

Evolution of Anoline Lizard Display Behavior

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SYNOPSIS. Based on my conceptual framework of anoline display behavior, I am suggesting the following evolutionary trends. Lateral presentation during display was probably promoted by monocular vision. Along with lateral presentation, postures evolved to increase lateral outline. These postures which magnified body size were probably of selective advantage within aggressive social contexts since larger animals tend to dominate smaller ones through bluff. Body movement evolved along with lateral orientation and size-enhancing postures. These movements would be most effective if they complemented lateral orientation. Effectors available for such movements were primarily pre-adapted for vertical motion. The patterns of movement generated were probably simple oscillatory bobbing movements by the head which were weakly stereotyped, interspecifically similar, appearing in many contexts, and having a weakly defined information content. Events having selective advantage for species recognition promoted stereotypy of bobbing behavior into species-unique displays; each species had its unique signature display which served in a manifold communicatory capacity. The signature display appeared in assertion, courtship, and challenge contexts. Its information content varied depending upon context and recipient of the display (*e.g.*, male or female). Besides the stereotyped aspects of the display, certain features remained variable with potential information significance. *Core variability* (see text) promotes individual recognition and may be the origin of new unique display patterns as sibling species emerge. *Display modifiers* (see text) are variable display features shared by members of a population (many being shared interspecifically) that provide a graded appearance to display performance; modifiers can indicate level of arousal and facilitate interspecific communication. For some species display repertoire size seems to have evolved from a single display (signature display) to repertoires of multiple displays; these subsequent displays are generally restricted to aggressive interactions.

INTRODUCTION

The ethologist has a difficult task. The phenomena from which he draws his data are ephemeral. Yet the essence of the observed behavior is the sum total, past and present, of an organism. The fleeting movements of effectors arise from the interpretation of immediate environmental and physiological events by a nervous system molded by the species' evolutionary history and the individual's ontological peculiarities. Virtually all biological phenomena could have an influence upon any one behavior under investigation. It is a humbling experience to attempt to iso-

late causal agents of behavior. However, because an animal's actions are the final expression of its biology, we must strive for an appreciation of behavior as a prime phenotypic character. This phenotypic character has historic roots and a current expression, and will be an influential determinant of future evolution.

Anoline displays can be studied as a narrow class of behavior within the expansive picture outlined above. These conspicuous visual signals are performed by a widely distributed versatile group of lizards and offer an excellent opportunity to approach the complex problems of causality, function, and evolution of behavior.

There are a number of factors which favor the study of anoline display behavior. *Anolis*, the largest genus of iguanid lizards, has members distributed among the Caribbean Islands, through the tropi-

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cal and subtropical Americas, and on a few islands in the Pacific. These lizards demonstrate a remarkable breadth of ecological radiation (Ballinger *et al.*, 1970; Campbell, 1973; Collins, 1971; Fitch, 1972; Fleming and Hooker, 1975; Heatwole *et al.*, 1969; Hicks, 1973; Jenssen and Swenson, 1974; Rand, 1964, 1967a; Rand and Humphrey, 1968; Rand and Williams, 1969; Ruibal, 1961; Ruibal and Philibosian, 1970; Schoener, 1968; Schoener and Gorman, 1968; Schoener and Schoener, 1971a, b; Sexton and Heatwole, 1968; Webster, 1969; Vanzolini, 1970; Vanzolini and Williams, 1970; Williams, 1972; Williams *et al.*, 1970) and diversity of social structure (Jenssen 1970a; Rand 1967b; Rand *et al.*, 1975; Stamps, 1973). Their social displays are species-typical (Carpenter, 1965; Echelle *et al.*, 1971a, b; Garcea and Gorman, 1968; Gorman, 1968; Jenssen, 1970a, 1977a; Kästle, 1963; Stamps, 1973) and largely stereotyped (Crews, 1975a; Hover and Jenssen, 1976; Jenssen, 1971; Jenssen and Hover, 1976; Jenssen and Rothblum, 1977; Stamps and Barlow, 1973), including those of hatchlings (Cooper, 1971; Jenssen, 1970a). From this evidence and the display characteristics which hybrids share with their parental species (Gorman, 1969; Jenssen, 1977b), it appears that display behavior has a strong genetic component. The anoles, particularly the males, perform displays frequently throughout the day (Andrews, 1971; Fleming and Hooker, 1975; Hicks, 1973; Jenssen, 1970a; Rand, 1967b; Ruibal and Philibosian, 1974). These signals play a significant role in territorial behavior of anoles, and also appear to function in mate selection and female receptivity (Crews, 1975b, c; Jenssen, 1970b). The number of signals within a species' repertoire, the complexity of these displays, and the patterning of the various displays show considerable interspecific differences (Jenssen, 1977a).

The data cited above indicate that anoline display behavior is a prominent phenotypic feature that is largely innate and is exposed to a plethora of selection pressures by its frequent use and many functions. Therefore, the study of anoline

displays should help: (1) to establish the genetic basis of behavior; (2) to evaluate behavioral evidence for phylogenetic relationships; (3) to correlate specific behavior (*e.g.*, stereotyped behavioral markers such as a display) with neural structure and function; (4) to identify communicative behavior and determine its function; and (5) to evaluate effects of environmental and social factors (*e.g.*, conspecific social structure, syntopic congeners, habitat characteristics, predator behavior, signal function of display) on the evolution of behavior.

DISCUSSION

In the following account I am providing a conceptual framework of anoline display behavior. Based on the perspective gained from this framework, I am suggesting some evolutionary events. Neither my present concepts of *Anolis* displays nor speculations about their evolution are intended to be definitive. These ideas are offered as an impetus for formulating new and productive questions. From these questions a broader data base should result to improve our understanding of behavioral evolution.

To begin the discussion, it is important to define the term, display. I am restricting "display" to body movements which (1) at least raise and lower the anole's head and/or dewlap, (2) are stereotyped, and (3) are shared for the most part by the population; implied in the definition is the hypothesis that the movement patterns have a strong genetic component and function as communication signals. Other terminology basic to anoline display studies (*e.g.*, signature display, display pattern, display type) are defined elsewhere (Jenssen, 1977a).

Source behavior

According to classical ethology, it is improbable that species-unique display behavior evolved *de novo*; more plausible is

"jigling"

The only iguanid lizard behavior which might closely resemble a primitive display behavior is the class of shallow, rapid head bobbing labeled as "jigling" (Evans, 1938; Ruitel, 1967), "shudder-bob" (Tinkle, 1967), "shuddering" (Ferguson, 1970); or "courtship nodding" (Greenberg and Noble, 1944; Carpenter, 1962a). This behavior is described as being interspecifically similar, although no graphic analysis has yet been made from high speed movie sequences. I suspect that there are some species-typical features in rapid head bobbing as evidenced by interspecific differences in display-action-pattern graphs for *Phenacosaurus heterodermus* (Jenssen, 1975), *Anolis aeneus* (Stamps and Barlow, 1973), and *Anolis lineatopus neckeri* (Jenssen, 1977b).

As the description implies, jigling is a simple pattern and superficially appears to be somewhat similar in different species. Jigling is only weakly stereotyped in *Uta stansburiana* (Ferguson, 1970) and *Sceloporus undulatus* (Rohblum and Janssen, 1977). There is no distinct beginning or ending to the sequence of shallow, rapid head bobbing; one can view it at any moment and identify jigling. Jigling is closely associated with locomotion, commonly occurring just before and during locomotion. Jigling, then, is principally effected by neck muscles and is independent of leg action. This is in contrast to species-unique display patterns which are always performed while the animal is planted and suggests a fundamental dichotomy between jigling and the other display behavior of a species repertoire.

From a contextual viewpoint, rapid head bobbing also fits the conception of a behavior transitional between a primitive, generalized signal and one that is unique, and is emancipated from its source behavior. Ruby (1977) found from field observations of *Sceloporus jarrovi* that jigling is performed in a variety of contexts: by solitary animals, by either sex during intrasexual encounters, by females to males and vice versa outside of the breeding season, and by males to females within the

the hypothesis that non-communicative behavior, which in some way was preadapted for signal value, became ritualized into stereotyped behavior having a communicatory function. Such "source" behavior could likely have been utilitarian and widely exhibited by already existing species. As one possibility, Barlow (1977) suggests rhythmic behavior derived from locomotion as being the origin for lizard pushup displays. The different pathways would already be available along with the neural organization for rhythmic, patterned motor output for leg extension and flexion.

Another behavior source for lizard displays might have been a common response of the somatic nervous system in "thwarting stimulus-situations" (Morris, 1956). For instance, displacement behavior can be elicited when there is a simple physical obstruction to aroused activity (Morris, 1956a). A personally observed example of displacement behavior within this thwarting context is the tail twitching of *Anolis nebulosus* when prey are not yet in the best position for seizing. Perhaps a similar somatic nervous response might produce small, quick vertical nods of the head when a lizard is aroused, but temporarily thwarted.

As another variation of Morris's (1956a) "thwarting stimulus-situations," Greenberg (1977) offers responses occurring during conflict situations as being raw material for signal behavior. He has observed an exchange in blue spiny lizards (*Sceloporus cyanogenys*) that suggests that the head nod may have evolved from an oscillating pattern of fear and aggression. Greenberg (1977) reports that when a dominant male raises its head, revealing its blue throat, a subordinate perching beneath will lower its head in apparent submission. Thus, head elevation is characteristic of an aroused, dominant animal, while head lowering is seen when a threatened animal is trying to be inconspicuous, or as a gesture of subordination. Morris (1956b) uses a similar logic to show how concurrent ambivalent behaviors of attacking and fleeing explain the origins of a number of stereotyped courtship rituals.

breeding season. Ruby suggests that jiggling, which is usually accompanied by other display types, at least represents a displayer's increased level of excitement. These observations are consistent with the analysis of jiggling in *Sceloporus undulatus* (Rothblum and Jenssen, 1977).

It would appear that jiggling may not have an intrinsic message content, but may merely indicate a state of arousal. When combined with other displays, jiggling could amplify the displayer's intent as signalled by the accompanying species-unique displays. In some species, however, jiggling has only been reported in male to female displaying during courtship (e.g., *Anolis nebulosus*, Jenssen, 1970a). In these species jiggling may have acquired a more specific message content, or at least is restricted to a single context.

In summary, rapid head bobbing (jiggling) comes close to a behavior pattern from which species-unique displays may have evolved. This evaluation is summarized by the following characteristics: (1) pattern appears interspecifically generalized; (2) pattern is simple; (3) pattern appears weakly stereotyped; (4) pattern has broad contextual usage for some species; and (5) pattern is probably generalized in message content.

Orientation and postures

Anoles, as well as iguanid lizards in general, present laterally while signalling to other lizards (Carpenter, 1967b). Since the lizards' prime modality for communication is vision, the characteristics of their visual receptors probably have influenced the evolution of both body orientation and body postures used during display.

With the exception of *Anolis*, which has a secondary fovea for binocular vision (Polyak, 1957; Underwood, 1951, 1970), iguanid lizards (and presumably their ancestors) possess a single fovea in the retina which is located for acute perception of objects lateral to the head (i.e., monocular vision) (Walls, 1942). Thus, while scrutinizing a conspecific, the longitudinal axis of the head would be at about a right angle to the viewed object to yield maximum visual

acuity. If the body is aligned with the head, this would logically lead to the evolution of lateral body presentation during signal exchange.

Lateral orientation also provides the best intermediate position from which an animal can approach or retreat; this orientation is quite reasonable if display movement evolved from ambivalent behavior within an agonistic context.

An evolutionary trend concomitant with lateral display presentation would be the exaggeration of lateral structures to enhance visual signals. Any anatomical structures and effectors which could increase the lateral area of the displayer would be advantageous to signal behavior. This would explain the ubiquitous occurrence of certain display postures in iguanid lizards (e.g., lateral flattening of body sides, elevated body position with arched back, lowering of the hyoid apparatus, extension of the retrobasal process of the hyoid apparatus, erection of a nuchal crest as in *Anolis*), and indicate that these postures made an early evolutionary appearance.

Because of strong ecological pressure, the conservative mechanisms for increasing lateral body area during display have been compromised in some species. For example, species of *Uma* dwell in loose sand where it is advantageous to be dorsal-ventrally flattened for "sand swimming." These species have only limited ability to compress their bodies laterally during display; to enhance lateral area they tilt their bodies with the dorsum toward the opponent as well as the dewlap extended (Carpenter, 1963).

Distinct markings and highly visible colors would logically be selected for signal enhancement. To avoid negation of cryptic coloration, these 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. Anoline lizards have exploited this approach more than any others of their family; they are characterized by having large extensible dewlaps (throat fans) which are vividly colored, but when the dewlap is folded the colors are hidden. Sceloporine species have colorful

belly and throat patches which become exposed by using a raised body posture, lateral body compression, and hyoid extension.

In summary, postures and distensible body structures which enlarge a lizard's laterally-viewed body outline are probably a very early evolutionary development. This hypothesis is based on the following observations. Lateral enlargement would enhance lateral presentation during display, especially if the behavior originally functioned in aggressive contexts (see Carpenter, 1967*b*: 100-101); it is well documented that the larger lizard usually wins an encounter even without physical contact. Lateral presentation during performance of stereotyped displays is universal in iguanid lizards, and many of the same mechanisms for lateral enlargement (*e.g.*, lateral body compression, lowered throat, dewlap extension) also appear to be held in common by iguanids.

Display movements

When displaying in the presence of another animal, the performer is stationary and orients laterally to the object of its attention. Given that this orientation is a primitive feature, the most effective display movements for maximum perception by an observer would be those at right angles to the line of sight (Fig. 1). Therefore, body movement along the X axis (anterior-posterior) or the Y axis (dorsal-ventral) would be more effective, hence energetically more efficient, than movement along the Z axis (lateral) since lateral movement would not enhance signal quality. Body movements along the Z axis during display are primarily restricted to lateral undulations of the tail.

However, movements along the X and Y axes are not equally probable. Most of an animal's effectors are preadapted for motion along the Y axis rather than the X axis (*e.g.*, neck muscles, caudal muscles, and to a significant extent the dewlap and limbs). Though the legs can produce anterior-posterior movement of the body, oscillating movements strictly along the X axis

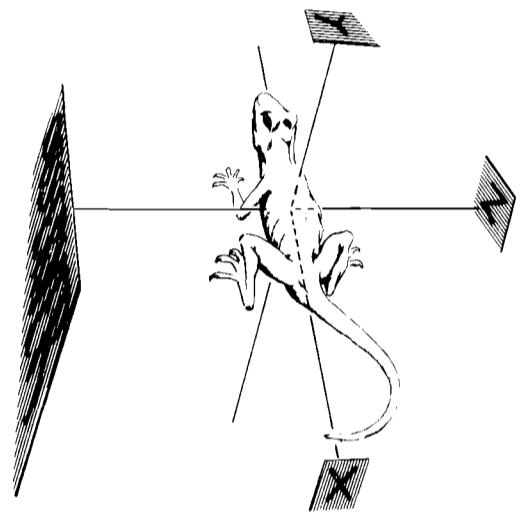


FIG. 1. Spatial planes along which a lizard can move while displaying laterally to an observer.

have not been described in display patterns of iguanids. The rhythmic, hesitant walk of *Polychrus guttuerosus* is closest to a behavior where movement vectors are bidirectional along the X axis. Lizards can perform intention movements which are along the X axis (forward for aggressive approach and backward for retreat); however, these are only in one direction, they do not accompany lateral presentation, and they are not incorporated into a stereotyped display pattern. The only reported displays which contain noteworthy fore and aft movements are those where the animal performs rocking motions [*e.g.*, *Anolis nebulosus* (Jenssen, 1970*a*) and *Phenacosaurus richteri* (Kästle, 1965) challenge displays]; these are usually produced by forelimb extension-flexion with neck and back arched. In summary, the vast majority of stereotyped display patterns are effected primarily by vertical movements (along Y axis) by the head and/or body (Fig. 1).

Signature display

In extant iguanids, the important work of Charles Carpenter and his students (Bussjaeger, 1971; Carpenter, 1961*a, b*; 1962*a, b*; 1963, 1965, 1966, 1967*a*; Carpenter and Grubitz, 1961; Clarke, 1965;

Lynn, 1965) has demonstrated that each species studied has its own unique display-action-pattern (DAP). From this work one may hypothesize that ancestral repertoires contained a single species-unique display per species, the signature display. These single display repertoires, in turn, may have been derived from simple head bobbing (*e.g.*, similar to jiggling) by pre-iguianid ancestors.

A number of different factors could have encouraged the trend toward species-typical display stereotypy. Females who used male behavior as a criterion for mate selection would have increased fitness if they could detect some consistent species-unique trait in the male display of their species, and thereby avoid investment in non-viable or uncompetitive hybrids. Ritualization of display behavior during agonistic interactions would be selected if an animal's intention, degree of motivation, and potential strength (*e.g.*, body size) relative to the viewer's strength were conveyed by some set of signals; this information could be used to predict who would win a physical encounter without the need to actually fight. Both contestants would benefit by avoiding excessive energy expenditures and chance of injury (see Smith and Price, 1973). For short-lived species genetic control over these signals and their meanings would also be favored.

Each species' signature display undoubtedly fulfilled a number of communication functions such as advertising a lizard's presence even when the displayer could not see another conspecific (assertion context), serving as ritualized aggression during territorial disputes (challenge context), and indicating sexual interest or lack of interest during male-female interactions (courtship context). Therefore, the signature display had different meanings depending on recipient of the signal and the context (see Smith, 1969 for these concepts).

The stereotyped aspects of the signature display pattern were useful for species recognition, but any residual variation in the signal could provide a recipient with more information about the displayer's identity, the displayer's level of arousal,

and the likelihood for the displayer to enact its intended behavior. Thus, the signal's information content was flexible and was defined by the context, the recipient, and the variable aspects accompanying the stereotyped display pattern (*i.e.*, core variability and display modifiers, see below).

Core variability and display modifiers

Past studies have overlooked the significance of variability in lizard displays. Before the functional significance and the possible evolution of display variability can be examined, a conceptual framework is mandatory to identify, inventory, and quantify the variable display features. I suggest the following categories for classifying display variability.

1) *Core variability*—For a given display type, no two performances by a lizard will be identical; however, basic to each display is a sequence of temporally patterned body movements which is predictable from one display to the next. This predictable sequence of behavior is what establishes a display type's pattern and *always* appears in each performance of that kind of display; it is the core (*i.e.*, maximum reliability of occurrence) of that display pattern. Yet variability (*e.g.*, temporal) is present even within this core display; this I am labeling as core variability.

2) *Display modifiers*—In contrast to core variability, modifiers are postures (static modifiers) or movements (dynamic modifiers) which are *not always* associated with a particular display pattern; they can be added to the core display pattern as an option employed by the entire population (Jenssen, 1977a; Jenssen and Hover, 1976).

After discerning where the source of variability resides within a display pattern (*i.e.*, core and/or modifier variability), one can determine for each source the relative amount of variability arising from comparisons of displays performed by each lizard (*within* lizard component) and from comparisons of displays by different lizards (*between* lizard component). When a measured display parameter shows a noticeable amount of variability, it may

have signal value if a major portion of the variance comes from only one of these two components.

If most of the variability is explained by the between lizard component, then *intra-individual stereotypy* exists; this condition favors individual recognition cues. On the other hand, if a large majority of variability resides in the within lizard component, then *intra-population variability* exists, with all lizards being able to vary the display parameter to a similar extent; this condition could be used to indicate relative arousal intensity of the displayers. Display behavior, then, can be partitioned into two sources of variability (core and modifier), with the observed variability attributable to within and between lizard components (Fig. 2).

With the present data base, I see several interesting trends which may have evolutionary implications. First, instances of large core variability primarily show intra-individual stereotypy and not intra-population variability (Fig. 2). As an example, all male *Anolis nebulosus* of a Nayarit, Mexico population performed identically patterned signature displays (Jenssen, 1970b). However, within the core portion of their signature displays there was significant temporal variation in display duration. This variability was slight for displays of any one lizard (2% within lizard), with each lizard having its own particular display duration. Comparisons

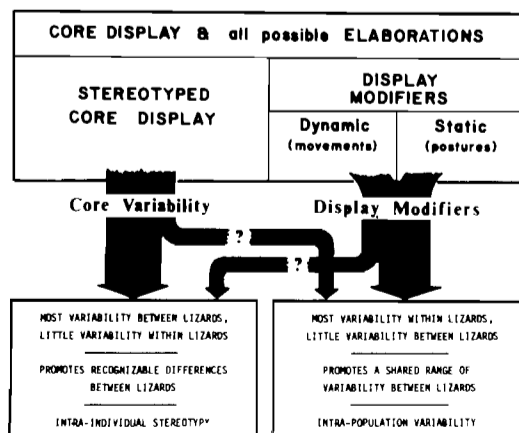


FIG. 2. A model for partitioning the source and kind of display variability.

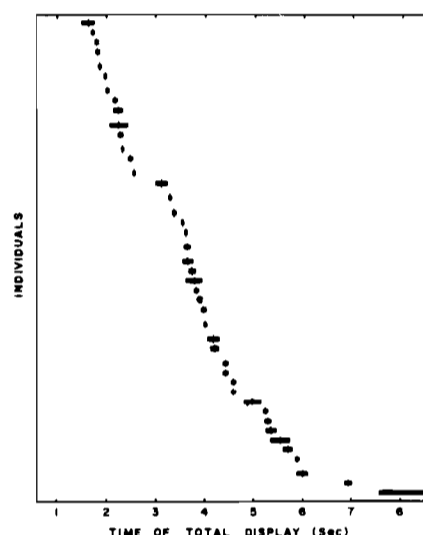


FIG. 3. Mean durations of the signature displays from 43 male *Anolis nebulosus*. Vertical line through black bars indicates mean value and ends of black bar give 95% confidence limits of mean.

of display durations between lizards, however, was great (98% between lizards), with the mean time for the fastest lizard being 1.7 s and the slowest 8.1 s (Fig. 3). This type of intra-individual stereotypy could serve as an individual recognition cue.

Another and more poignant example of intra-individual stereotypy for core variability is the Type B display of *Sceloporus undulatus hyacinthinus* (Rothblum and Jensen, 1977). This display was extremely stereotyped for each male, but for some males there were significant differences between their B displays (Fig. 4). These differences were so pronounced that the B display could not be represented by a single display pattern.

I propose as a generalization that any significant amount of variability in the core display promotes stereotyped, individually unique aspects to a lizard's display that can function as individual recognition cues. This in turn can provide the raw material for character displacement and sympatric speciation where female mate selection operates on display features. In short, core variability may be the origin of new, unique display patterns for newly evolving sibling species.

A second trend concerns display mod-

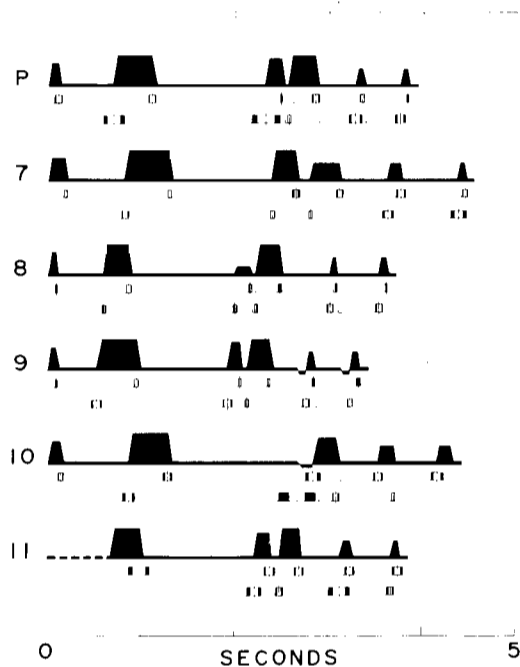


FIG. 4. From 79 Type B displays from 11 male *Sceloporus undulatus hyacinthinus* are constructed some of the individual-unique patterns for males 7-11, and the pooled pattern (P) for six other males whose patterns were somewhat similar. The Y-axis gives head amplitude movement and the X-axis gives elapsed time. Blocks under graph provide mean unit durations (vertical line), standard error of the mean (ends of white blocks), and 99% confidence limits of the mean (ends of outer black blocks).

ifiers. In contrast to core variability, modifiers seem to exhibit primarily intra-population variability (Fig. 2). Examples of *static modifiers* are lateral body compression, lowered throat, dewlap extended, mouth open, tongue out, raised nuchal crest, widely opened eyes and dilated pupils, elevated four-legged posture, and other optional postures; examples of *dynamic modifiers* are introductory body movements (with or without dewlap extension) immediately preceding the core display, variable repetition of the display pattern's concluding body movements, the variable amount of inter-display leg extension-flexion, tail movements, and other optional movements associated with a particular display pattern. Most modifiers are shared by many species, and some modifiers, particularly the static modifiers (*e.g.*,

postures for enhancing lateral body area), seem to be universally used in the family Iguanidae.

The evolutionary implication is that modifiers tend to be conservative, some being quite primitive (see *Orientation and postures* above). They are shared interspecifically, and, therefore, could function in interspecific communication. Within a species, all lizards share a common repertoire of modifiers. Every lizard can perform a similar range of modifier variations. For example, many species can perform their signature displays using only their neck muscles; however, during more intense social interaction, the display movements can be executed with varying degrees of extension and flexion by the fore limbs, or by all four legs. The variability in such a dynamic modifier produces a graded elaboration of the display. Use of particular modifiers can be correlated with the appearance of other modifiers and with certain contexts (Hover and Jenssen, 1976; Jenssen and Hover, 1976; Stamps and Barlow, 1973). Modifiers give the core display a greater signal flexibility (*i.e.*, a graded signal), and at the very least seem to indicate increasing arousal which should be recognizable between species.

Display repertoire size

Before discussing the evolution of display repertoire size, one must first establish criteria for determining different displays. My criteria are restrictive and produce conservative counts. The display behaviors which I am counting as separate display types for anoline lizards are those species-unique head and/or dewlap movements which are stereotyped and descriptively distinct from each other. I do not count a pattern more than once even though it may have a constellation of possible modifier combinations associated with it or appear in a host of contexts (*e.g.*, assertion, courtship, challenge).

Behaviors excluded from repertoire size are those which are not obviously stereotyped and those interspecifically shared. For example, common to all anoles I have seen is the use of dewlap movement

divorced from stereotyped body movement. For the most part such "dewlapping" is non-stereotyped and can appear: (1) after eating, (2) during shedding, (3) when the animal enters a part of its domain with which it was previously out of visual contact, and (4) as a reaction to the beginning or tailing-off of a social encounter. Undoubtedly there are a few anoles whose dewlapping may be stereotyped and an important display of the formal repertoire. With the exception of these species, I am not considering dewlapping in the discussion of repertoire size. Also excluded is "jiggling," a generalized behavior with weak stereotypy performed by many iguanid lizards.

As mentioned above, every iguanid lizard appears to have its own species-unique signature display. The signature display pattern of a species can be very simple, such as the brief sine wave-like bobs of *Anolis lineatopus neckeri* (Jenssen, 1977b) (Fig. 5). Most species' signature displays, however, are more involved. One means by which display complexity may have increased is through the incorporation of dynamic modifiers into the core display. One likely possibility could involve the fixation of optional head bobbing which may follow the core display.

For example, the signature displays of *Anolis limifrons*, *Anolis townsendi*, and *Anolis sericeus* can be compared to illustrate a possible progression of increasing display complexity based on a greater incorporation of dynamic modifiers into the termi-

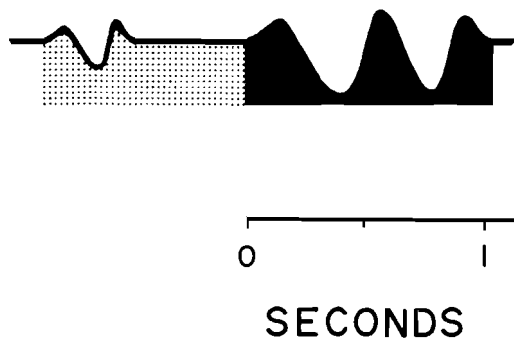


FIG. 5. Signature display of *Anolis lineatopus neckeri*. The Y-axis gives head amplitude movement and the X-axis gives elapsed time. Grey area shows bobbing not always present with the signature display.

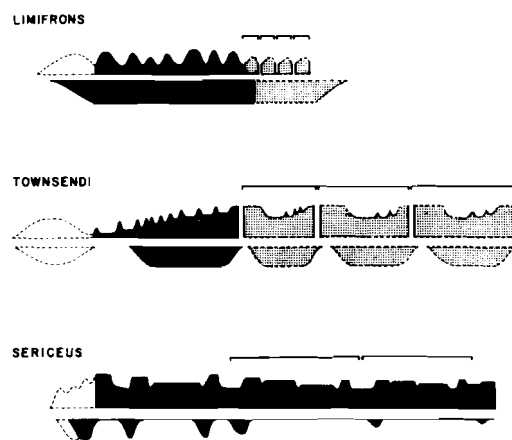


FIG. 6. Signature displays of *Anolis limifrons*, *A. townsendi*, and *A. sericeus* comparing repetitions of terminal display movements as indicated by overhead brackets. Under the brackets, the grey areas represent dynamic modifiers and the black areas represent part of the core display. Splits in the graph indicate where the lizard may terminate its display. Upper block of each figure shows head amplitude through time and lower block shows dewlap extension through time.

nal portion of the core display. The display of *A. limifrons* is depicted as the initial phase of evolving greater complexity. The display core of seven bobs can be followed by a varying number of single bobs (Jenssen and Hover, 1976) (Fig. 6). In *A. townsendi* the terminal portion of the signature display is also variable (Jenssen and Rothblum, 1977); but in this species, there is a varying number of acts (Fig. 6). Each act is a complex stereotyped behavior involving the coordination of head and dewlap movement. Once an act is begun it is performed to completion. In *A. sericeus*, which has a long stereotyped signature display (approximately 30 s), there is a repetition of complex behavior in the last two thirds of the pattern (Fig. 6); this repeated pattern is part of the core display. One can hypothesize that there once had been optional repetitions of acts, as seen in *A. townsendi*, which have become fused into one long signature display pattern.

Not all species have a single display pattern in their repertoires. I am finding that *Anolis* tends to have multiple display repertoires. In species having a two-

display repertoire, there is the species-unique signature display (which I will call the Type *A* display), and a second display pattern (a Type *B* display). For those species having more than one display pattern, the *B* pattern is similar to the *A* display. If one assumes that a repertoire of genetically determined signals usually evolves from small to large, it is reasonable to expect the evolution of subsequent signals to share many aspects of the previous signal or signals (Barlow, 1977). This appears to be the case for the Type *B* displays (Fig. 7).

To detect multiple display repertoires, one needs to be alert for small, but statistically significant distinctions in movement patterns. This is especially true if the *B* display closely resembles the *A* pattern. To determine whether two subtly different patterns truly merit separate classification, controlled social situations should be provided to observe if the two displays are used within different circumstances. Correlations between contexts and differential use of display patterns would infer a func-

tional distinction between the two display patterns as well as a descriptive difference.

In lizards having two displays in their repertoires, the Type *A* (signature) display is performed in all social contexts (*e.g.*, assertion, courtship, challenge). In contrast to the *A* display the Type *B* display is generally restricted to agonistic encounters (*i.e.*, challenge context). This second display type seems to have evolved as an elaboration of ritualized territorial interactions. A more extensive bluff system has been suggested as a favorable mechanism for species which interact throughout a long breeding season (Jenssen, 1977a); this would possibly decrease the occurrence of physical combat for winning and maintaining territories. With a computer model, Smith and Price (1973) show it is disadvantageous to use potentially dangerous offensive weapons in intraspecific contests; a stable strategy does, however, require that contestants should respond to an "escalated" attack by escalating in return. For anoles with a large agonistic display repertoire, this escalation is facilitated with less chance for injurious contact.

Some species have proliferated the number of agonistic-related display patterns to include *C*, *D* and even *E* displays in their repertoires (Hover and Jenssen, 1976; Jenssen and Rothblum, 1977). For example, *Anolis limifrons* (Hover and Jenssen, 1976) has five display types (*A-E*) in its repertoire (Fig. 8). All five are used in male-male encounters. As the encounter ensues and the animals move closer toward each other, they progressively perform more elaborate display types (*A*→*B*→*C*→*D*). In the exchange of displays the responder performs a similar display or the next more elaborate type. When the males are within biting distance of each other, they give the *E* display, which is of short duration and has no dewlap extension. This least elaborate display minimizes the chance of injury to the displayer as the display is of short duration and the dewlap is not extended and vulnerable.

When viewing the displays of a large repertoire like that of *A. limifrons*, there are clues to indicate how these patterns evolved. Presumably the *A* (signature) dis-

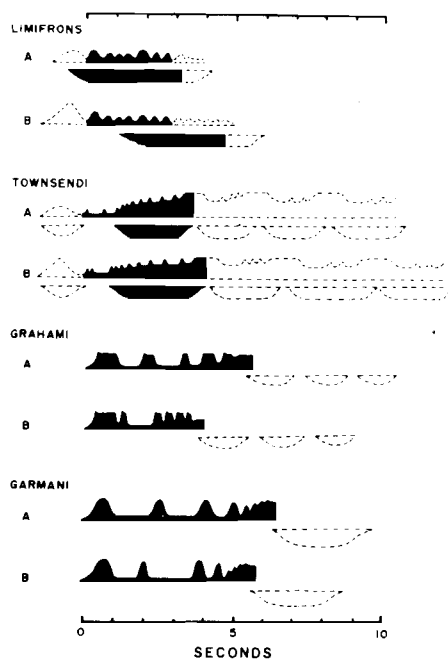


FIG. 7. Comparisons of the Type *A* and *B* displays in the repertoires of *Anolis limifrons*, *A. townsendi*, *A. grahami*, and *A. garmani*.

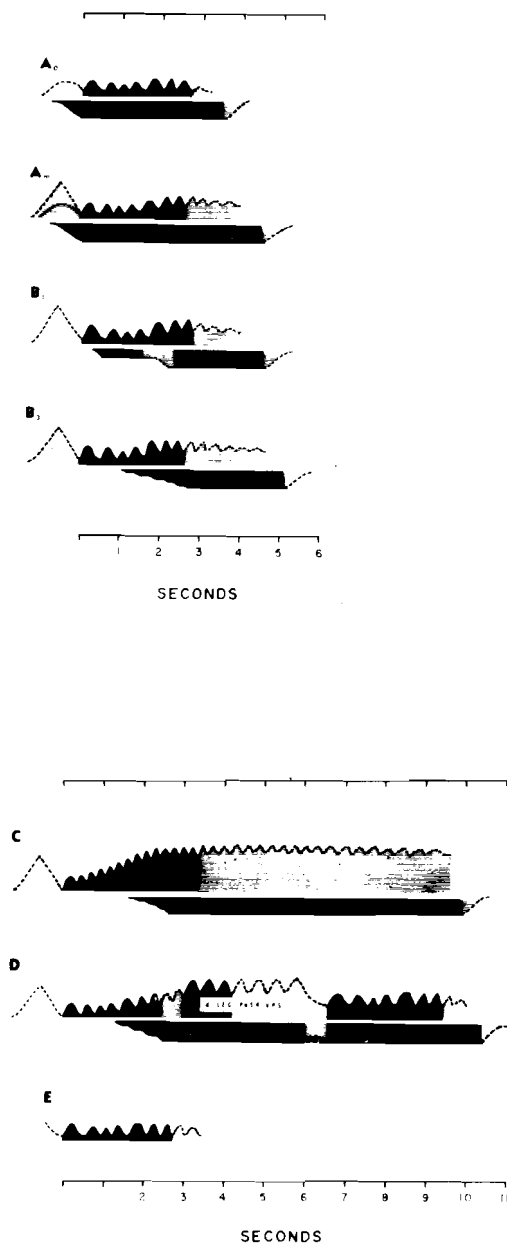


FIG. 8. Display repertoire of *Anolis limifrons* males constructed from an analysis of 666 displays by 23 lizards. Black areas denote portions of the display always present, and grey areas are of variable appearance.

play evolved first. From this pattern was derived the *B* display. A diagnostic feature of *B* displays is the initial appearance of the dewlap during the bobbing, whereas it first appears before bobbing in *A* displays

(Fig. 8). The Type *C* display was probably derived from the *B* display. The *C* display begins like a *B* display, but then diverges by finishing with a long series of bobs. The *D* display is the most elaborate and diverges more from the *A* display than the preceding *B* and *C* patterns. The *D* display is the last bluff performed before the disputing lizards are within physical range of each other. The *D* display appears derived from three pre-existing behaviors: the *B* pattern, a series of four-legged pushups, and the *A* display pattern. An indication that the *D* pattern is an amalgamation of separate core patterns is the fact that after each of the three intra-display patterns there is a varying number of bob repetitions (grey areas on *D* DAP graph of Fig. 8). This is very reminiscent of the optional terminal bob repetitions that serve as a dynamic modifier at the end of many displays. In the *D* display these segments with bob number variability may represent vestiges of three separate patterns having been welded together to produce the most elaborate of the *limifrons* displays. Last, the *E* display, which could have evolved before the *D* display, is the *A* pattern without dewlap extension.

In conclusion, *Anolis* represents an advantageous vertebrate group for studying display evolution. Among lizards, the genus has a relatively rich social behavior. Anoles are easy to study in the field. Because of the group's extensive ecological radiation, there are many potential case studies to correlate display characteristics with effects of diverse biotic and abiotic environmental conditions. This genus of versatile lizards offers an excellent opportunity to approach the problems of causality, function, and evolution of behavior.

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