

TONGUE DISPLAY IN ANOLES AND ITS EVOLUTIONARY BASIS

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Use of the tongue as a component of visual display has been reported for several lizards (e.g. Carpenter & Murphy, 1978; Murphy et al., 1978), but is particularly widespread among anoles (Kastle, 1963, 1965; Rand, 1967; Ruibal, 1967; Echelle et al., 1971a,b; Greenberg, 1977; Hover & Jenssen, 1976; Jenssen & Hover, 1976; Jenssen & Rothblum, 1977; Jenssen, 1979; Ortiz & Jenssen, 1982; Losos, 1985). It is likely, however, that tongue display in some form is characteristic of many taxa, given the ubiquity of gaping as a threat display among lizards (see Carpenter & Ferguson, 1977).

In this preliminary report we review information about tongue display in anoline lizards (true anoles, sensu Etheridge & de Queiroz, 1988) and clarify some ambiguities in the literature regarding its form and content. We emphasize that there are two different lingual displays exhibited by anoles and argue that these have been evolutionarily derived from two different, more fundamental, patterns of tongue use that are primitive for squamates generally.

Tongue display in anoles. Although some form of tongue display has been described for a variety of species (references above), our own observations and some literature accounts indicate that there are two distinctly different displays that have been erroneously equated in some cases. The distinction is not a trivial one because it is likely that the two displays have inherently different signal contents and separate evolutionary histories. They are easily confused, however, particularly in the field, because they share certain similar features of form and context.

The first display we call "tongue-bunch" (after Losos, 1985). This behavior is almost certainly equivalent to Greenberg's (1977) "tongue-gorge," may be partly synonymous with Carpenter & Ferguson's (1977) "protrude tongue" in that this designation very likely includes both tongue displays described herein, and may also be partly synonymous with Jenssen & Hover's (1976) "open mouth" in which the tongue is said to usually be clearly

exposed. During tongue-bunch the mandible is depressed to a greater or lesser extent, revealing the tongue within the oral cavity. The tongue is moved anteriorly between the mandibular rami, the tongue tip is curled ventrally and sometimes posteriorly so that the tip is hidden from view, and the tongue dorsum is steeply arched anteroposteriorly (Fig. 1A). Salient features of this display are: a. the arched or "bunched" form of the tongue body; b. the tongue is protruded only slightly, or not at all, beyond the jaws; c. if the tongue is protruded, it is protruded with the dorsal surface, not the tip, as its leading edge, due to the curled conformation of the tongue.

The second display we call "tongue-protrude" (after Jenssen, 1979). This behavior is probably equivalent to Greenberg's (1977) "tongue-out" and Ruibal's (1967) "tongue everted," although the equivalency of the latter is somewhat problematic (see below). During tongue-protrude, the jaws are parted as in the tongue-bunch, but usually to a lesser degree so that the gape angle remains small. The tongue is protruded beyond the jaws with the tip directed anteriorly (Fig. 1B). The tongue is usually engorged with blood. Salient features of this display that distinguish it from tongue-bunch are: a. most of the lingual dorsum remains more or less flat anteroposteriorly; b. the tongue is always protruded beyond the jaws; c. during protrusion the tongue tip remains pointed anteriorly, although it may bend somewhat ventrally, so that the ventral surface of the tongue touches the mental scale (see Fig. 3 in Jenssen, 1979:25); in any case, the tongue tip is never tucked completely ventrally or posteroventrally, resulting in an arched tongue as in tongue-bunch.

Both tongue-bunch and tongue-protrude can be exhibited by the same individual at different times, making careful observation and description necessary to distinguish them. To highlight this point, we note the case of Anolis lineatopus. Rand (1967:41) described clearly a tongue-bunch display in this species: "Frequently the mouth is opened slightly and the tongue, which is short and broad, is raised and pushed forward so that the tip appears as a small ball between the ends of the jaws." In describing the threat display of the same species, Ruibal (1967:129) noted only, "The tongue is sometimes everted," a description we interpret as probably meaning the tongue is protruded. Both descriptions are equated by Jenssen (1979) with each other and with "protruded tongue" in A. opalinus. We, however, equate unequivocally Jenssen's (1979) "protruded tongue" with our "tongue-protrude." Distinguishing between the two displays is made particularly difficult given that tongue-bunch can involve some protrusion. Only careful note of the form of the tongue during display can unambiguously distinguish. For example, Losos (1985) observed tongue-bunch in A. marcanoi, but noted that tongue protrusion sensu Jenssen (1979), never occurred in this species.

Display context and signal content. Tongue-bunch in anoles and other iguanian lizards in which it occurs is always a component of threat or defensive display. It often precedes a bite, or sometimes an attack without a bite (e.g. Losos, 1985;

KS & GCM, pers. obs.). Tongue-bunch is often observed when a lizard is directly threatened by an observer's hand or finger, particularly if the lizard is restrained (KS & GCM, pers. obs.). In general, tongue-bunch seems to be a component of high-level agonistic behavior and is similarly used in defensive behavior, indicating that an attack or bite is imminent.

Tongue-protrude remains more difficult to characterize. It is most likely a "static modifier," as suggested by Jenssen (1979), that serves to boost, or in some way alter, an agonistic behavior. As such, it is always associated with some other more prevalent behavior, and occurs only during some fraction of these (Jenssen, 1978). Jenssen (1979) noted that such static modifiers are used by A. opalinus principally during male-male agonistic encounters and are invoked in an "additive heirarchy" apparently associated with increasing arousal.

It is worth noting herethat color may be an important element of the signal content of tongue display in anoles. Anole tongues are unusual among iguanian lizards in a number of aspects of their microscopic structure (Schwenk, 1988; Schwenk & Williams, in prep.) For example, they exhibit a distinct zonation of papillar morphology along the length of the tongue (Rabinowitz & Tandler, 1986; Schwenk, unpublished data). This zonation appears to be associated with the distribution of melanophores and other chromatophores, as well as differences in vascular and epithelial structure that might relate to blood engorgement and its consequent red coloration of the tongue. Thus, there is the potential for species-specific pattern and color in the anole tongue. One of us (GCM) has observed in the field tongue-bunch displays in which contrasting coloration of the anterior half of the tongue seems to be a result of dermal chromatophores. Gordon Burghardt has long noted the variety of color and pattern in the squamate tongues and thinks it likely that such patterns are related to the signal content of lingual displays, particularly in some snakes (Burghardt, unpublished data, pers. comm.). Jenssen (1977:206) noted that "signal markings and colors would be most beneficial if they appeared on structures normally out of sight, but which became visible during lateral area enlargement." This observation, relating to the evolution of anoline dewlaps and sceloporine belly and throat patches, could easily be applied to tongue displays as well.

Finally, we note in this context that the principal difference between tongue-bunch and tongue-protrude is in the form and display of the tongue tip. In tongue-bunch the tip is tucked ventrally or curled under the tongue. It is hidden beneath the body of the tongue and/or beneath the level of the sublingual plicae (containing the sublingual glands). Our very preliminary observations suggest that it is the tongue tip that is most brightly colored during engorgement. Therefore, hiding the tip during tongue-bunch, as opposed to displaying and engorging it during tongue-protrude, could relate to differences in the signal content of the displays. Alternatively, these differences might relate only to the different behavioral substrates from which they evolved (see below).

Evolution of tongue displays in anoles. It is generally thought that species-specific, stereotyped displays evolve by exploitation of pre-existing "source" behaviors that have no communicative function (Barlow, 1977; Jenssen, 1977). This is the behavioral equivalent to the classical concept of pre-adaptation (or exaptation, sensu Gould & Vrba, 1982). Such exploitation of pre-existing, non-communicative behaviors has the advantage of economy in its use of already available structures and motor patterns. Therefore, elaborate displays need not be viewed as having arisen de novo without behavioral precedent. We believe that we have identified the source behaviors for tongue display in anoline lizards. Our observations are appealing because they not only elucidate the origin of tongue display generally, but also provide an historical basis for the presence of two distinct displays in anoles.

The source behaviors for tongue-bunch and tongue-protrude are lingual feeding and chemosensory tongue protrusion, respectively. Feeding and chemoreception are the two fundamental functions of the tongue in squamate reptiles. These two functions have been viewed as competing evolutionary demands that have shaped the morphology of the tongue (e.g. McDowell, 1972; Schwenk, 1982), although this has been disputed by Smith (1986). In any case, these behaviors are widely distributed among squamates.

Use of the tongue during feeding characterizes all lepidosaurs (Sphenodon + squamates) except varanid lizards and snakes. However, salient to this discussion is the fact that use of the tongue as a prehensile organ during the initial, or ingestion, stage of feeding is limited to the Iguania (Iguanidae, Agamidae, Chamaeleontidae), including anoles (Schwenk, 1988; Schwenk and Throckmorton, 1989). During a prey capture sequence, the jaws are parted and the tongue is moved forward in the mouth. As soon as it is visible, the tongue is seen to be curled with the tip tucked ventroposteriorly and the dorsal surface arched anteroposteriorly (Fig. 1C). The tongue continues to move anteriorly until it is protruded beyond the jaws, dorsal surface foremost. It is the arched, dorsal surface of the tongue that contacts and apprehends the prey item, rapidly drawing it back into the mouth (Schwenk & Throckmorton, 1989). The same pattern of tongue movement is used when a large object, such as an observer's finger, is attacked and bitten. The resemblance between the display tongue-bunch and the morphology of the tongue in the early stages of a lingual ingestion sequence is striking (compare Figs. 1A and C; also Fig. 3 with Figs. 7, 8 and 12 in Kastle [1965]; see also plates and figures in Schwenk & Throckmorton [1989]). Furthermore, the behavior in both cases can indicate an imminent attack or bite. It is significant that the extra-oral component of anterior tongue movement during lingual feeding is not a fait accompli; rather, the feeding sequence is often aborted at an early stage, with the tongue "bunched" within the mouth, depending on the status and movement of the prey item. Aborted feeding attempts, which sometimes last several seconds owing to ambiguous prey signals, are indistinguishable from tongue-bunch displays.

Tongue-mediated chemosensory behavior is a derived feature of squamate reptiles (Schwenk, 1986, 1989). Such chemosensory tongue protrusion is universal among squamates (see reviews by Burghardt, 1970, 1980; Simon, 1983; also Gove, 1979) and is usually called "tongue-flicking." Tongue-flicking is presumed to stimulate the vomeronasal organs, as has been clearly demonstrated for snakes (e.g. Kubie & Halpern, 1979), although gustation may also be used in some cases (Schwenk, 1985). Two types of tongue-flick occur: those in which the tongue touches the substrate (tongue-touch or substrate-lick) and those in which only the air is sampled (tongue-flick proper, or air-flick). These comprise either a single tongue extension, or multiple dorsoventral oscillations of the tongue before its withdrawal into the mouth. Multiple oscillation is characteristic of most scleroglossan squamates, whereas iguanians (including anoles) have never been observed to use more than a simple extension (Gove, 1979; Schwenk, 1988).

Among iguanians, the rapidity and relatively short distance of tongue protrusion sometimes makes tongue touches difficult to distinguish from air-flicks; however, some workers have done this successfully (e.g. Greenberg, 1985; Burghardt et al., 1986). Such differences in the kinematics of tongue-flicking seem to relate to different aspects of exploratory behavior (Greenberg, 1985; Burghardt et al., 1986) and might be associated with stimulation of different sensory modalities (Schwenk, 1985). However, both tongue-touches and air-flicks are initially similar in form and are distinctly different from tongue protrusion associated with feeding. Chemosensory tongue protrusion in iguanids always begins with a small gape angle and a relatively flat (unarched) tongue. Most important, the tongue is protruded with its tip foremost (Fig. 1D). Some downward deflection of the tip occurs at the end of the flick. The form of the tongue during a tongue-flick appears very similar to the anole tongue-protrude display (compare Figs. 1B and D; also see Jenssen [1979] Figs. 1 and 3).

We suggest that the fundamental iguanian behaviors of lingual feeding and chemosensory tongue protrusion were exploited by anoline lizards in their evolution of complex visual displays. These source behaviors are phylogenetically primitive for squamates and have no communicative function. They continue to exist in all iguanian lizards, including anoles, and were ideally preadapted in form, function and context for signal value in displays associated with agonistic and assertive behavior. Furthermore, the presence of two distinct lingual source behaviors helps to explain the presence of two distinct displays in anoline lizards. We note that tongue protrusion during feeding and chemosensory behavior are not only different in superficial form, but result from fundamentally different mechanisms of movement, hyoid protraction and hydrostatic deformation, respectively (Smith, 1984; Schwenk & Throckmorton, 1989; Schwenk, unpublished data). These mechanisms rely on different muscles for their action, and therefore involve different motor patterns. Thus, differences between these displays are not merely subtle modifications of a single basic

pattern, but have evolved from separate neural substrates. This putative dichotomy in CNS patterning underscores our assertion that tongue-bunch and tongue-protrude are indeed separate "units" of behavior (see Barlow, 1977), an hypothesis testable by electromyographic and electrophysiological techniques.

An observation, a solicitation, and a plea. At the Anolis symposium at the ASIH meetings in San Francisco, we noted with interest that many of the slides used to illustrate talks on a variety of topics showed anoles exhibiting tongue displays, both tongue-bunch and tongue-protrude. Since speakers usually choose photographs with the most impact, this informal observation highlights the fact that tongue display adds a dramatic visual addendum to an anole's usual repertoire, sufficient at least to catch the eye of a human observer. We believe that tongue displays are more widespread among anoles than has been reported (see Jenssen, 1979) and solicit unpublished observations on the presence (and absence) of such displays in anoles and other lizards. We urge workers to consider the differences in displays we have outlined here in order to test their consistency and generality with additional observations. We are continuing this work, and would appreciate greatly hearing about all such observations, old and new. Correspondence should be addressed to the senior author. All such data will be credited to its source.

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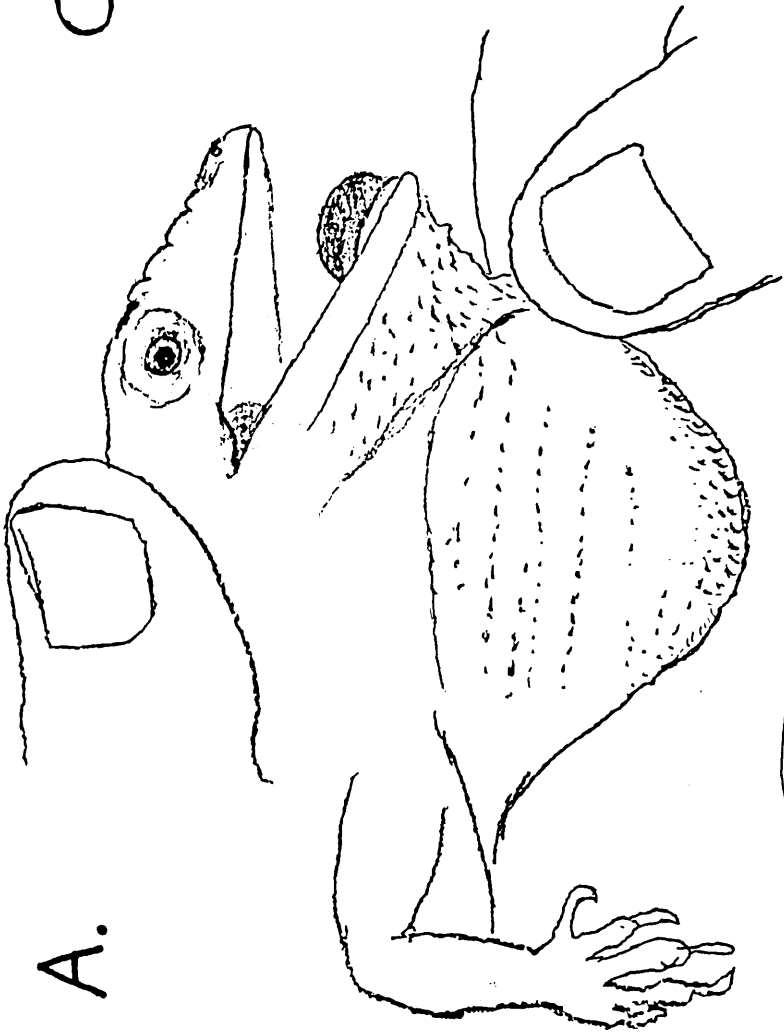
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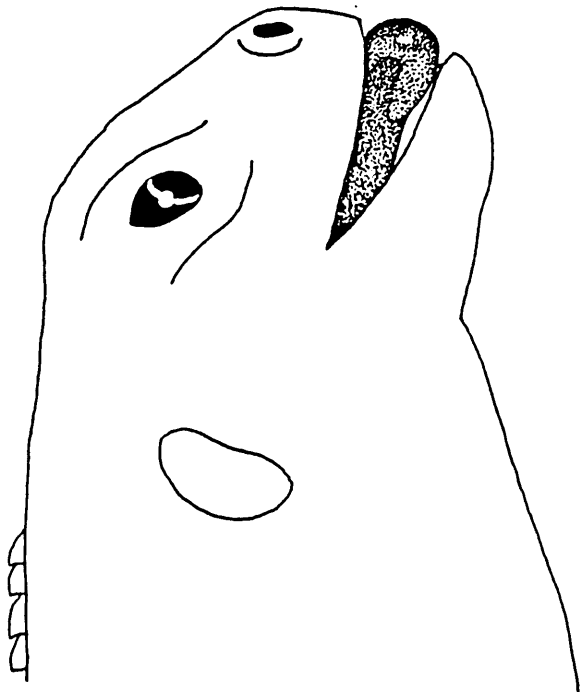
Figure 1. A. Tongue-bunch exhibited by Anolis barahonae from Isla Saona, Dominican Republic, while being held by hand. The tongue is not engorged with blood. Traced from a transparency by Roy McDiarmid. B. Tongue-protrude exhibited by Anolis stratulus from Guana Island, British Virgin Islands, while engaged in male-male agonistic display. The tongue is engorged and reddened with blood. This lizard is at a very high level of arousal, with dewlap extended, nuchal and dorsal crests erected, skin around eye darkened, and body raised on all four limbs. Traced from a Kodachrome transparency. C. Lingual feeding by Dipsosaurus dorsalis (see Schwenk & Throckmorton, 1989). Traced from 16 mm cine film. D. Chemosensory tongue protrusion by Dipsosaurus dorsalis. Traced from 16 mm cine film.

Erratum: "Anolis barahonae" should be "Anolis baleatus".

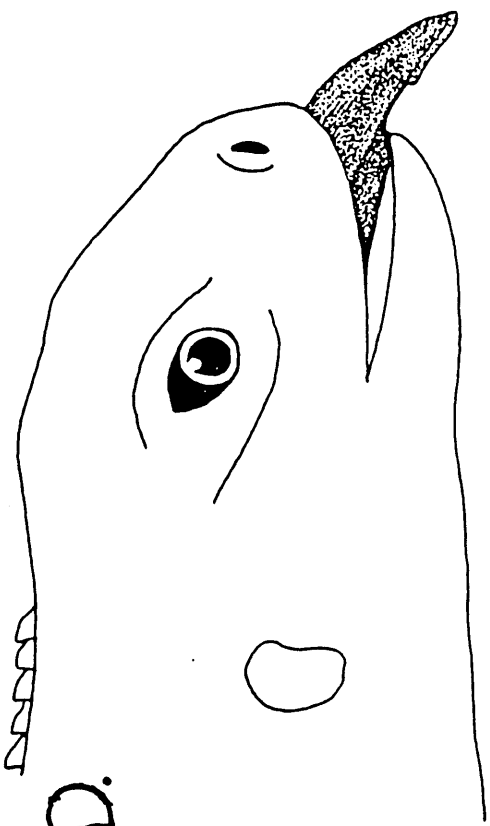
A.



C.



D.



B.

