



Population differences in a lizard communicative display: evidence for rapid change in structure and function

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ABSTRACT

Population differences in a communicative display can lead to reproductive isolation and speciation, and are an indicator of the potential for rapid change in the display. Herein, we describe differences in the push-up displays produced by three populations of sagebrush lizards, *Sceloporus graciosus*, in the field. Lizards from these three populations differ in the use of display body postures, the number of legs extended to produce the up-and-down motion of the display, and the number of headbobs produced in each of three segments of the display. In addition, there is at least one behaviour that is unique to one of the three populations (the 'nodding run'). These differences among populations suggest that both the structure and the function of the push-up display are undergoing far more rapid change than was previously thought.

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New species are formed when populations become reproductively isolated from one another and continue to evolve independently. Evolutionary changes in the communicative displays used in courtship, mate choice or other aspects of reproduction can result in prezygotic isolation and ultimately speciation. Recent research has found substantial differences in the production of communicative displays among populations of most groups of animals including insects (e.g. Ritchie & Kyriacou 1994; Butlin 1996; Shaw 1996), fish (e.g. Endler & Houde 1995), frogs (e.g. Gerhardt 1994; Ryan et al. 1996), birds (e.g. Lynch & Baker 1994; Tubaro & Segura 1994; Byers 1996; King et al. 1996), and some mammals (e.g. Ford 1991). Relatively few (Ferguson 1970; Martins & Lamont 1998) have considered population differences in the communicative displays of reptiles. In this study, we describe the push-up displays of three populations of the sagebrush lizard, *Sceloporus graciosus*, and discuss the potential importance of the measured differences to our understanding of the evolution of communicative displays.

Lizards of the Iguania group communicate with each other primarily through the use of visual displays (Carpenter & Ferguson 1977). In the most common of these displays, the animals raise and lower their heads and torsos in a series of headbobs or push-ups, sometimes also using a number of display-specific body postures.

The combination of headbobs and body postures is quite complex and rivals the communication systems of many birds and mammals (including passerine bird song, Martins 1994). The display contains substantial information about the individual, sex and species identities of the displaying animal (e.g. Rothblum & Jenssen 1978; Bels 1986; Martins 1991). In at least three species, structural differences in the display (the number and timing of headbobs, the use of body postures and the numbers of legs extended) are also related to the use of the display in different contexts, which suggests that different forms of the displays may have different meanings (Martins 1993; Decourcy & Jenssen 1994; Lamont 1997). There is a set of rules governing the combination of display components into these different forms of the display, and that set of rules is sufficiently complex that it resembles a primitive syntax or form of grammar (Martins 1994).

Very little is known about population level variation in the structure of lizard push-up displays. Ferguson (1970) considered the headbob displays of 12 populations of *Uta stansburiana*, and used the variation he found to elucidate the patterns of radiation and the character evolution for that species. Considering only variation in the number and timing of headbobs in the display, Ferguson found that *Uta* populations differed in several measures of the display. For example, the average number of up and down motions in a push-up display was highly variable, ranging from 2.8 to 7.4 (SEs range from 0.02 to 0.30). This range is only slightly less than the variation usually found among species (e.g. 2–15 bobs/display for *Sceloporus*, Carpenter 1978). In contrast, Ferguson (1970) found that the total

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duration of *Uta* displays in different populations ranged from 0.1 to 1.2 s (SEs range from 0.01 to 0.02), which is substantially less than that found among species (e.g. 3–21 s for *Sceloporus*, Carpenter 1978). Ferguson (1970) did not consider other aspects of the display (e.g. the use of body postures, number of legs extended) that have been shown to carry much of the information content of these displays (Martins 1993).

Furthermore, it was recently shown that three populations of *Cyclura nubila*, the Cuban ground iguana, differ substantially in terms of the number and timing of headbobs in their displays (Martins & Lamont 1998). Specifically, one population of *Cyclura nubila nubila* from Cuba produced displays that were more similar to those produced by a population from a different subspecies (*Cyclura nubila lewisi*, found in the Cayman Islands) than they were to those produced by a second population of the Cuban subspecies. Unfortunately, however, the results of this study are not conclusive because data were obtained from small numbers of individuals and because two of the three measured populations consisted of captive and introduced animals with unknown histories.

In the current study, we add to our knowledge of population differences in lizard communication by describing the push-up displays of three populations of sagebrush lizards in the field. The three populations belong to two subspecies, and are relatively separate from each other geographically (Oregon, Utah and southern California). The Oregon and Utah populations belong to *S. g. graciosus*, a subspecies which also ranges east into Colorado and south into Arizona (Stebbins 1985). In contrast, the California subspecies (*S. g. vandenburgianus*) consists of a few, isolated populations separated from *S. g. graciosus* by a third subspecies, *S. g. gracilis* to the north and east. Because the three populations are roughly the same distance apart geographically, all three have probably been evolving independently for a very long time.

METHODS

Subjects

Sagebrush lizards were studied on Coyote Butte in eastern Oregon and on Red Butte in northern Utah. Coyote Butte is in a high-altitude sagebrush desert, and we found the lizards either on the sand or in the brush. In Utah, we found the lizards on the sides of a small, forested canyon near the University of Utah campus (in Salt Lake City) on rocks and in the brush. For comparison, we also included data previously collected on Table Mountain in the Angeles National Forest of southern California (a high-elevation, ponderosa pine woodland where the lizards live on fallen logs; Martins 1991). Animals in Oregon and Utah have a slightly longer activity season (March–October), and occasionally lay two clutches of eggs each year (personal observation; L. Carroll, personal communication). Animals in this California population have a shorter season (April–September) and usually only lay a single clutch (personal observation). We conducted observations in Oregon from

18 to 30 June (when most females were gravid with their first clutch), and in Utah from 23 to 31 July (when many females were gravid with their second clutches). We collected data in California during July 1989 (after the breeding season, Martins 1991).

Sampling Procedure

We observed lizards during peak activity periods (roughly 0900–1200 and 1400–1700 hours Pacific Standard Time at all three sites). We conducted focal animal observations on each individual for up to 30 min or until the animal moved out of sight. We selected animals for focal animal samples by wandering through the area and stopping when we located an animal. Thus, results may be biased towards active, conspicuous animals (usually males). To avoid problems with pseudoreplication, we individually marked all animals. In Oregon, we paint-marked animals from a distance (using a water pistol and dilute paint) to avoid observing any individual more than once. In Utah, several of the animals had been previously marked (by L. Carroll) with coloured beads strung on surgical wire through their tails. The remainder were paint-marked as in Oregon. Animals in California were all individually marked with coloured beads and were observed weekly as part of a long-term study (Martins 1991). The sexes of the animals were easily determined at a distance from size and shape (most females were gravid), general behaviour and colour (more blue on males, more orange on females), and were confirmed for most of the animals when they were captured and marked.

Data Collection

Observations were conducted by a single observer (E.P.M.), from a distance of at least 2 m, often with binoculars. Whenever the animal produced a push-up display, the details of the display structure were recorded. These details included the number and order of single and double headbobs, the number of legs extended (all four, the front two only or none), and the use of body postures (lateral flattening, gular extension, arching of the back and tail raise; see Martins 1994 for detailed descriptions). Each display was also categorized as Broadcast (when no animals were known to be within 1 m of the displaying animal), Courtship (displays directed by males towards females during reproductive interactions) or Agonistic (displays directed by either sex towards either sex during aggressive encounters) based on the context in which the display was produced (Martins 1993).

Statistical Analyses

We used chi-square tests to determine whether populations differed in terms of display type (Agonistic, Broadcast or Courtship), display frequency, the numbers of legs extended and the use of display body postures. We conducted multiple regression analyses using the SAS

Table 1. Population differences in push-up display structure

	Oregon	Utah	California
Number of displays observed	320	244	406
Number of lizards			
Males	49	20	15
Females	16	15	12
Display type			
Broadcast	90.3%	88.5%	89.7%
Courtship	8.4%	11.5%	7.4%
Agonistic	1.2%	0.0%	3.0%
Display frequency (displays/h)			
Total	9.6	15.1	6.7
Females	5.0	6.5	4.3
Males	12.1	21.1	9.1
Use of body postures	2%	0%	21%
Percentage of displays with			
Four legs extended	3%	<1%	27%
Two legs extended	29%	55%	53%
Zero legs extended	68%	45%	20%
Mean (+SE) number of headbobs*			
Initial double headbobs, A	1.0 (0.01)	1.0 (0.00)	0.6 (0.02)
Single headbobs, B	1.3 (0.04)	1.0 (0.02)	1.8 (0.04)
Final double headbobs, C	0.6 (0.04)	1.1 (0.06)	2.0 (0.07)
Total headbobs, A+B+C	3.0 (0.06)	3.2 (0.06)	4.4 (0.10)
Typical display type	ABBC	ABC	ABBCC

*All differences were significant at $\alpha=0.05$.

GLM procedure (SAS Institute 1989) to determine how well the number of headbobs in the push-up display (the response or *Y*-variables) was explained by the source population in which the lizards are found (the predictor or *X*-variable). Because the push-up display has previously been shown to vary with individual, sex, display type and the use of display body postures, these factors were also taken into account as predictor variables in the regression model.

Recent studies have shown the importance of taking phylogenetic relatedness among taxonomic groups (e.g. species or populations) into account when doing standard statistical analyses such as those described above (see Martins & Hansen 1996 for review). Failure to do so will not bias the results of most parametric statistical tests, but may inflate the number of significant hypothesis tests. Unfortunately, little information is available about the relatedness of these three *S. graciosus* populations, other than that the Oregon and Utah populations are classified as members of one subspecies (*S. g. graciosus*), whereas the California population is classified as a member of a second subspecies (*S. g. vandenburgianus*). Because the three populations are approximately equidistant from one another geographically, however, it seems reasonable to consider the three populations essentially independent of one another (radiating in a 'star' phylogeny) for the purposes of these statistical analyses. A second possibility is to apply a conservative significance level (e.g. $\alpha=0.01$) to counteract the effects of phylogenetic dependence on significance tests whenever all three populations are considered. Note that analyses considering only two of the three populations would not suffer from any of the potential problems of phylogenetic

dependence, and should thus be considered at the usual alpha level of 0.05.

RESULTS

A total of 564 displays (320 Oregon, 244 Utah) produced by 99 individual lizards (16 females and 49 males in Oregon, 15 females and 20 males in Utah) were observed during this study. For comparison, we combined these data with previously published information on 406 displays produced by animals in southern California (in 1989, Martins 1991).

In all three populations, about 90% of all displays were Broadcast displays (produced without any other animals within 1 m of the displaying animal), about 10% were directed by males towards females in a courtship context, and fewer than 3% were produced during agonistic interactions. The distribution of displays across these three main display types was similar in the three populations (Table 1, $\chi^2_4=0.37$, $P>0.3$), suggesting that the three populations were indeed sampled at similar points of their seasonal cycles.

As shown previously for lizards in California (Martins 1991, 1993), display frequency varied consistently between individuals and between the sexes. Display frequency also varied significantly between populations. Male sagebrush lizards displayed at least twice as often as females in all three populations (Table 1). Male lizards in Utah, however, produced about twice as many displays as did males in Oregon or California (about 20/h in Utah, as opposed to about 10/h in Oregon and California, Table 1). Females produced roughly the same number of displays (about 5/h) in all three populations.

Table 2. Mean squares from multiple regression analyses

	Response (dependent) variables				
	Headbobs				Number of legs extended
	Initial	Single	Terminal	Total	
Predictors (df)					
Population (2)	2.16**	1.89**	2.73*	2.15	36.02**
Individual (79)	0.30**	1.67**	2.52**	4.93**	2.76**
Sex (2)	0.06	1.75**	5.93**	12.33**	3.70*
Display type (2)	0.01	0.37	2.68*	1.55	3.17*
Body postures (1)	1.62**	0.16	14.08**	29.43**	150.73**
Number of legs extended (2)	0.60**	5.86**	41.02**	69.13**	—
Overall model (88)	0.02**	3.26**	11.28**	18.52**	11.24**
Error (881)	0.10	0.26	0.73	1.04	0.93
Model r^2	45%	56%	61%	64%	55%

* $P < 0.05$, ** $P < 0.01$.

We also observed male lizards in Utah engage in at least one behaviour pattern that was not seen in lizards from Oregon or California, or in the behaviour of females. In almost all long bouts of locomotion (when the animal moved more than 20 cm), males would nod their heads while running. These nods were simple up-and-down motions which occurred repeatedly at a frequency of approximately one nod per 10 cm. Longer bouts of these nodding runs often occurred as the male approached a female, and may be involved in courtship. (Note that courtship behaviour patterns have been observed throughout the active season in all three populations.)

The use of display body postures also varied among populations (Table 1; $\chi^2_2 = 33.6$, $P < 0.01$). About 21% of the displays produced by sagebrush lizards in southern California included the use of up to four body postures (L: lateral flattening; A: arching of the back; G: gular extension; and T: tail raise) either alone or in combination (Martins 1994). We observed lizards in Oregon using the same display body postures, but at a much lower frequency (in only six Broadcast and one Courtship display or 2% of all displays). Specifically, we observed the following combinations: L (in two displays), G, T, LG (in the single Courtship display), LAG and LAGT. We never observed animals in Utah using display body postures (although apparently they do occasionally use them; L. Carroll, personal communication). The very low number of displays in which body postures were observed prohibited further analyses to examine variation between individuals or between the sexes.

The actual up-and-down motion of the display is produced by extending all four legs, the front two legs alone, or by moving the head and shoulders alone (a zero-legged display). The three populations differed in the relative proportion of four-legged, two-legged and zero-legged displays (Table 1; $\chi^2_4 = 277$, $P < 0.01$). First, although California lizards produced all three types of displays, lizards in Oregon and Utah produced almost no four-legged displays. Furthermore, whereas more than half the displays produced by Utah and California lizards were two-legged displays, Oregon lizards produced mostly

zero-legged displays. Multiple regression analyses considering the effects of individual (nested within sex), sex (nested within population), display type (Agonistic, Broadcast or Courtship), the use of body postures (any or none), and population (Oregon or Utah) on the number of legs extended (treated as a continuous variable) showed significant effects for all factors (Table 2; $P < 0.03$ in all cases). As found previously for the California population alone (Martins 1991), four-legged displays were more likely to include the use of body postures and somewhat less likely to be Broadcast displays (Fig. 1; Table 2).

Most dramatic, though, were the differences in the headbob pattern across the three populations. Sagebrush lizard push-up displays from all three populations can be described as a series of double (A), single (B), and then again double (C) headbobs (Martins 1994). The actual number of each of these three components in the series, however, varies among populations (Tables 1 and 2). Lizards in Oregon almost always produced one initial double headbob followed by one single headbob (AB); about half the time this series was followed by another single headbob and/or one terminal double headbob (ABBC or ABC or ABB). In Utah, animals typically produced only one of each type of headbob (ABC). Lizards in California produced the initial double headbob in about half the displays, but usually included two single headbobs and two terminal double headbobs (ABBCC or BBCC). Differences between populations in the number of headbobs in each part of the display (but not the total number of headbobs combined) were statistically significant (Table 2).

We also used multiple regression models (Table 2) to consider the effects of individual (nested within sex), sex (nested within population), display type (Agonistic, Broadcast or Courtship) and the use of body postures (any or none) on the number of headbobs in each of the three segments of the display, on the total number of headbobs (single and double combined), and on the number of legs extended during displays. All of these models fit reasonably well with all factors in the model (i.e. good residual plots, r^2 ranging from 45 to 64%; Table 2). As in

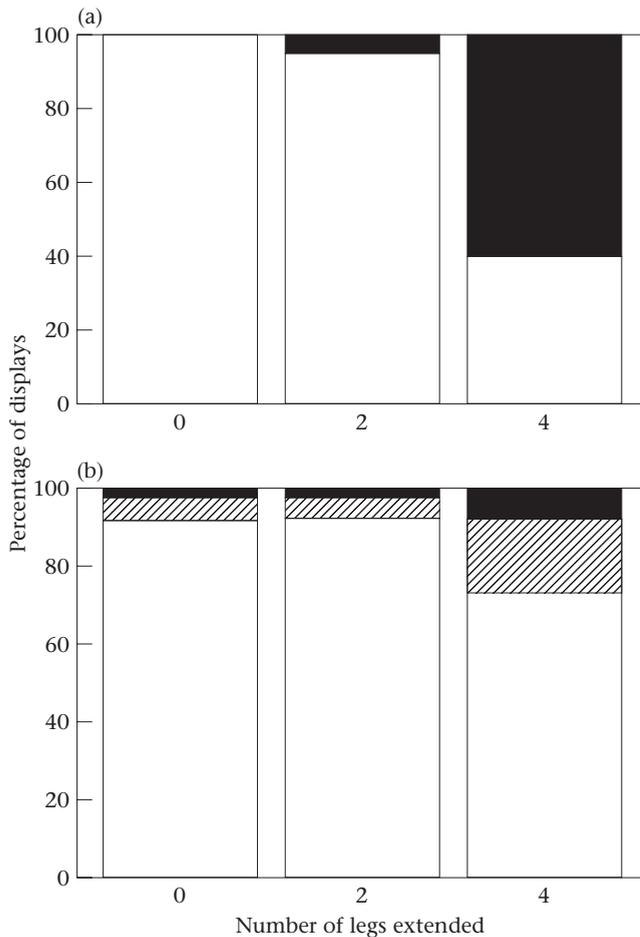


Figure 1. Relationship between the number of legs extended (zero, two or four) and the use of (a) body postures: ■: with body postures; □: without body postures; and (b) display type: ■: Agonistic; ▨: Courtship; □: Broadcast. Data are from all three populations combined (a total of 970 displays).

Martins (1991), all analyses revealed significant differences between individuals and between the sexes, except for a lack of sex difference in the initial double headbob ($P > 0.05$). Only the number of terminal double headbobs differed among display types ($P < 0.02$): fewer terminal double headbobs were produced in Broadcast displays (Fig. 2). Except when considering the number of single headbobs (Table 2), headbob number increased with the use of body postures and the number of legs extended (e.g. Fig. 2).

DISCUSSION

In this study, we show that there are marked differences in the push-up displays of three populations of sagebrush lizards. Specifically, lizards from the three populations observed in the field differed in the use of display body postures, the number of legs extended to produce the up-and-down motion of the display, and the number of headbobs produced in each of three segments of the display. Population differences in the push-up display are large, making it relatively easy for a human observer to

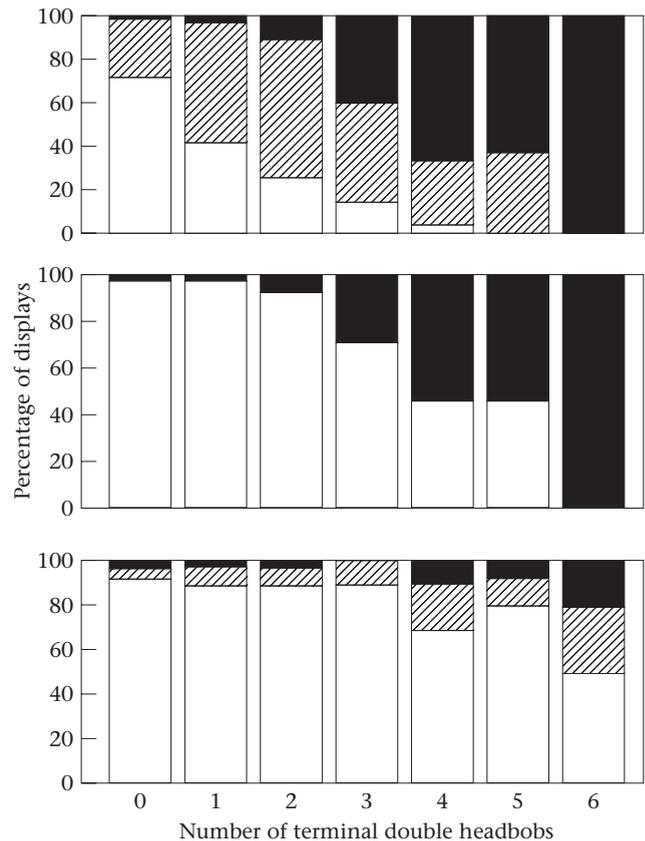


Figure 2. Relationship between the number of terminal double headbobs and the number of legs extended (a: □: zero; ▨: two; ■: four), the use of body postures (b: designations as in Fig. 1) and display type (c: designations as in Fig. 1). Again, data are from all three populations combined (a total of 970 displays).

distinguish lizards from the three populations on the basis of their displays.

Differences in the displays of California lizards and those of animals from Oregon and Utah were most dramatic, as would be expected by the subspecies distinctions. *Sceloporus graciosus vandenburgianus* in California produced more variable and more 'intense' displays than did the *S. graciosus graciosus* of Oregon and Utah. Lizards in California produced zero-, two-, and four-legged displays frequently, as opposed to animals in Oregon, which produced mostly zero-legged displays, and animals in Utah, which produced both zero- and two-legged displays. California lizards also included display-specific body postures far more often and produced a longer series of headbobs in each display. These latter differences were such that Oregon and Utah animals rarely produced the structurally more intense displays observed in most California social interactions (Agonistic or Courtship, as opposed to Broadcast displays).

Differences between Oregon and Utah lizards were more subtle. Utah animals produced roughly equal numbers of zero- and two-legged displays, as opposed to the zero-legged displays usually produced by Oregon animals. In contrast, Utah animals actually produced less 'intense' displays in terms of body postures or number of

headbobs. The number of headbobs produced in displays by Oregon animals was slightly greater (sometimes ABBC as opposed to ABC), and slightly more likely to include display body postures (although neither population used these body postures often). Although these differences were statistically large, whether the animals from the two populations recognize the differences between each other remains to be shown.

Population differences in a communicative display may occur for a number of reasons. For example, consider that display-specific body postures are used frequently by California sagebrush lizards during aggressive social interactions (but not in broadcast displays), and seem to be involved in transmitting information about the aggressive intent of the display producer (Martins 1993). Animals in Oregon and Utah, however, hardly ever used these display body postures at all. One possibility is that the decreased use of body postures by lizards in Oregon and Utah may be due to a decrease in the frequency of agonistic interactions and the corresponding decrease in the need to convey aggressive information. Alternatively, animals in Oregon and Utah may apply a different set of semantic rules than do the animals in California, possibly even using a different set of displays to convey information about aggressive intent. The existence of the nodding run, a behaviour entirely unique to the Utah population, lends support to the latter hypothesis.

Large population differences in the structure of the visual displays of side-blotched lizards (*Uta*; Ferguson 1970) and rock iguanas (*Cyclura*; Martins & Lamont 1998) also suggest that lizard headbob and push-up displays can and do change rather quickly. In the latter study, differences between populations within a subspecies were as large as those found between species. Despite the prevalence of dialects and other structural variation in bird song, a shift in the semantic content of displays across populations is also quite unusual. Thus, the results of the current study suggest that the structure and function of the push-up display may be more plastic, or evolving more quickly than many other types of communicative signals.

Future studies considering the causes of population differences, and measuring the relative importance of genetics and learning in display ontogeny may help determine whether the observed differences are the result of genetic or cultural evolution, or whether they are simply evidence of phenotypic plasticity. Other researchers (J. Archie, personal communication) are currently using molecular genetics to determine the genetic relatedness of these and other populations of *Sceloporus graciosus*. Their results will also help determine how long the populations have been apart and how quickly display evolution has occurred. Further studies are also needed to determine how such changes might affect the reproductive isolation and phenotypic differentiation characteristic of speciation.

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