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Clubbed Regenerated Tails in *Agama agama* and Their Possible Use in Social Interactions

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In response to attack by a predator or aggressive conspecific, many lizards can shed their tail and later regenerate a facsimile of the original structure (Bellairs and Bryant, 1985). Autotomy and other tail loss by lizards is usually regarded as an effective adaptation to elude attacking aggressors (Vitt et al., 1977; Arnold, 1984). Here we suggest a possible additional benefit of tail loss and regeneration in the African rainbow lizard, *Agama agama*. New growth at the site of tail breaks in male rainbow lizards usually forms a hard swollen mass, or club. During agonistic contests, male *A. agama* whip one another with their tails. We propose that the clubbed structure of regenerated tails in *A. agama* plays a role in social interactions between males by augmenting the effectiveness of tail whipping.

While handling a large number of *A. agama* collected at 21 sites scattered about Sierra Leone, west Africa, we (JJS and CRB) scored the frequency of injured tails and the appearance of the regenerated portion. Injured tails were less common in *A. agama* (16% of 1381 adult males; 10% of 1031 adult females) than in populations of several other species of lizards we have studied that possess fracture planes (typically about 25%) (Werner, 1968; Schall and Pianka, 1980; Schall et al., 1982). Nevertheless, the tails of *A. agama* break readily; tails of 11% of 2412 sampled lizards broke while the lizards were being chased and captured.

In lizards that lack fracture planes in the caudal vertebrae, tail breaks are usually intervertebral and are not followed by regeneration of a long, pliable, tapered replacement (Werner, 1961; Etheridge, 1967; Arnold, 1984). For example, *Agama* lack autotomy planes in the caudal vertebrae, as is true of agamids in general (Arnold, 1984). The appearance of regenerated tails of *A. agama* from Sierra Leone varied considerably (Fig. 1). Some formed hard spiny clubs which were generally elongate, being 2 to 3 times as long as their diameter which exceeded that of the stump. Some clubs were nearly spherical. Such clubs can form anywhere along the length of the tail where it has been broken. The most striking examples we have seen were spherical clubs at the tip of the tail. Other regenerated tails were quite different, forming a much longer structure that, although not pliable, more nearly resembled the tapered regeneration of species with autotomy planes. The shape taken by these regenerated structures may depend on the kind of damage, if any, done to the caudal vertebrae during tail loss (Etheridge, 1967; S. Moody, pers. comm.).

The typical shape of the regenerate tail differed between males and females. Scoring of the shape, however, contains a significant subjective component. We, therefore, independently scored tails on two samples of lizards from Sierra Leone, one collected during the wet season, the other during the dry period. In the wet season sample of regenerated tails scored, 65.5% of 55 adult males and 36.4% of 22 adult females possessed clubs rather than the more tapered structure. In the dry season sample, 84.4% of 127 males versus 13.1% of 61 females had formed clubs. In both samples, males were more likely to form clubs, and females to form more elongated structures (χ^2 test, $P < 0.05$). Combining the two data sets shows males were four times more likely to replace a broken tail with a clubbed growth than were females (78.6% of 182 males; 19.3% of 83 females). Dividing the data by site retained a similar pattern. For example, at Njala 86% of 43 regenerated tails of male lizards and only 8% of 26 tails of females took a club form. At Taiama 85% of 13 males and 14% of 7 females possessed clubbed tails.

This observed difference between sexes in the form of regenerated tails might conceivably result from differences in the type of injury suffered during tail loss. Males, for unknown reasons, may typically break the tail between caudal vertebrae, whereas females might more often injure the bone. Whatever the relevant internal morphology, which we could not verify, we propose an alternative explanation, one that

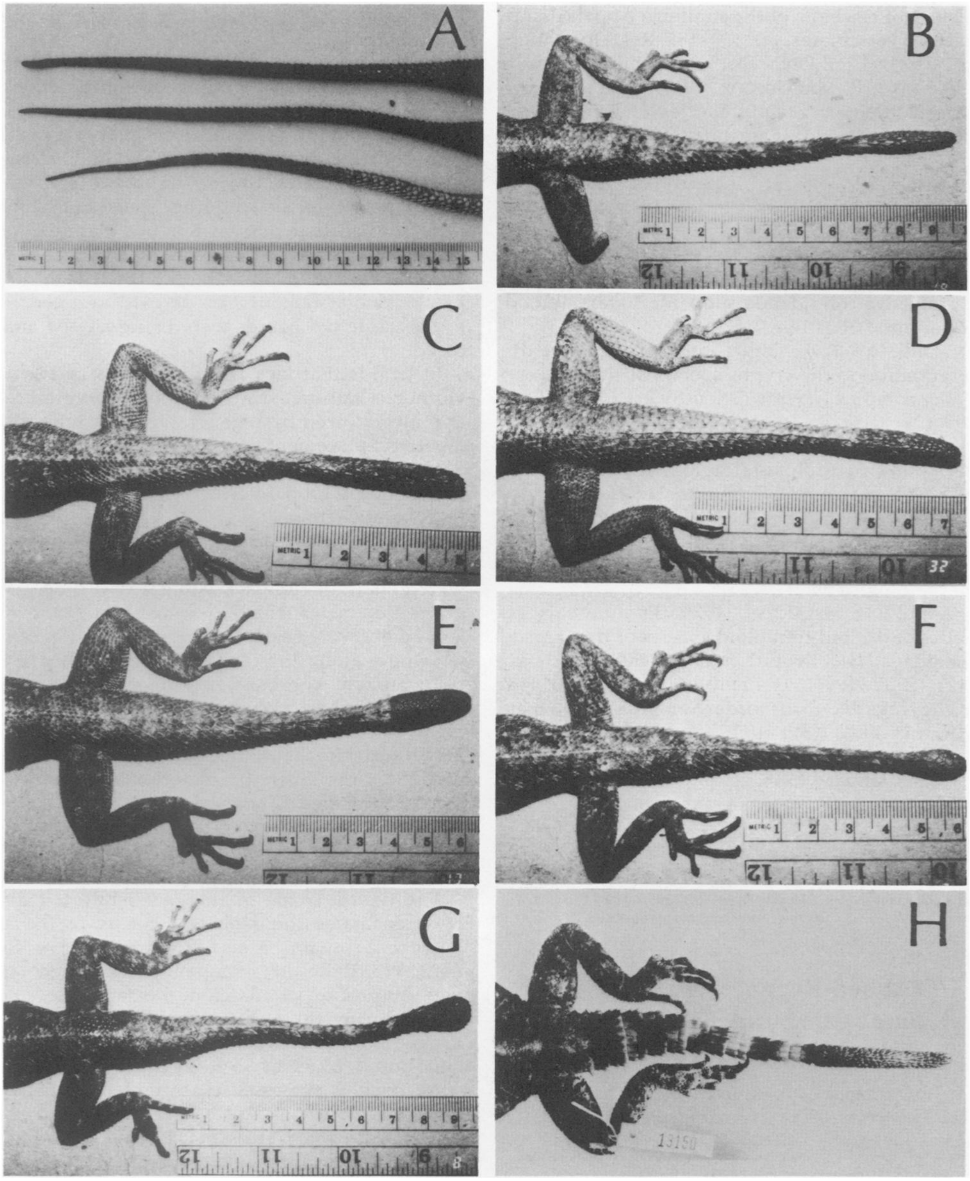

FIG. 1. Tails of *Agama agama* from Sierra Leone, west Africa (A–G) and *A. stellio* from Israel (H). "A" shows unbroken tails; "B–D" show regenerated tails that form more-or-less a tapered structure; "E–G" show regenerated tails forming a clubbed structure; H shows a tapered regenerated tail of *Agama stellio* which usually forms much shorter regenerated structures.

views the tendency to produce clubbed tails as having an adaptive significance for male *A. agama*. Harris (1964) reported that male *A. agama* in Nigeria whip each other with their tails during social interactions. We have observed this behavior at least six times in Sierra Leone. Two males aligned themselves in a parallel configuration, then tailwhipped each other. Sometimes these encounters appeared as wild whipping, whereas at other times one male precisely delivered a blow with its tail to the other lizard's head. Lizards with clubbed tails may have an advantage in such social conflicts, especially if the original break occurred toward the distal portion of the tail, because such blows from a club could aid in displacing its opponent.

This proposal is supported by a control case: *Agama stellio* in Israel does not use tail whipping during social interactions (Arbel, 1980). Arbel (1979 and pers. comm.) has studied the behavior of both *A. agama* in Kenya and *A. stellio* in Israel and notes that clubbed regeneration was common in *A. agama* but very rare in *A. stellio*. To confirm the last statement, we (YLW and JM) examined 543 *A. stellio* (360 adults and 183 juveniles) from most of the range of the species (Greece, Turkey, Cyprus, Lebanon, Jordan, the Sinai, and the mesic portion of Israel [⅔ of the sample]), preserved in the Zoological Museum of the Hebrew University of Jerusalem. These had been collected without bias of tail condition. For the adult sample, 35% showed broken or regenerated tails, with no difference in frequency of injuries between sexes (χ^2, $P > 0.05$). Most of the tail injuries were fresh breaks, so only 27 broken tails were sufficiently regenerated to be scored for shape. Most of these were short, blunt structures, but one exceptionally long regenerated tail measured 39 mm (Fig. 1). In none of the tails was the regenerated portion significantly thicker than the stump. Although Arnold (1984) attributes considerable regenerative capacity to *A. stellio*, these data contradict this conclusion. The situation in *A. stellio* instead parallels that observed in the gecko *Stenodactylus sthenodactylus*, which also has a reduced autotomy system and regenerates only abbreviated nontapering blunt tails (Werner, 1961, 1965, 1968).

In summary, *Agama stellio* does not engage in tail whipping behavior and does not regenerate broken tails into clubbed shapes. *A. agama* males, in contrast, use the tail in social interactions, and males of this species are more likely to form clubbed regeneration. We have no data to support the proposal that clubbed tails are actually more effective during tail whipping bouts that are tapered tails. Clearly, experimental staged bouts between males with different tail forms is the only way to properly confirm our hypothesis. Even if such experiments demonstrate the value of clubbed tails during social interaction between males, this would not necessarily indicate that the tendency of male *A. agama* to produce clubbed tails is an adaptation. Perhaps clubbed regeneration is simply a developmental quirk that influenced selection leading to tail whipping behavior. Alternatively, the use of the tail in social contests may have antedated the origin of clubbed tail regeneration, and acted as the selective force that favored clubs over more tapered regenerated tissue. *A. agama* is a very wide ranging species (Harris, 1964), so this issue perhaps could be resolved through studies of the distribution of tail whipping behavior and club-forming tail regeneration among widely spaced populations.

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Deimatic Behavior in *Pleurodema brachyops*

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Deimatic behavior consists of intimidating postures or actions that occur in animals which cannot flee very fast, or which have been caught by a pursuing predator (Edmunds, 1981). Puffing up the body, elevating the hindparts, and displaying bright colored marks, glands and eyespots are known deimatic displays in frogs (Sazima and Caramaschi, 1988). *Physalaemus nattereri* and *Physalaemus deimaticus* puff up the body and display glands that resemble eyes when disturbed (Edmunds, 1981; Sazima and Caramaschi, 1988). Seven of 12 known species of *Pleurodema* have a pair of prominent lumbar glands; these glands are generally black with other contrasting colors (Duellman and Veloso, 1977). Cei and Espina (1957) reported on the deimatic behavior in *Pleurodema thaul* and Cei (1962, fig. 46) found it in *Pleurodema bufonina*. Duellman and Veloso (1977) did not observe this behavior in the other five species of *Pleurodema* having lumbar glands (including *P. brachyops*). During a study of the reproductive biology of frogs inhabiting the savanna in northern Brazil, I observed deimatic behavior in *Pleurodema brachyops* under laboratory conditions.