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Water Collection and Drinking in *Phrynocephalus helioscopus*: A Possible Condensation Mechanism

KURT SCHWENK¹ AND HARRY W. GREENE²

¹*Department of Oral Anatomy, University of Illinois at Chicago, 801 S. Paulina St., Chicago, Illinois 60612, USA*

²*Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, USA*

ABSTRACT.—The drinking behavior of nine captive *Phrynocephalus helioscopus* was observed. When wetted, animals assumed a stereotyped posture in which the head was depressed to within several mm of the substrate, the limbs splayed, and the hindquarters and tail elevated. Drinking involved repeated, slight tongue protrusion, but without lapping from the substrate. This behavior was elicited in no other context. Simple experiments showed that the interscalar channels transport water across the skin to the mouth by capillary action. This mechanism is compared with that reported for another agamid, *Moloch horridus*. We hypothesize that the drinking posture 1) facilitates drinking rain water and/or 2) facilitates drinking water condensed on the skin and moved to the mouth by capillary action. We conclude that derived features of water collection and transport shared by *Phrynocephalus* and *Moloch* are convergent.

Recently, Gans et al. (1982) examined the water-collecting mechanism of *Moloch horridus*, an Australian agamid squamate. They elaborated upon an earlier study (Bentley and Blumer, 1962) which found that the integument acts as a "blotting paper," soaking up standing water through capillary action, ultimately moving it to the mouth. The more recent study showed, however, that the water moves through interscalar channels rather than through grooves created by ridges on the scalar surfaces, as suggested by Bentley and Blumer (1962). Gans et al. (1982) went on to point out that standing water is a rarity in the arid habitat occupied by *Moloch* and that the integumentary mechanism might serve instead to collect drinking water through condensation. Water condensing on the skin would move through the interscalar channels to the corner of and into the mouth. They further suggested that the numerous spines present on *Moloch* might act as "condensation foci," thereby speeding the wetting process. No behavioral correlates of *Moloch's* integumentary water-collecting mechanism have been noted.

In this paper we report a potentially similar water-collecting mechanism and associated behaviors in another agamid, *Phrynocephalus helioscopus*. This species inhabits arid regions of moderate elevation

in western Asia and Asia Minor (Nikolsky, 1915). Lizards typically occur in open areas with scattered rocks and bushes, and rely largely on crypticity to escape detection (Clark and Clark, 1973; Clark et al., 1966; Nikolsky, 1915). In nature they feed on small insects, largely beetles and ants (Clark et al., 1966; Nikolsky, 1915).

MATERIALS AND METHODS

Nine specimens of *Phrynocephalus helioscopus* were housed in two glass aquaria, seven in one, two in another. The substrate at one end of each cage was heated. Fluorescent white and ultraviolet light was provided on a 12/12 cycle. Lizards were fed irregularly with mealworms and crickets dusted with a mineral supplement, and watered every day. Observations were made on the lizards for a period of several months. No differences in behavior between residents of each cage were observed. Several experiments were performed on the two individuals in one cage; these are described below.

OBSERVATIONS AND RESULTS

Behavior.—When misted with water from a plant mister, or especially when wetted with an eye dropper, the lizards assumed an unusual posture, usually within several seconds after wetting (Fig. 1A). The puta-

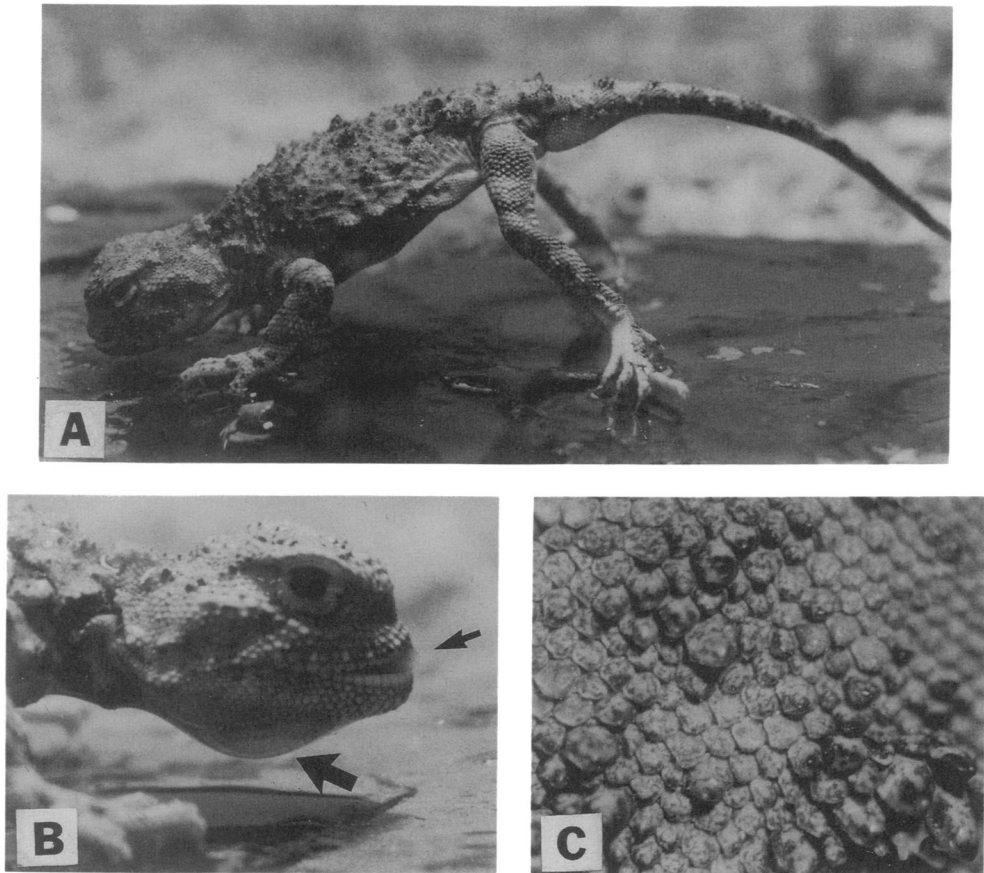


FIG. 1. Drinking and integument of *Phrynocephalus helioscopus*. (A) *P. helioscopus* in stereotyped drinking posture. The head is depressed, but remains above substrate; hindquarters and tail are elevated; limbs are splayed. Note that jaws are slightly parted to allow tongue protrusion. (B) Head of another individual while drinking. Head remains elevated above the substrate during entire drinking bout. Small arrow indicates moving tongue during retraction. Maximal protrusion of tongue is only slightly greater than shown. Large arrow indicates depression of buccal floor accompanying tongue retraction. (C) Enlargement of skin on lizard's back shows slightly imbricate nature of scales. In lower right corner a cluster of large scales forms protuberances visible in Fig. 1A. Anterior is at top of figure.

tive drinking posture involves depression of the head to within several millimeters of the substrate and concomitant elevation of the hindquarters, so that the base of the tail is the highest point on the animal's body. The limbs are splayed, particularly the hindlimbs. The posture is assumed in a stereotyped manner and varies little among individuals or among trials with the same individual. It is elicited only during wetting and has not been observed in any other context. When small pieces of aquarium gravel of approximately the same mass as a water drop were dropped onto

the lizard's back, only a mild defensive reaction was elicited (see below). The drinking posture is also in contrast to that assumed during basking under a heat lamp, in which the head is elevated and the hindquarters, including the hindlimbs, are adpressed to the substrate.

Several seconds after the posture is assumed the lizards begin to drink. The salient feature of this behavior is that it does not involve lapping of water from the substrate as is typical among squamate reptiles. Rather, the head remains elevated somewhat off the ground (2–10 mm) and

the tongue is protruded only slightly from between the parted jaws (Fig. 1B; small arrow). The frequency of tongue protrusion is ca. twice per sec. Tongue retraction is accompanied by depression of the buccal and pharyngeal floor (Fig. 1B, large arrow) which probably indicates swallowing. On several occasions lizards regurgitated water after drinking for a long time (ca. 1 min). This confirms that water was ingested during this behavior. Tongue protrusion is distinct from that observed during lingual prey prehension, which involves extension of the entire tongue beyond the mandible (pers. obs.). The fact that lapping of water from the substrate rarely occurs (we have observed it infrequently) indicates that the animals are drinking water that is entering their mouths from the surface of the body.

Although we did not test explicitly other lizards during the course of this study, we have not observed this behavior in any other species. Our experience with captive lizards includes dozens of species. None were observed to assume a similar posture, even under similar conditions.

Schleich (1976) noted that his captive *P. helioscopus* from Iran clambered over each other to get under a stream of water. They then stood there, pumping air in and out, apparently moving water through their skin (his interpretation). Some of Schleich's animals drowned in a water dish in their cage, but others drank from a petri dish without difficulty.

Given the observations noted above and the water-collection mechanism of *Moloch* described by Gans et al. (1982), we hypothesized that the drinking posture of *P. helioscopus* might facilitate a similar water-collecting mechanism. We tested this hypothesis by examining the integument of *P. helioscopus*, comparing it with *Moloch* as described in Gans et al. (1982), and by performing several simple experiments.

Integument.—Scales covering most of the dorsum appear to be very fine and granular. Closer examination, however, revealed that they are slightly imbricate (Fig. 1C). Though slight, scale overlap is greater than in *Moloch*. Scales are most imbricate on the ventral surface and along the dorsal

midline. Nearly granular, non-imbricate scales occur along the flanks. These become increasingly imbricate dorsally, but remain granular anteriorly, in the shoulder region dorsal to the forelimb, and on the neck. Scales on the head are also mostly non-imbricate and are smallest at the corner of the mouth and neck. Thus, a band of granular scales runs along each side of the body from hindlimb to head. The small protuberances covering the animal's dorsum (Fig. 1A) comprise clusters of enlarged scales (Fig. 1C). They are neither sharp nor stiff and are unlike the pronounced spines of *Moloch*.

We did not examine the scales of *P. helioscopus* with an SEM so we are unable to comment directly on their surface architecture. However, E. E. Williams (in Peterson, 1984) found a "honeycomb" pattern of ridges in *Phrynocephalus* (species unspecified) similar to that reported by Gans et al. (1982) for *Moloch*. A honeycomb scale-surface morphology is present in many iguanids and all agamids so far examined and is probably the plesiomorphic state for Agamidae (Peterson, 1984).

Experiments.—We tested the ability of the integument to hold and transport water by using water dyed with food coloring. The dark-colored water allowed visualization of the water on the integument of *P. helioscopus*. Four experiments were performed on each of two specimens: 1. Water dropped from a height of ca. 8 cm onto the dorsum of a completely dry lizard; 2. Water dropped onto the dorsum of a lizard previously wetted under a faucet and blotted dry with a paper towel; 3. The venter of a dry lizard placed in a puddle of water; 4. The venter of a previously wetted and blotted specimen placed in a puddle of water.

Results of the experiments were identical in both specimens. When a dry lizard is exposed to dyed water in either manner, no movement across the integument is observed. The surface tension of a drop placed on the dorsum is not disrupted; the drop retains its integrity and does not wet the surface. Similarly, when the lizard's venter is placed in water, no movement of water up onto the dorsum is observed, as reported for *Moloch* (Bentley and Blumer,

1962; Gans et al., 1982). In contrast, results of experiments performed on previously wetted specimens were dramatic. A drop placed on the dorsum spread almost instantly across the surface of the lizard, moving anteriorly and posteriorly equally as fast as ventrally. Likewise, movement of dyed water from the venter over much of the body was almost instantaneous. In both experiments with the previously wetted specimens, movement slowed considerably after the first instantaneous burst. Nonetheless, within one minute dyed water was observed half way down the length of the tail and on the head at the corner of the mouth. Because we did not attempt to observe directly dye on the tongue or in the mouth, we cannot confirm absolutely that water entered the mouth during the experiments.

The dyed water was clearly observed to fill the interscalar channels, as described by Gans et al. (1982) for *Moloch horridus*. Thus their discussion of capillary action in the integument of that species is probably equally applicable in the case of *P. helioscopus*. However, given the greater degree of scale overlap in the latter species, it is likely that the capillary force generated is not as great (see Gans et al., 1982, for discussion of the relationship between capillary force and scale overlap).

DISCUSSION

The principal, salient difference between *Moloch* and *Phrynocephalus* is that the integument of *Moloch* is wetted easily, even in a completely dry animal (Gans et al., 1982). Gans et al. (1982) described the scalar surface as "hygroscopic" and attributed this fact to the honeycomb surface morphology of the scale surface. Since *Moloch*, *Phrynocephalus*, *Amphibolurus* (also tested by Gans et al., 1982), and other agamids share this morphology (see above) it is unlikely to be the cause of *Moloch's* hygroscopic integument. However, it is possible that variation among species in height of the honeycomb walls (Peterson, 1984) might account for differences in wettability. It is also possible that the putatively greater capillary force generated by the integument in *Moloch* is sufficient to over-

come the water's surface tension, thereby drawing it into the interscalar channels and causing it to spread, wetting the surface. Alternatively, other features of the scale surface that are larger than the honeycomb cell junctions might cause the meniscus to break. Such features include the bumps or low spines covering each scale and the ridges that roughen the bases of the numerous spines on *Moloch* (Gans et al., 1982). Without comparative morphological data and additional experiments these suggestions are purely speculative.

It was noted above that there is regionalization in the distribution of granular vs. imbricate scales in *P. helioscopus*. It was our impression during the experiments that dyed water was mostly held and transported in the granular region and that movement from the venter onto the dorsum was considerably slowed toward the dorsal midline where scales are most imbricate. The path taken by dyed water to the corner of the mouth seemed to correspond to the band of granular scales described above.

Many lizards exhibit a distribution of granular scales similar to *P. helioscopus*. This distribution seems to correspond to regions of skin movement and flexibility, hence its role in water collection and transport may be fortuitous. More species with a variety of scale types need to be tested in order to assess adaptive explanations.

Some care must be taken in interpreting a postural response to a stream of water as actually involving drinking. Certain salamanders (*Ensatina*, R. B. Huey, pers. comm.) and snakes (*Cylindrophis*, pers. obs.) will immediately assume an antipredator posture if a small jet of water is squirted on their backs. However, the only responses of *P. helioscopus* to simulated predation in the field (Nikolsky, 1915; Clark et al., 1966; Clark and Clark, 1973) and in captivity are immobility and crouching, or rapid locomotion. Captive *P. helioscopus* were observed by Obst (1959) to assume a defensive display in which the venter is pressed to the substrate, the fore- and hindfeet raised slightly off the ground, and the tail curled over the body. The spectacular threatening displays seen in *P. mystaceus*

(Mertens, 1952) and *P. scutellatus* (Minton, 1966) are not exhibited by *P. helioscopus*. It is also worth emphasizing that feeding by these lizards is kinematically different from drinking. Our captives fed readily on small mealworms, crickets, and termites. These insects were captured by rapid approach with the body elevated on all four feet, head lowered and posterior raised, then capture with a quick protrusion of the long tongue.

In summary, *P. helioscopus* assumes a stereotyped drinking posture when wetted. Water enters the mouth by movement through the interscalar channels created by capillary forces. In order for this to happen, the animal must first be sufficiently wetted to allow spreading of water across its integument. *P. helioscopus* shares the behavior of drinking water from the integument with *Moloch horridus*, another agamid.

We offer two possible explanations for the unusual drinking posture: 1. Rain water would flow downward along the animal's dorsum toward the head where it could be drunk. In this scenario, movement of water across the integument to the mouth by capillary action would be a secondary, possibly unimportant mechanism of water-collection. 2. The posture somehow enhances the degree of water condensation on the lizard's body. In this case, movement of water by capillary action would be the principal means of delivering water to the mouth for drinking. If the source of moisture-laden air for condensation were a breeze or moving fog, then orientation of the posturing lizard with its head into the breeze would increase the surface area directly exposed, thereby increasing the amount of condensation. If, however, the source of condensed water is dew, then there would seem to be little benefit in assuming the head down posture. It is clear that our ability to interpret this species' behavior is hampered by our lack of sufficient natural history data.

Phrynocephalus is similar to *Moloch* in general body form and in the potential for integumentary water movement by capillary action. In a recent phylogenetic study

of relationships among agamid genera, Moody (1980) found *Moloch* and *Phrynocephalus* to be only distantly related, hence it is likely that these derived features are convergent and not due to common ancestry.

Species of the iguanid genus *Phrynosoma* are North American, desert-adapted lizards that are similar in body form to *Moloch* and *Phrynocephalus*. Mayhew and Wright (1971) found that *Phrynosoma m'calli* did not take up and transport water like *Moloch*, despite convergence in form and ecology. However, they did not try wetting animals first as we did with *Phrynocephalus*. It is possible that water uptake would be similarly enhanced. Gans et al. (1982) pointed out that nocturnal emergence is required by the hypothesis of water collection through condensation (assuming dew as a source) and that *Phrynosoma* is a burrower that probably spends most nights below ground. However, we have found *Phrynosoma platyrhinos* on the surface at night in the Mojave Desert; hence water collection through condensation might occur in this genus.

Water collection through capillary action of the skin may be important in other vertebrates as well. For example, Lillywhite and Licht (1974) described water movement across toad skin through epidermal channels analogous to interscalar channels. The extent to which such disparate morphologies are convergent might provide tests of adaptive hypotheses. In order to test adequately hypotheses of water-collection and drinking presented here and in Gans et al. (1982), additional comparative tests on sister- and outgroup taxa are necessary. Only in this way can the generality of condensation and capillary action mechanisms be determined and their status as an adaptation to arid habitats assessed.

It is clear from the above observations that the posture and associated behavior that we observed repeatedly when the lizards were wetted is elicited only by application of water to the skin. Carpenter (1977) did not include drinking among the many stereotyped postures used by lizards, but

careful observations might yield interesting comparisons with the behavior we have described for *P. helioscopus*.

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