two segments of the display in 1990 (during the mating season). This decrease in variability of the female display can be clearly seen in the drop in Evenness ($V = 0.52$ in 1989 vs $V = 0.33$ in 1990 for Type B; $V = 0.85$ in 1989 vs $V = 0.24$ in 1990 for Type C; Table 1). Males also became less variable in their displays in 1990, but this drop in variability led to the use of a smaller number of categories, thus leading to an increase in the Evenness of male displays ($V = 0.59$ in 1989, $V = 0.66$ in 1990 for Type B; $V = 0.81$ in 1989, $V = 0.69$ in 1990 for Type C). Thus, the difference between the sexes was more pronounced during the mating season (1990) than after it (1989), and the interaction

TABLE 2. FREQUENCY OF OCCURRENCE OF EACH COMBINATION OF THE THREE DISPLAY ELEMENTS.

Legs flexed	Number of head-bobs	Body postures		
		None	Any	Total
0	1	101	—	102
	2	57	—	57
	3	32	—	32
	4	53	—	53
	5	35	—	35
	6	26	—	26
	7	7	—	7
	8	1	—	1
	9	—	—	—
Total	312	—	312	
2	1	36	1	37
	2	48	4	52
	3	38	2	40
	4	89	7	96
	5	98	6	104
	6	72	4	76
	7	19	2	21
	8	2	—	2
	9	1	—	1
Total	403	26	429	
4	1	1	1	2
	2	3	1	4
	3	17	4	21
	4	40	15	55
	5	65	22	87
	6	62	48	110
	7	47	35	82
	8	16	22	38
	9	3	8	11
Total	254	156	410	
Grand total	1	138	2	140
	2	108	5	113
	3	87	6	93
	4	182	22	204
	5	198	28	226
	6	160	52	212
	7	73	37	110
	8	19	22	41
	9	1	8	12
Total	969	187	1151	

effect between sex and year was significant (Table 1).

Overall, females used fewer total head-bobs in displays than did males, and produced displays consisting of only one double head-bob (Type A) more often. Both sexes produced somewhat fewer head-bobs in displays during the mating season (1990) than after it (though this difference was not statistically significant);

and this shift in behavior was substantially greater for females than for males (i.e., the interaction effect between sex and year was statistically significant; Table 1). The average male head-bob pattern during both years was ABBCCC, whereas the average female display was AB in 1989 (postmating), and A alone in 1990 (during mating). In terms of Evenness of total number of head-bobs, females tended to have less Even display distributions than did males, and this difference between the sexes was greater in 1989 than in 1990 (Table 1).

In summary, year and sex differences were found in all three of the primary components of the push-up display. Males were more likely to use body postures, extend more legs and produce more head-bobs than were females. No differences were found in use of body postures between the two years. However, in terms of number of legs extended and number of head-bobs produced, the sex difference was greater in 1990 (during the mating season) than in 1989 (after mating had ended) in all cases except for that of the number of initial double head-bobs. Displays in 1990 were more likely to include the initial double head-bob (Type A) and omit the single head-bob (Type B) than displays in 1989 (Table 1).

Signal system openness.—Finally, we can compare the relationship between the frequency at which a particular type of display is used and the rank of this frequency to determine whether the push-up display is an open system. As stated earlier, 172 combinations of elements into push-up displays were actually observed. Figure 2 shows a graph of the probability of use of these combinations with their frequency rank. From this figure, we can easily see that, if the curve continues as it does within the measured sample, it will never reach an asymptote at zero probability of use (i.e., a vertical line). In other words, the system is the second nonhuman communicative system which has been shown to be generative, such that increasingly rarer patterns will be encountered as larger samples of displays are examined. Furthermore, although the data are not well described by the actual line predicted by Zipf (the straight dashed line in Fig. 2), they are fairly well described by Mandelbrot's modification of Zipf's Law. More surprisingly, they are described reasonably well by the same curve that Hailman et al. (1985) used to describe the chick-a-dee call of the black-capped chickadee $(P = 14 \ (r + 19)^{-1.9})$, where P is the probability of occurrence of the rth-ranked word. Although statistically derived parameter estimates and hypothesis tests would be extremely useful to test the validity of these patterns, the tight relation-

ship between data and curve shown in Figure 2 seems unlikely to be the result of chance alone.

DISCUSSION

Display structure.—The push-up display of *S. graciosus* may be succinctly described as a simultaneous combination of three components: (1) the use of four body postures; (2) the number of legs extended (zero, two, or four); and (3) the number, type, and sequence of head-bobs in the display. Structurally, each of these components of the push-up display can take several forms, and these forms might all be ranked theoretically by level of structural intensity. The head-bob pattern might be made more intense by increasing the number of head-bobs in any of the three segments; the number of legs extended during the display might be increased from zero to two or from two to four; and the number of body postures used in combination might be increased to produce a more intense display than one that did not use any specific body postures at all. Increasing this level of intensity in any of the three components may be comparable to increasing the number of times note types or phrases are repeated in a bird call or primate vocalization.

Martins (1993) suggested that the number of head-bobs, the number of legs, and the probability that display body postures would be used increased with the level of arousal experienced by the displaying animal. Push-up displays are often produced immediately after an animal has run from one place to another, and the actual form of each of the three components is closely related to the distance moved immediately before the display was produced. The results of the current study show that, given the limits defined by the variables themselves (i.e., zero, two, or four legs extended and up to 10 head-bobs), all possible combinations of numbers of legs extended and number of head-bobs are used by *S. graciosus* during push-up displays. Thus, the number of head-bobs and the number of legs extended could function as graded signals of the level of arousal or intensity involved. This is similar to what Jenssen (1979) found for the visual displays of *Anolis opalinus*, in which all of the display components were viewed as graded signals of the level of display intensity.

In contrast, the use of body postures in push-up displays did not seem to show graded or progressive variation. Almost all of the push-up displays in this study either exhibited no body postures at all or a particular combination of three of the postures (lateral flattening, arching of the back, and extension of the gular flap).

Other combinations were rare, suggesting that the use of body postures functions primarily as a discrete rather than a graded signal. Martins (1992) shows that display body postures are used by *S. graciosus* as a signal of aggression in agonistic territorial interactions and are not used during bouts of courtship or reproductive behavior. A much larger sample of displays would be necessary to determine whether rare occurrences of other body posture combinations are used as signals of intermediate levels of aggression, but the results of the current study support the suggestion that body postures are a discrete signal of aggressive intent.

Push-up display grammar?—Not all of the possible combinations of the three components are produced by *S. graciosus*, and some combinations are far more likely to occur than are others. The three components of the push-up display are related to each other, with certain combinations being allowed by the system whereas others are not. As was also found by Jenssen (1979) for *A. opalinus* displays, *S. graciosus* displays that include the use of body postures also occur with the extension of at least two, and usually four, legs. These displays also tend to occur with more head-bobs than do other types of displays. Finally, displays in which a greater number of legs are extended also occur with a greater number of head-bobs. Thus, all three display components seem to be positively related to each other along a continuum, such that an increase in the number of any one of the components increases the probability that an increase in the number or intensity of the other two elements will also occur. In other words, the three components of the display impose structural constraints on each other, and there seems to be a grammatical rule requiring that the three components increase or decrease together.

Male and female lizards used different forms of the push-up display preferentially, suggesting that different rules apply to each of the two sexes. Males used more head-bobs, extended more legs, and used display body postures more often than did females. Although there was no difference between years in the use of the four body postures, males increased in the number of legs extended from 1989 to 1990 (after the mating season to during the mating season), whereas the reverse occurred in females. Both sexes decreased in the number of head-bobs (except in the first segment of the display) from 1989 to 1990, but this decrease was more pronounced in females than in males. The average male head-bob pattern consists of a double head-bob, followed by two single head-bobs, followed by a series of three double head-bobs (ABBCCC). The average female head-bob pattern consists of a double head-bob alone (A) during the mating season (1990) but followed by a single head-bob (AB) after mating had ended.

Overall, these differences resulted in a greater degree of sexual dimorphism during the mating season than afterward. During the mating season (in 1990), females used few body postures, extended few legs, and used few head-bobs in comparison to males. After the mating season (in 1989), females still used few body postures, but they increased both the number of head-bobs and the number of legs flexed in displays. Because males decreased the number of legs flexed in displays after the mating season, the sexes were more similar in display behavior after the mating season than during it. With the information on push-up display structure and function reviewed above (see particularly Martins, 1993), these results imply the existence of separate functions for the components of the push-up displays of male and female lizards. Display body postures serve as an aggressive signal produced by males year-round, whereas the number of head-bobs and the number of legs extended are used as graded signals of the level of arousal by both sexes after mating has ended but primarily by males during the mating season.

Comparisons with other signal systems.—Several comparisons can be made between the *S. graciosus* push-up display and the signal systems of other animals. For example, the push-up display is "combinatorial" in that it is a simultaneous combination of three elements. Similarly, many bird calls and primate vocalizations are produced by combining simple notes into more complex strings or phrases. For example, the chickadee call of *Parus atricapillus* is a sequential combination of four note types, each of which may be repeated several times or not at all before continuing to the next note type (Hailman et al., 1985). This pattern is directly analogous to the repetition of double and single head-bobs in the head-bob pattern of the *S. graciosus* push-up display. The push-up display also exhibits a combinatorial pattern at a higher level, because of the simultaneous combination of head-bob pattern, leg extension, and body postures.

Furthermore, the push-up display system is generative and open in that the number of different types of displays observed will increase with the sample size. As was shown by the examination of Zipf's Law (Fig. 2), there does not seem to be an upper limit to the number of display combinations that are used. This is true of human language and the chick-a-dee call of

the black-capped chickadee (Hailman et al., 1985) and may be true of other species as well (although it has not yet been tested). More surprisingly, both the push-up display and the chick-a-dee call had the same form of curve for the probability of use by frequency-rank graph. With a sample size of two species, it is difficult to make any generalizations, but the possibility of a general pattern merits further examination.

When all possible combinations of the three elements are considered, the Maximum Entropy of the push-up display is 12.74 bits/display. This is substantially smaller than the maximum Entropies reported for the chick-a-dee call of the black-capped chickadee (48.4 bits/call; Hailman et al., 1985), the communicative dance of the honey bee (25.4 bits/dance; Gould, 1975, as reported by Hailman et al., 1985), or written English (1908.4 bits/word; Hailman et al., 1985). However, because each of these estimates is based on approximate determinations of the extent of theoretical systems, this may be a rather unfair comparison. A more reasonable comparison may be of the Actual Entropies obtained or of the relationship between Actual and Maximum Entropies for each of these systems.

The Actual Entropy of the push-up display is 6.15 bits/display, yielding an Evenness of 0.48. The Actual Entropy of the chick-a-dee call as measured by Hailman et al. (1985) is 6.7 bits/call, whereas the Evenness of the chick-a-dee call is 0.14. The Actual Entropy of written English is 11.8 bits/word (Pierce, 1980), yielding an Evenness of 0.01. The Evenness of a system can be interpreted as a measure of the degree of constraint of the system and the corresponding level of code efficiency. The push-up display is less constrained than either the chick-a-dee call or human language and, thus, also uses more of its capacity (i.e., is less redundant) than either of the other two systems.

Snowdon (1990) broadly defined syntax as "any rule-based system that generates predictable sequences of behavior." Although conventional wisdom might deem it absurd to conclude that lizards have language, the push-up display of *S. graciosus* does indeed have a distinct structure with explicit rules governing the combination of elements into displays. By Snowdon's (1990) definition, it has a syntax. *Sceloporus graciosus* push-up displays include a hierarchical combinatorial pattern more complex than many bird songs or primate vocalizations and the use of both graded and discrete signals. They also exhibit substantial variation between the sexes and across seasons. Earlier studies have shown high levels of semantic complexity and repeat-

able differences among individuals in display structure and use (Martins 1991, 1992, 1993). Thus, although the push-up display system has somewhat less overall complexity or potential for complex information content than do the communicative systems of other animals that have been studied, it exhibits many of the main factors of interest in the modern study of animal communication. With the added bonus of social groups with relatively few participants and virtually no parental care, the push-up display system can serve as an excellent model of animal communication systems in general.

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